# The Journal of Comparative
# Neurology and Psychology

Founded by C. L. Herrick

---

VOLUME XVII, 1907

OFFICE OF ADMINISTRATION
HULL LABORATORY OF ANATOMY, THE UNIVERSITY OF CHICAGO
C. JUDSON HERRICK, Managing Editor

# The Journal of
# Comparative Neurology and Psychology

## CONTENTS OF VOLUME XVII, 1907

---

### Number 1, January, 1907.

### Number 2, March, 1907.

### Number 3, May, 1907.

### Number 4, July, 1907.

### Number 5, September, 1907.

### Number 6, November, 1907.

# SUBJECT AND AUTHOR INDEX.

## VOLUME XVII.

Author's names are in small caps. References to subjects and authors of original articles are marked with an asterisk.

The Journal of
Comparative Neurology and Psychology

VOLUME XVII JANUARY, 1907 NUMBER 1

# ON THE PLACE OF ORIGIN AND METHOD OF DISTRIBUTION OF TASTE BUDS IN AMEIURUS MELAS.

BY

F. L. LANDACRE.

(*Associate Professor of Zoölogy, Ohio State University.*)

WITH PLATE I AND FOUR FIGURES IN THE TEXT.

CONTENTS.

## INTRODUCTION.

The present investigation was undertaken with the object of ascertaining, if possible, at what time and in what order taste or terminal buds appear in the anterior oral cavity and on the outer body surface of Ameiurus melas as compared with those situated in the pharynx.

The siluroids, owing to the enormous number of taste buds scattered over practically the whole of the body surface, seemed the most favorable group for such a study and Ameiurus melas in particular was selected on account of the very complete description of the distribution of the gustatory fibers which has been given for this type by C. J. HERRICK ('01).

Owing to the fact that all taste buds wherever located are innervated by communis fibers and that those in the endoderm of the pharynx appear in some forms before buds appear in the ectoderm, it was thought that buds would be found to spread from endodermic into ectodermic territory.

This has proven not to be the case in Ameiurus and if a study of less specialized or more primitive forms shows this supposition to be the general rule, a view which has been advanced by JOHNSTON ('05a), the condition in Ameiurus will have to be explained on the basis that the gustatory system is so highly specialized that phylogenetic relationships have been materially modified or obscured.

While the results obtained do not show a derivation of ectodermic from endodermic buds nor the reverse, as suggested by COLE ('00, p. 320), still a careful study of the time of appearance and the direction of spreading has brought to light a number of interesting facts, which, when related to the nerve supply, throw light on the problem of the distribution of ectodermic buds, if they do not answer the question as to how these two groups are related to each other primitively.

## I. HISTORICAL.

The attempt to correlate the distribution of taste buds with the distribution of gustatory fibers in the various cranial nerves is rendered possible by two somewhat distinct lines of research. The first culminated in the complete isolation, both structurally and functionally, of the taste or terminal buds from all other cutaneous sense organs. The second culminated in what is commonly called the theory of nerve components in which we have the isolation of the various components of the cranial nerves, such as the gustatory, the lateral line and general cutaneous, based on a difference in the size of their fibers, and the isolation of their central endings or nuclei in the brain from each other as well as on the difference in types of sense organs supplied.

In the brief historical outline which follows no attempt is made to give a digest of the earlier literature on the cranial nerves of fishes, much of which is confusing and still more of which is of little value for the present purpose, owing to the fact that it depends for its analysis of the cranial nerves on the method of gross dissection, a method which is totally inadequate where it is possible to separate the various components only by a microscopic study of serial sections.

The review of the theory of nerve components makes no claim to completeness either, it being the writer's intention to present the salient points of that theory as far as they would be of value for the present paper, which is concerned solely with the communis system. For a comparison of the results of the microscopical analysis of the cranial nerves with the earlier attempt by gross methods the reader should consult the papers of STRONG, HERRICK, JOHNSTON, KINGSBURY, COLE and others.

(*a*) *Taste or Terminal Buds.*—The taste buds were first discovered on the palatal organ of the carp in 1827 by WEBER ('27) and their function correctly inferred. In 1851 LEYDIG ('51) discovered the taste or terminal buds on the outer skin of fishes but gave a somewhat faulty description. In 1863 F. E. SCHULZE ('63) described the same organs and distinguished structurally between the sensory and supporting cells and inferred their function to be the same as similar buds found inside the mouth. The same author showed in 1870 that the terminal or taste buds differ in structure from the lateral line organs or neuromasts of whatever form in that the sensory cells of the taste buds are elongated cells and pass down from the surface of the epithelium entirely to the basement membrane, while the sensory cells of the lateral line organs and of all superficial organs related to them are pear-shaped and do not reach the basement membrane.

MERKEL ('80) in 1880 confirmed these structural differences, but confused the subject by attributing the same function, namely, touch, to both terminal or taste buds and neuromasts or lateral line and related organs.

In 1904 C. J. HERRICK ('04) demonstrated by experiments that the function of the terminal buds is undoubtedly gustatory, and in addition showed that the cat fishes, at least, can locate sapid substances by the sense of taste and can learn to distinguish between gustatory and tactile stimuli, although ordinarily these are probably used in conjunction in locating food. These experiments, reinforced by the complete isolation of the gustatory fibers and gustatory centers microscopically, leave no doubt that we have here a sensory system quite distinct functionally and structurally from any other cutaneous sense organs.

As to the exact time and place of appearance and the direction of spreading of the buds, less work seems to have been done.

ALLIS ('89) calls attention in Amia to the time of appearance of what he takes to be terminal buds and describes briefly the manner of spreading posteriorally from the anterior parts of the head back to the body. He describes (p. 509) and figures the terminal buds as appearing as whitish lines, usually parallel with the lateral lines of the head, that later break up into individual buds. The serial arrangement disappears as the buds become more numerous.

JOHNSTON ('05a) states that buds are present in the branchial region only of the Ammocœtes stage of Petromyzon but that they are present in the skin also of the adult. Corregonus and Catostomus sp. were studied also in serial sections, and the taste buds of the pharynx found to be much more numerous and highly developed than elsewhere. Buds were found in the œsophagus and on the roof and floor of the mouth but in both places were smaller than those in the pharynx. No buds were found on the skin of the body except in a specimen taken some days after hatching. These facts, *i. e.*, the earlier appearance of the pharyngeal buds, their larger size, and the fact that all taste buds are innervated by communis fibers, inclined JOHNSTON to the opinion that buds have spread from the endoderm to the ectoderm.

(*b*) *The Communis System.*—The need of the application of histological methods in the study of peripheral nerves and the substitution of components as physiological and morphological units instead of nerves may be traced to GASKELL ('86, '89). The two-root theory of BELL had dominated the study of spinal and cranial nerves from the time BELL's law was enunciated in 1810 until GASKELL proposed what is called the four-root theory. According to GASKELL a typical spinal nerve contains four roots, somatic sensory, somatic motor, splanchnic sensory and splanchnic motor.

STRONG ('95), following a suggestion of H. F. OSBORN ('88) that it might be possible to analyze the cranial nerves on the basis of structural differences in their components and peripheral distribution, made the first successful attempt at such an analysis on the sensory portions of the cranial nerves of the tadpole of the common frog. As a result of this analysis STRONG found that the sensory portions of the V, VII, VIII, IX and X nerves could be resolved into three components.

1. The general cutaneous component, characterized peripherally by having medium sized fibers and free nerve endings, and centrally by ending in the spinal fifth tract which is a continuation of the dorsal horn of the cord.
2. The acustico-lateralis component, characterized peripherally by having coarse fibers and innervating the ear and lateral line and related organs, and centrally by ending in the tuberculum acusticum.
3. The communis component, characterized peripherally by innervating unspecialized mucous surfaces and specialized organs in the form of terminal or taste buds, by having fine fibers, and centrally by ending in the lobus vagi and lobus facialis, which are really one nucleus morphologically.

STRONG's work was followed and confirmed in all essential details by that of HERRICK on Menidia ('99), on Gadus ('00), on Ameiurus ('01); and by COLE on Gadus ('98) and on Pleuronectes ('01); and by COGHILL on Amblystoma ('02) and on Triton ('06); and by JOHNSTON on Acipenser ('98) and on Petromyzon ('05), and others, so that we have a thorough knowledge of the components of the cranial nerves based on a careful microscopic study of serial sections for the cyclostomes, teleosts and amphibia. In all these papers the necessity of correlating the peripheral distribution of the nerve with its central endings and the unraveling of the nerve throughout its whole course has been kept in mind and accomplished with an unexpected degree of success. A study of the central endings of the cranial nerves in the medulla and their homologies with the centers of the four roots of GASKELL has been made particularly by KINGSBURY ('95a, '97) and by JOHNSTON ('98, '01, '02a), in addition to the papers mentioned above, while the larger problem of the morphology of the vertebrate head has been attacked by JOHNSTON ('05b) from the functional standpoint and in accord with the work on nerve components.

Since taste buds are innervated wherever situated exclusively by communis fibers, we may confine our attention to this component. As mentioned above, all communis fibers end in a morphologically single center, those from the ninth and tenth nerves in the lobus vagi and those from the VII nerve in the lobus facialis, which correspond in the position in the medulla to the visceral sensory or region of CLARKE's column in the cord. All communis fibers running out through the VII nerve trunk and through what are commonly designated as the fifth rami come from the geniculate ganglion of the VII nerve, while those running out through the ninth and tenth nerves come from ganglia situated on those nerves. The communis fibers coming from the geniculate ganglion enter the brain anterior to the position of their nucleus and pass back as the fasciculas communis or fasciculus solitarius of mammals to the facial lobe.

The communis component consists of unspecialized fibers supplying mucous surfaces and specialized fibers supplying taste buds situated in both ectoderm and endoderm. These specialized and unspecialized divisions cannot be accurately separated centrally although HERRICK ('05) has worked out the reflex gustatory paths both ascending and descending in the cyprinoids and siluroids. This is the first successful attempt to trace definitely the secondary and tertiary gustatory paths in any vertebrate, and from being the least known system centrally, the communis system, at least in teleosts, is one of the best defined systems both peripherally and centrally of any of those contained in the cranial nerves.

The communis fibers running out through the IX and X nerves are fairly constant in their distribution. The IX nerve may send fibers to the surface of the body, as in Menidia, but the distribution seems usually to be confined to mucous surfaces as in Ameiurus. The communis fibers arising from the geniculate ganglion, however, show the greatest diversity in the number of rami through which they pass to the surface and in the extent and variety of the surface innervated. They may pass out through only one ramus, as in Petromyzon (JOHNSTON '05), or two as in Rana (STRONG '95), or three as in Amblystoma (COGHILL '02) and Triton (COGHILL '06) and Amia (ALLIS '97), or five as in Pleuronectes (COLE '01), Gadus (HERRICK '00), Menidia (HERRICK '99), or even as many as twelve rami in Ameiurus (HERRICK '01).

Since both ectodermic and endodermic buds are innervated from the geniculate ganglion and it shows such a diversity in the number of rami of the V and VII nerves used, and since the interest in the relation of ectodermic to endodermic buds centers in the distribution of these nerves, a table has been arranged to show these relations.

TABLE I.

Table showing the rami of the V and VII nerves which carry communis fibers in types in which they have been worked out fully. In this table rami carrying communis fibers are indicated by (x). In the Amphibia and Petromyzon the presence of the ramus or truncus is indicated by (″), and when a ramus is known to be absent it is indicated by (—). The rami as outlined here are fairly constant for the Teleosts and Amia and the main rami are also present in the Amphibia and Petromyzon, although no attempt has been made to analyze these and determine their homologies. The ramus oph. profundus is probably not present in Teleosts, and on the homology of the ramus max. acces. and ramus max., see COGHILL ('01).

| | AMEIURUS | MENIDIA | GADUS | PLEURONECTES | AMIA | RANA | AMBLYSTOMA | TRITON | SPELERPES | PETROMYZON (LARVA) |
|---|---|---|---|---|---|---|---|---|---|---|
| Ramus oph. prof. | | | | | | ″ | ″ | ″ | ″ | ″ |
| Ramus oticus VII | x | | | | | | | | | |
| Ramus lat. acc. VII | x | x | x | x | x | | ″ | ″ | | ″(?) |
| Truncus supra-orbit. | | | | | | | | | | |
| Ramus oph. sup. V | x | x | x | | | ″ | | | ″ | ″ |
| Ramus oph. sup. VII | | | | | | ″ | ″ | ″ | ″ | ″ |
| Truncus infra-orbit. | | | | | | | | | | |
| Ramus mand. V | | | | | | ″ | | | ″ | ″ |
| Mand. ex. V | x | | | | | | ″ | ″ | | |
| Mand. int. V | x | | x | x | x | | | | | |
| Ramus max. V | | | | | | ″ | ″ | ″ | ″ | ″ |
| Max. lat. V | x | x | x | | | | | | | |
| Max. mes. V | x | | | | | | | | | |
| Ramus max. acces. | x | | | | | ″ | | | | |
| Ramus buc. VII | | | | | | ″ | ″ | ″ | ″ | ″ |
| Buc. exter. VII | | | | | | | | | | |
| Buc. inter. VII | | | | | | | | | | |
| Ramus palatinus VII | x | | | x | x | x | x | x | x | x |
| Ramus pal. post. VII | x | x | x | x | | | x | x | | |
| Truncus hyomand. | | | | | | | | | ″ | ″ |
| Ramus oper. sup. VII | — | | | | | | | | | |
| Ramus hyoideus VII | x | | | | | ″ | ″ | ″ | ″ | |
| Ramus mand. ex. VII | x | | | | | ″ | ″ | ″ | | |
| Ramus mand. int. VII | — | x | — | x | | x | x | x | x | |

Although the work on nerve components has shown several of the names commonly used to designate these rami to be inappropriate in a number of types, in order to get some basis on which a comparison of the number of rami carrying communis fibers could be made, the current nomenclature has been used. The table is open to criticism, of course, in this regard, but it does bring out the fact that of the rami usually attributed to the V and VII nerves a great variation exists in the number carrying communis fibers. In the case of Petromyzon, one branch of the hyomandibular trunk carries communis fibers and JOHNSTON does not state, so far as I am aware, its homology with corresponding rami of the teleosts. In the case of Rana, I have catalogued only two rami as bearing communis fibers, namely, the ramus palatinus and the ramus mand. int. VII, but the ramus palatinus near its peripheral distribution forms anastomoses with the ramus oph. V and with the ramus mand. int. VII, so that there are really four rami in the frog carrying communis fibers, although they do not enter these rami near their ganglia. The teleosts, owing to their close relationship and the constancy of these rami, furnish the best basis for comparison.

Of the fourteen rami usually found in teleosts, two, the ramus mand. int. VII, and ramus oper. sup. VII, are absent in Ameiurus, and of the twelve remaining, ten contain communis fibers and these fibers are absent from the ramus oph. sup. VII and ramus buccalis VII only. An examination of Menidia shows only five rami carrying communis nerves; the same is true of Gadus, but while these two types have the same number of rami carrying communis fibers the rami are not identical. Menidia has communis fibers in the ramus mand. int. VII, which is absent in Gadus while Gadus has communis fibers in the ramus mand. int. V which is present in Menidia but contains no communis fibers. The distribution of the taste buds on the ectoderm is correlated more or less closely with this variation in the rami carrying communis fibers, although peripheral anastomoses sometimes materially modify the distribution of taste buds from what we should expect to find, judging from the number of rami carrying communis fibers at a point near the ganglia.

The same variation is found in Amphibia. Amblystoma and Triton each have three rami which carry communis fibers that run out with these rami from near the ganglia, while the frog has only two.

These differences cannot be explained on the basis of a larger or smaller number of communis fibers in a particular ramus in various types, such as the teleosts, for while no enumerations have been made, it is altogether probable that Ameiurus not only contains more rami bearing communis fibers, but contains more communis fibers in a given ramus than either Gadus or Menidia or Pleuronectes, if we may judge from the number of taste buds on the surface in a given area. Of course, we would have to except from this general rule the nerves supplying the palatal organs in the cyprinoids. Judging by the variable number of rami of the V and VII nerves used by communis fibers in the teleosts, it would seem that the constancy of these rami in this group is not maintained primarily by the communis system, but has to be accounted for by the phylogenetically older and more constant general cutaneous system and in some cases the lateralis system of fibers. In an attempt to explain how this variation came about it is important to keep in mind the proximity of the ganglia of the communis, general cutaneous, and lateralis components in the trigemino-facial complex, which seems to furnish a clue to the way in which communis fibers have used them in some types and have not used them in others. In Ameiurus we have an extreme case of this usurpation where ten out of twelve rami carry communis fibers. Since the brain center is constant in position and morphologically single in all these types, and since fibers grow both peripherally and centrally from the ganglion cells, it would seem that our attention should be given largely to the ganglion as a source of variation. The question of the relation of the fibers to the taste buds will be taken up under the general survey of the oral and cutaneous groups.

## 2. MATERIAL AND METHOD.

In order to determine the place of first appearance and the rate and manner of distribution of the taste buds, a number of series of young Ameiurus melas were taken and the total number of buds enumerated and their locations tabulated.

The most complete series and the one from which most of the tabulations were made was found in a nest at Sandusky, Ohio, on July 1, 1905, at 3.30 p. m. Both parents were on the nest and the eggs were apparently just being deposited and fertilized. The nest was conveniently located near the edge of a pond so that the eggs could be removed with a pipette at desired intervals without disturbing the male parent. As segmentation had not begun when the nest was found, no eggs were removed until the following day at 3 o'clock, when the blastoderm was found to cover about half the yolk. Forty-nine hours after the nest was found eggs were removed and as the embryo was sufficiently developed to render the presence of taste buds possible, series were taken at intervals ranging from four to fourteen hours up to the eighth day, and on the ninth day a thirty-one hour series was taken when the eggs in the nest were exhausted. After examination it was found that in the oldest embryo of this series buds were not present back of the operculum on the body and later series were taken the following year. Since no nests were found in which the eggs were being fertilized, so that the exact age could be determined, these embryos were arranged according to measurement rather than age. The oldest embryo of the first series was 9.4 mm. in length, and the later series were selected so as to complete this, embryos being cut which measured 11, 14¾, 15½, 17½ and 20¼ mm., respectively.

In the first series five lots were taken for each stage and fixed in the following fluids, (*a*) HERMANN'S, (*b*) FLEMMING'S, both the weak and the strong solution, (*c*) a chromo-aceto-osmo-platinic mixture, and (*d*) ZENKER'S fluid.

A number of stains were tried but HEIDENHAIN'S iron hæmatoxylin after ZENKER gave the best results. This stain gives a sharp differentiation to the taste buds, sometimes staining the sense cells and sometimes the supporting cells. In the ear and lateral line organs it usually stains the pear shaped sensory cells quite black, thus rendering the separation of the neuromasts from taste buds quite easy.

Every alternate series beginning with the earliest was cut, but no buds were found until series K′ (113 hours). This is about 24 hours before hatching, the incubation period being about six days.

The earliest buds to appear are of course very immature, but little or no difficulty was experienced in recognizing them as soon as the first rudiments appeared. The only organs with which they could possibly be confused would be the teeth in the oral and pharyngeal cavities and the neuromasts in the cutaneous regions. The teeth appear first as invaginations of the Malphigian layer of the epidermis, while the taste buds always begin as an evagination of the same layers. On the outer surface the same distinction exists between the taste buds and the neuromasts. All neuromasts are in the form of more or less well defined depressions of the epidermis at the time taste buds appear, while the taste buds, as in the mouth and pharynx, begin as elevations. Even in cases where the neuromast does not begin as a well defined depression, the presence of two layers of cells, the outer one of which is rounded and lies quite near the surface and will later become the pear shaped sensory cell so characteristic of neuromasts, makes the separation of these two types of organs easy.

In order to avoid any possibility of confusion all the lateral line organs of all the series in which taste buds occur and all the neuromasts present in the earlier stages have been located, and at the time the first taste buds appear all the placodes of the lateral line organs are present and accounted for.

In this connection it may be of interest to note the difference in time of maturing of these two types of organs. Perfectly formed lateral line organs with the sensory cells having the same shape as in the adult and with their free borders exposed can be found as early as series N, 138 hours. This is about the time of hatching and is probably correlated with the effort of the young fish to right and orient themselves, which occurs about this time, although no notes were taken of the exact time when this occurs; nor were any notes taken of the exact time at which the young orient themselves in the nest after they can maintain an erect position. This orientation is quite a characteristic phenomenon of larvæ of very young cat fish, however.

On the other hand, no taste buds are found in my series that could be considered mature until much later, probably in series Q, 174 hours. It is much more difficult to determine when taste buds mature on account of the irregularity in the staining of the sensory cells in the taste buds. There are, however, in series Q, both in the oral cavity and in the pharynx, buds that resemble mature buds of the oldest embryo studied in all essential details except size. The later maturing of the taste buds is probably correlated with the reduction in amount of yolk and the beginning of feeding on food secured from the surrounding water.

As to the relative time of maturing, there is no apparent difference between the oral, pharyngeal and cutaneous regions. Mature buds appear in the pharynx, and in the oral cavity, and on the maxillary barbule, at the same time as nearly as I can determine. Nor does the difference in size between the buds in the three regions which JOHNSTON ('05) finds in Catostomus and Corregonus exist in Ameiurus. This was to be expected after it was found, as will be shown later, that buds arise in the oral and pharyngeal cavities simultaneously.

Series were all cut 7 microns in thickness and all tabulations are based on serial sections, since nothing could be made of the distribution of taste buds from surface views, largely on account of the amount of pigment in the epidermis.

Since the question as to whether a given group is spreading forward or backward from the position in which the buds first appear in a preceding series depends upon the actual length of the specimen compared with the limits of the groups in the two series, a table is given showing the exact age and the age increment, and the average length in all fixing fluids, of the specimens of each age with the average increment in length of each age.

TABLE II.

Table showing ages in hours after fertilization of series K′ to U and the average lengths in mm. of these embryos in all fixing fluids and the increments in age and length in each case.

| EMBRYO. | AGE. | AGE INCR. | LENGTH. | LENGTH INCR. |
|---|---|---|---|---|
| K′ | 113 | 8 | 5.73 | |
| L | 120 | 7 | 6.55 | .82 |
| M | 128 | 8 | 6.36 | .09 |
| N | 138 | 10 | 7.06 | .70 |
| O | 146 | 8 | 7.33 | .27 |
| O′ | 155 | 9 | 7.54 | .21 |
| P | 163 | 8 | 7.59 | .05 |
| Q | 174 | 11 | 7.82 | .23 |
| R | 183 | 9 | 8.33 | .51 |
| S | 199 | 16 | 8.50 | .17 |
| T | 213 | 14 | 8.70 | .20 |
| U | 244 | 31 | 9.40 | .70 |

There are three possible sources of error to be taken into consideration in attempting to determine the exact position of a group of buds located on structures that are not segmental and the manner of their spreading. (1) All embryos probably do not shrink uniformly. Although a table prepared, but not given in this paper, shows a rather remarkable uniformity in the various fluids, still some variation may be due to this factor. Greater shrinkage in an embryo in which a group of buds had appeared in an earlier period would make the group seem to spread forward if measured in sections from the anterior end. (2) All the earlier series were not taken directly from the nest; for the first three days two lots were taken each day and intermediate series were taken from those brought in at a previous trip. Embryos reared in the laboratory from the earlier stages until the time of hatching probably do not grow so fast and undoubtedly do not become so thoroughly pigmented as those reared in the nest, but this probably does not materially affect the rate of differentiation of taste buds in the series under discussion, since the intervals were too short. (3) The most puzzling question that arises in attempting to determine whether a group of taste buds, not located on structures segmentally arranged, is actually spreading in a given direction arises from the unequal growth of various regions of the body. When we give the limits of a group of buds in various ages in sections counted, as must be done sometimes, from the anterior end of the body, we assume that the anterior end of the body is a fixed point. This of course is not true. A group of buds might show if measured in this manner a well defined spreading backward and still not be spreading backward at all, but be simply increasing in a given area which owing to the growth of that area and of areas in front of it, comes to lie further from the anterior end; or it might be moving bodily back with reference to other structures near it. The branchial apparatus, for instance, owing to its functional importance elongates much more rapidly than other structures occupying similar segments of the embryo and comes to occupy many more segments in the adult than in the embryo (JOHNSTON '05b), and the anterior taste buds situated on the proximal hyoid and suspensorium move backward almost as rapidly as the posterior buds, showing a backward movement of these two structures, while on the other hand some portions of the nasal group of buds remain practically stationary.

For practical purposes in determining how fast and in what direction a group is spreading the best means seems to be to reduce the older embryo to terms of the younger in length. That is, if a group of buds extended twice as far from the anterior end in series B as in A and series B had increased less than twice as much in length as A we would be warranted in thinking that the group had actually spread back and had not simply moved with the area on which it was situated. Both these conditions are found, as will be shown in the analysis of the groups. This rule seems to be particularly applicable to the solid parts of the head and body, rather than to the gills, where the spreading can be determined segmentally much more accurately.

### 3. THE ORAL, PHARYNGEAL AND CUTANEOUS GROUPS.

In order to ascertain whether taste buds appear first in areas that are undoubtedly ectodermic or in areas that are endodermic, buds were classified roughly into three groups:

(*a*) The oral group, comprising buds lying on the anterior portion of the mouth, both roof and floor, and extending as far back as and including the proximal hyoid arch and suspensorium.

(*b*) The pharyngeal group, comprising buds lying on the roof and floor of the pharynx, on the gills, and extending as far forward as and including the ventral portion of the hyoid arch and extending posteriorally into the œsophagus.

(*c*) The cutaneous group, including all buds lying on the dorsal and ventral portions of the head and on the barblets, operculum and posterior portions of the body back of the operculum. This group is, in the anterior portion of the head at least, a continuation of the anterior oral group, and is catalogued separately for the purpose of a preliminary survey only.

In tabulating the buds of the barblets it was not practicable, of course, to place them in the sections in which they were found, since they might lie in almost any position, nor in the sections in which the proximal portions lie, since the base varies in size at different ages and always occupies a number of sections; nor was it possible to ascertain accurately their number in later series, since they are very numerous. The barblet buds are not included in Table II, since the main object of this tabulation is to show the place of first origin and the rate of progression from this point. They will be given in separate tables and discussed fully. The buds of the barblets should be added to the total of Table II to ascertain the exact number of buds in a given series.

From Table III it will be seen that buds appear simultaneously in the anterior portions of the mouth (really on the inner surface of the lips and breathing valve, which cannot be distinguished at this age) and in the pharynx. The buds of the pharyngeal group appear simultaneously on the first, second and third gill arches. No buds appear on the skin of the outer surface of the head until in series N, 25 hours after they appear in the oral cavities and the pharynx. The first to appear on the outer surface of the head spread continuously from those just inside the lips.

TABLE III.

Table showing gross distribution in oral, pharyngeal and cutaneous groups.

| EMBRYO. | AGE IN HOURS. | NO. OF BUDS IN MOUTH. | INC. | NO. OF BUDS IN PHARYNX. | INC. | NO. OF BUDS IN SKIN. | INC. |
|---|---|---|---|---|---|---|---|
| K′ | 113 | 4 | 4 | 10 | 10 | — | — |
| L | 120 | 10 | 6 | 10 | 0 | — | — |
| M | 128 | 21 | 11 | 12 | 2 | — | — |
| N | 138 | 52 | 31 | 47 | 35 | 14 | — |
| O | 146 | 56 | 4 | 69 | 22 | 30 | 16 |
| O′ | 155 | 65 | 9 | 80 | 11 | 23 | 7 |
| P | 163 | 84 | 19 | 102 | 22 | 34 | 11 |
| Q | 174 | 94 | 10 | 147 | 45 | 36 | 2 |
| R | 183 | 86 | 8 | 201 | 54 | 35 | 1 |
| S | 199 | 113 | 27 | 210 | 9 | 49 | 14 |
| T | 213 | 146 | 33 | 352 | 142 | 72 | 23 |
| U | 244 | 188 | 42 | 477 | 125 | 117 | 45 |

In the case of the maxillary barblet buds, an exception to this statement might be taken. In discussing those buds later they are catalogued as appearing in K′; but, since the lateral portions of the upper lips are continuous with the inner and lateral portions of the maxillary barblet, it is impossible to state positively, owing to the relation of the barblet to the lips, whether they are inside the mouth or on the outer surface of the head. The above statement is correct for all cutaneous buds aside from the doubtful ones on the maxillary barblet.

From the table it will be seen also that the total number of buds in the oral cavity is greater than that in the pharyngeal for the first four series excepting in K′; from series O′ on the total number of buds in the pharynx is greater than in either the oral or cutaneous groups excepting the maxillary barblet buds and after series Q is greater than both of them combined. This inequality may possibly disappear after the cutaneous group secures its full complement of buds, which is much later than any series studied.

The relation of the oral and cutaneous buds will be discussed later under the analysis of the smaller subdivisions of which these are composed. So far as Tables II and III are concerned, the cutaneous group may be considered as an extension of the oral buds out over the upper and lower lips and so to the head and body. It is almost impossible to tell whether a bud situated on the anterior edge of the lip is to be counted as oral or cutaneous. For these particular areas buds above the dorsal boundary of the oral epidermis of the upper lip were counted as on the top of the head and the same arbitrary rule was applied to those of the lower lip. And while the appearance of buds on the body is by discontinuous groups, as will be shown later, we may consider them for the present as simply extensions of the buds within the mouth with which they are continuous at that point.

The simultaneous appearance of the two primary groups and their wide separation, one lying in the ectoderm of the extreme anterior portion of the oral cavity and the other in the endoderm of the pharynx, renders the exact determination of the anterior limits of the pharynx unnecessary so far as this type is concerned, at least.

The anterior limits of the pharyngeal group are definite and do not move forward, while the posterior limit of the oral group moves steadily backward (see Table IV) until it reaches the anterior limit of the pharyngeal group; and in the absence of definite knowledge of the limits of the pharynx it is much more probable that oral buds, as will be seen later, may spread into endodermic territory than that the reverse process takes place. Except for the spreading of the pharyngeal group back into the œsophagus, it is much more constant in its position than the oral and cutaneous groups, which in addition to spreading back in the mouth also spread out from the lips and finally cover nearly the whole surface of the body.

These buds of the oral and cutaneous groups which are innervated by the gustatory fibers from the geniculate ganglion show a much greater adaptability to the functional needs of the organism than those of the pharynx which are innervated by the ninth and tenth nerves.

These three groups seem to represent three more or less well defined functional groups of which the oral and cutaneous are much more closely related to each other structurally and functionally than are either of them to the pharyngeal; and it is in the functional needs of the organism, *i. e.*, in the appearance of the buds simultaneously on areas where they could be stimulated at the same time, that we shall have to look for an explanation of the place of appearance and manner of spreading of the various groups of buds.

TABLE IV.

Table showing the extent of the oral, cutaneous and pharyngeal groups given in sections of 7 microns each.

| Embryo. | Oral. | | Pharyngeal. | | Cutaneous. | |
|---|---|---|---|---|---|---|
| | Limits in Sec. | Length in Sec. | Limits in Sec. | Length in Sec | Limits in Sec. | Length in Sec. |
| K′ | 10–15 | 5 | 68–73 | 5 | — | — |
| L | 3–21 | 18 | 116–141 | 25 | — | — |
| M | 3–41 | 38 | 105–121 | 16 | — | — |
| N | 3–65 | 62 | 90–163 | 73 | 2–36 | 34 |
| O | 2–73 | 71 | 90–167 | 77 | 8–59 | 51 |
| O′ | 2–67 | 65 | 67–173 | 106 | 5–38 | 33 |
| P | 2–76 | 74 | 88–180 | 92 | 2–45 | 43 |
| Q | 2–70 | 68 | 75–192 | 117 | 2–60 | 58 |
| R | 2–122 | 120 | 86–207 | 121 | 2–44 | 42 |
| S | 2–153 | 131 | 93–227 | 134 | 2–64 | 62 |
| T | 2–154 | 132 | 96–248 | 152 | 2–67 | 65 |
| U | 2–174 | 172 | 93–301 | 208 | 2–68* | 66 |

*The opercular buds catalogued in Table VIII, C, for the 9.4 mm. embryo (U) are not included in this summary.

The relations of these groups to each other and particularly their limitations are shown in Table IV, where the anterior and posterior boundaries of the groups are given in sections of 7 microns each. From this table it will be seen that the isolation of the oral and pharyngeal groups is quite marked in the earlier series and even up to series R they do not overlap, but in this series the two groups overlap. Those of the oral group occupy the roof and dorso-lateral portion of the palate and extend posteriorly beyond the anterior end of the pharyngeal buds which occupy the floor and sides of the pharynx.

In the regions in which the overlapping occurs the oral group includes in this table all buds of the anterior and posterior palatine groups, the latter including the proximal hyoid and suspensorium buds. All these groups have a certain degree of continuity as they spread backward and all are innervated by the seventh nerve in common with buds in the anterior oral regions.

The pharyngeal group includes, in the region of the overlap, buds on the floor of the pharynx, on the distal portion of the hyoid and on the gills. These are all innervated by fibers from the ninth and tenth nerves, and, with the exception of the distal portion of the hyoid, appear in segmental order from the first gill backward.

The oral group begins at the extreme anterior end of the mouth and in series U extends back to section 174, the most posterior buds of the oral group at this time being situated on the proximal portion of the hyoid.

The pharyngeal group begins at section 68 in K′ and appears in 116 in L and its anterior buds then remain constantly near the 89th section in the remaining series. The most striking exception is in O′, in which the group extends forward to section 67.

The most anterior buds of the pharyngeal group as catalogued here always lie in the median ventral line in front of the union of the hyoid with the copula and the overlapping described above is due to the growth of the oral group backward over the pharyngeal and not to the growth forward of the pharyngeal, since the anterior pharyngeal buds lie grouped about the 89th section and the oral move back from the 15th to the 174th section.

In series S, T and U the œsophageal buds are included with the pharyngeal. If we subtract 3 sections from S, ten from T and 26 from U, it will give the exact limit of the pharyngeal group. This makes the total in the three groups, respectively, 131, 142 and 182 sections.

The preponderance of taste buds in the pharynx where there are 477 in U as compared with 188 in the oral group is not accompanied with a corresponding elongation of the pharyngeal areas as compared with the oral areas in the early stages of Ameiurus. Even in U, where the areas occupied by oral and pharyngeal buds are nearly equal, being 172 and 182, respectively, the number of buds in the pharynx is more than two and a half times as great as that in the oral group.

A comparison of the posterior limit of the oral and cutaneous groups shows a much slower rate of progression in the cutaneous group. In series N, for instance, where the cutaneous buds first appear, the posterior limit of the oral group is section 65, while the posterior limit in U is 174. In the cutaneous group the corresponding limits in N and U are 36 and 68. This slower rate of progression, accompanied as it is by the later appearance of the cutaneous buds, probably indicates the phylogenetic relation of these two groups to each other. The oral group would be functionally important regardless of the condition of the eye, while the appearance of the cutaneous buds is probably associated with the reduction of the relative functional importance of the eye in seeking food, which is so characteristic of Ameiurus. The spreading of buds from the oral areas to the cutaneous areas does not involve a very great change, since the two areas are really continuous on the lips and both lie in ectoderm and both are supplied by communis fibers from the geniculate ganglion of the seventh nerve. The simultaneous appearance of buds in the oral and pharyngeal areas is, however, much more striking, since one lies in ectoderm and the other in endoderm. This difference might be minimized by lessening the radical distinction which is usually made between endodermic and ectodermic areas, since endoderm is always derived from ectoderm, if it were not for the fact that buds lying in ectodermic areas are supplied by communis nerves. JOHNSTON's suggestion that buds spread from endodermic into ectodermic territories, if found to be true in more generalized types, would lessen the difficulty of explaining this curious condition.

Since taste buds do not spread from endoderm into ectoderm in Ameiurus, some other explanation of their appearance there must be sought which will explain the conditions here, as well as in other types. In the following sections an analysis of the various subdivisions of the three principal groups mentioned has been made to ascertain if possible what factor has determined the time and place of appearance of taste buds and in particular to see if the distribution was correlated with or controlled by the nerve supply.

In this analysis four things have been kept in mind: (1) To determine the time of first appearance of taste buds situated in different areas but innervated by fibers from the same nerve, *i. e.*, to see if buds not parts of the same functional unit but having a common innervation appeared at the same time. (2) To determine if buds that are a part of the same functional unit but have their fibers from different nerves appear at the same time. If this proves to be the case, the functional unit is the prime factor in determining the time of the appearance and direction of spreading of groups. Neither of these questions can be answered, of course, except in groups of buds, the smaller subdivisions of which have a single innervation. (3) To determine, if possible, whether buds appear first on the peripheral or proximal distribution of a nerve. This ought to throw some light on the manner in which gustatory fibers reach the areas they innervate. (4) To determine if buds appear in any definite order on structures segmentally arranged, such as those in the gill region.

The description of the relations of the various areas to the nerve supply is based, as mentioned before, on the account of the communis system of Ameiurus by C. J. Herrick ('01), mainly, although not entirely for the pharyngeal regions. The reader is referred to that paper for a fuller description of these nerves; only so much of it is incorporated here as is deemed necessary to make the correlation clear.

The term "functional unit," as used in the following description, is applied to groups of buds, discontinuous at the time of their appearance, which from their position on the body would seem to function as units, that is, be stimulated in unison. They are characterized, first, by having areas between them and other groups devoid of buds at the time of their appearance, although they may become continuous later with these groups; and, second, by differences in time of appearance, this difference varying from a few hours up to one hundred or more for adjoining groups which may later become continuous. The units are composed of smaller subdivisions closely related to the number of nerves supplying the unit. These show the same manner of spreading as the larger unit of which they are part.

### 4. THE DORSAL LIP AND MAXILLARY BARBLET GROUP.

This group includes buds lying on the upper lip both inside the lip and on the outside, buds lying on the maxillary barblet and on the dorsal breathing valve. The first buds to appear in this group are situated on the lateral portion of the upper lips, the dorsal breathing valve and the region of the premaxillary teeth and on the base of the maxillary barblet. Buds appear on the base of the maxillary barblet of K′ (118 hours). As mentioned before, these may be really internal lip buds and not on the outer surface. It is not possible to distinguish between the buds on the lip, on the breathing valve and on the region of the premaxillary teeth. Teeth are not present at this stage and the premaxillary bone, being a membrane bone, is not present and the breathing valve is not yet differentiated from the lip. The breathing valve can, however, be distinguished easily from the roof of the mouth at this stage. The epithelium of the lip and breathing valve is thick, while that of the roof of the mouth is thin. This enables one to separate these two structures from the roof of the mouth, which receives buds much later. All these areas receive buds simultaneously and all are innervated by communis fibers running out through the ramus maxillaris (excepting one twig from ramus mand. V to the barblet), the buds of the maxillary barblet and the skin of the upper lip just in front of the maxillary barblet and continuous with it being supplied with the lateral branch of that nerve and those of the lateral parts of the upper lip and the region of the premaxillary teeth by the mesial stem of the same nerve. The buds of the maxillary barblet are supplied by three twigs from the same nerve. HERRICK ('01), in his description of the distribution of the ramus maxillaris, does not mention the upper breathing valve and I infer that it is included in the description of the innervation of the lateral lip region and the premaxillary region.

Table V shows the number of buds and the number of sections occupied in this group for series K′ to P.

TABLE V.

Table showing time of appearance, rate of increase and length of area measured in sections occupied by the dorsal lip and maxillary barblet groups. Under each age the first column gives the number of buds present, the second column the extent indicated by the section numbers between which they are found.

| EMBRYO. | K′ | | L | | M | | N | | O | | O′ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | No. | EXTENT. | No. | EXTENT. | No. | EXTENT. | No. | EXTENT. | No. | EXTENT. | No. | EXTENT. |
| Lip and breathing valve.. | 4 | 11–15 | 8 | 3–16 | 13 | 3–20 | 9 | 3–21 | 29 | 2–40 | 38 | 2–53 |
| Max. barblet .......... | 2 | 36 | 13 | 36–54 | 11 | 43–58 | 18 | 40–74 | 23 | 21–59 | 34 | 31–73 |

This area, although innervated by several nerves, would undoubtedly function as a unit. The only exception to this statement that might be taken is in regard to the maxillary barblet, but as stated above its first buds appear at the base of the anterior surface where they are continuous with the inner and lateral portion of the lip. And when buds appear later distally on the barblet, they are accompanied by other buds farther back on the body which would increase the area innervated from the lip region, that is, the long maxillary barblet bearing buds on its distal portion is equivalent to enlarging the cutaneous group by spreading over the head and body.

This group is isolated in position from buds on the top of the head by an area devoid of buds between it and the nasal group which appears later and from the anterior palatine group by the later appearance of that group as well as by the different histological character of the epithelium on which they are situated. The buds on the maxillary barblet supplied by the ramus mand. V cannot be separated from those supplied by the ramus maxillaris. There is no reason, however, for supposing that they do not appear along with the other maxillary buds in point of time rather than with buds appearing later in other areas which are innervated by the ramus mand. V. The almost invariable rule is for buds to appear with their functional group regardless of the various nerves supplying them.

### 5. THE VENTRAL LIP AND BARBLET GROUP.

This group includes buds lying inside the mouth on the lower lip and mucosa covering the mandible and on the outside covering the outer anterior surface of the mandible and on the mental and post-mental barblets. All these buds are placed under one head because those lying on the anterior portions of the lips are continuous both with those inside the mouth and with those under the lips on the outside of the body. They probably comprise two groups, however, at least functionally. Those lying inside the mouth would function with those buds occupying a similar position on the upper lip and breathing valve and the region of the premaxillary teeth, while those lying under the lower jaw and on the mental and post-mental barblets would function with the buds situated on the maxillary barblet and those of the nasal group.

Structurally this group is isolated, both those lying inside the mouth and those outside, from groups lying farther back by well defined areas devoid of buds at the time the posterior groups appear and by the later appearance of those groups.

(*a*) Buds of the lower lip inside the mouth on the lower breathing valve and on the mucosa of the mandible.

In separating the buds of the extreme anterior portions of the lip into those inside the mouth and those outside the mouth the same arbitrary rule was followed as in the case of the upper lip. Buds lying below the ventral border of the mucosa of the lip were tabulated as on the outside of the body. It is not possible to separate buds of this subdivision which lie on the lip from those on the mucosa of the mandible. Meckel's cartilage extends almost into the extreme anterior portion of the lip and there is no perceptible difference between the epithelium of the lip and the breathing valve and that of the mandible.

Table VI shows the number of buds in this subdivision up to series O′, where there are 24. The backward movement of the buds up to this time is not marked, although present; in later stages buds extend much farther posteriorly and in the $20\frac{1}{4}$ mm. embryo they occupy four-fifths of the total extent of Meckel's cartilage.

TABLE VI.

Table showing time of appearance and extent of subdivisions A and B in the lower lip and the two ventral barblet groups.

| Embryo. | A. Mucosa. | | B. Skin. | | C. Mental Barb. | | D. Post Mental Barb. | |
|---|---|---|---|---|---|---|---|---|
| | No. of Buds. | Extent. | No. of Buds. | Extent. | No. of Buds. | Extent. | No. of Buds. | Extent. |
| L | 1 | 20 | 1 | 27 | — | — | — | — |
| M | 7 | 30–41 | — | — | — | — | — | — |
| N | 20 | 27–65 | 2 | 27 | 7 | 48–55 | 7 | 63–75 |
| O | 21 | 17–70 | 8 | 17–31 | 10 | 36–48 | 10 | 43–58 |
| O′ | 24 | 19–66 | 6 | 19–30 | 9 | 47–61 | 12 | 55–67 |

The taste buds on the mucosa of the mandible are innervated by twigs from the internal branch of the ramus mand. V. Those of the middle of the lower lip and lower breathing valve are innervated by the lip twig of the same nerve. This nerve also gives off two twigs farther back for the mental and post-mental barblets which acquire buds somewhat later.

Buds on the edge ("lateral portion") of the lower lip are innervated by the external branch of the ramus mand. V along with those throughout the whole length of the outer surface of the mandible. The buds of the middle of the lip cannot be separated from buds of the lateral portion of the lip even in the earlier stages, although innervated separately by the internal and external branches, respectively, of the ramus mand. V. They would undoubtedly function as a unit.

If we compare the posterior limit of the dorsal lip and breathing valve group (Table V) with the anterior limit of the lower lip and mandible group (Table VI), it will be seen that there is no overlap. The posterior limit of the former group for series K′, L, M and N are sections 15, 16, 20 and 21, respectively, and the anterior limit of the latter group for series L, M and N are 20, 30 and 27, respectively. The ventral group underlies the dorsal in later series, however, and its failure to do so in the earlier series is due probably to the elongation of the upper parts of the head on account of the rapid growth of the brain. This is equalized later by the growth of the lower jaw to fit into the upper.

The posterior limit of buds on the mucosa of the mandible moves backward, as stated above, until in series N it comes to the region occupied by the most anterior buds of the anterior palatine group, and in series O′ reaches the anterior buds of the mid-ventral pharyngeal group which, however, had appeared first in an earlier series (N).

The spreading of the buds back from the anterior portion of the mandible both on the mucosa and on the skin, as will be shown presently, toward the posterior or proximal portion and the manner in which the nerve runs along the mandible from the proximal toward the distal portion is conclusive evidence that in these two cases the more peripheral buds supplied by these nerves receive fibers before the proximal buds do.

The functional need of the organism, represented by the more or less continuous spreading of the buds from the lips out over the surface of the body and back in the oral cavities, seems to furnish the key to the explanation of the methods of spreading rather than the anatomical arrangement of the nerves. Buds rarely or never in the oral and cutaneous groups appear on the shortest twigs or the proximal distribution of a nerve first, but always on the distal or longest portions, since this maintains the continuity in the anterior-posterior method of spreading.

(*b*) Buds lying on the skin of the mandible outside the mouth, and on the mental and post-mental barbules (groups B, C and D).

From Table VI it will be seen that buds appear first on the skin of the mandible (group B) in series L where there is one bud. None are present in M and two in N. In series N buds appear on the mental and post-mental barbules, but there are a few sections in O′ and P lying between the buds on the mental barbules and those of the lower lip devoid of buds. Notwithstanding this slight discontinuity, there seems to be no doubt of the propriety of including the barblet buds with the anterior mandibular or lip group, since buds situated farther back on the lower jaw do not appear until series U, when buds appear on the posterior portions of the operculum. Buds which would be most likely to be confused with these in later stages are those of the posterior mandibular divisions of the post-orbital and opercular group, which do not appear until the 11 mm. embryo, so that the group is quite homogeneous in distribution and time of appearance compared with any other group with which it might be confused. Functionally this group probably serves the same purpose for the lower jaw that the buds of the nasal group do for the dorso-lateral portion of the head. Buds of the lower jaw, for instance, have extended as far back as section 30 in O′, while those of the nasal group have extended to the 38th section.

It is not possible to make a comparison of the mental and post-mental barbules with the maxillary and nasal on account of the pliable character of the structures.

The posterior limit of the anterior mandibular group moves posteriorly slightly in the earlier series until it reaches a point just back of the post-mental barblet, but in series U the posterior buds of this group lie in section 53, so that there is probably up to this time little actual spreading. This must occur in later series, however, since according to HERRICK the buds of this group supplied by the ramus mand. V occupy the whole extent of the mandible.

The innervation of buds on the lateral portion of the lip and mandible is by the external branch of ramus mand. V, while that of the mental and post-mental barblets is from the internal branch of that nerve along with the middle of the lower lip, the lower breathing valve and the mucosa of the mandible.

It is of interest to note in this group, first, the slight discontinuity in the appearance of mental and post-mental barbule buds, since they represent the posterior extension of the lower lip group and have their innervation in common with that, and, second, the fact that the buds on the mandible supplied by the ramus mand. ex. V appear first on the anterior portions of the mandible; that is, on the distal distribution of the nerves, and later spread back to the posterior portion of the mandible at a time corresponding to the appearance of buds in post-orbital and opercular group.

### 6. THE NASAL GROUP.

A second group of taste buds isolated by position and by time of appearance includes those lying in front of the nasal barblets, on the skin at the base of the nasal barblet, about the nasal opening and those between the nasal barblet and the eye.

All these buds are innervated by the ramus oph. sup. V (WORKMAN, '00). This group can be broken down into four, or possibly five, subdivisions separated by differences in position of the first buds appearing and by a very slight difference in time of appearance, although the group as a whole is quite homogeneous in both these respects. This group lies in the region where the anterior and posterior nasal openings are formed, and it is possible that the subdivisions in which this group appears are due in some measure to the presence of this organ, although at least three of them are indicated by divisions of the nerves supplying them.

The nasal opening is an antero-posterior slit still open throughout its whole length in series L, but closed in series M. The formation of two nasal openings from a single slit-like opening is accomplished by the approximation of the dorsal and ventral lips of the slit in the middle region, leaving an opening at either end around which the nasal cones appear later. The nasal barblet occupies a position slightly posterior to the middle of the dorsal lip in the embryo but comes to have a more posterior position in the adult quite near the posterior opening.

The subdivisions of the group are as follows:

(A) A group in front of the nasal barblet, on the top of the head, and extending forward toward the snout and innervated by one of the last four large divisions of the ramus oph. sup. V.

(B) A group lying on the nasal barblet and innervated by the remaining three of the last four divisions of the ramus oph. sup. V.

(C) A group in front of the eye and back of the nasal barblet and over the supra-orbital line and innervated by the first four main branches of the ramus oph. sup. V.

(D) A group lying under the line of closure of the nasal slit whose innervation WORKMAN does not give, or at least does not distinguish from the other buds about the nasal opening.

(E) A group in front of the eye and under the supra-orbital line and probably innervated by some of the fibers supplying group C.

TABLE VII.

Table showing the number of buds at different ages in the various subdivisions of the nasal group and their extent as indicated by the section numbers between which buds are found (sections 7 microns thick).

| EMBRYO. | A | | B | C | | D | | E | |
|---|---|---|---|---|---|---|---|---|---|
| | NO. | EXTENT. | NO. | NO. | EXTENT. | NO. | EXTENT. | NO. | EXTENT |
| N | — | — | 1 | 1 | 33 | 1 | 36 | — | — |
| O | — | — | 3 | 2 | 32-40 | 2 | 54-59 | — | — |
| O′ | 2 | 19-23 | 2 | 2 | 30-38 | 1 | 33 | — | — |
| P | 2 | 15-22 | 4 | 2 | 30-40 | 2 | 42-45 | — | — |
| Q | 3 | 19-23 | 5 | 2 | 35-43 | 2 | 49-60 | — | — |
| R | 3 | 16-22 | 5 | 2 | 31-43 | 1 | 44 | — | — |
| S | 5 | 17-32 | 5 | 2 | 33-60 | 4 | 35-55 | 1 | 64 |
| T | 5 | 15-21 | 6 | 2 | 41-50 | 5 | 35-59 | 1 | 67 |
| U | 9 | 19-34 | 25 | 2 | 73-89 | 9 | 48-68 | 1 | 101 |

The single columns of Table VII show the number of buds and the double columns give the extent of groups expressed in sections. It will be seen from the table that three of these subdivisions appear in N and one additional in O′. The presence of two buds on the skin in front of the nasal barblet, group A, indicates that possibly the later appearance of this subdivision is an individual variation. It is possible that series E which lies in front of the eye and below the supra-orbital line belongs to D, though I have catalogued it separately, and that the sections in which these buds are located indicate the posterior extent of that group.

The first buds in this group appear 25 hours later than the first buds of the preceding group and are isolated from them in position. All the buds of this group lie about the nasal opening and on the dorso-lateral portions of the head, while those of the preceding group are on the lip and maxillary barblet. The posterior buds of the lip and barblet group lie farther from the anterior end of the head than the anterior buds of this group in the later series owing to the more rapid growth posteriorly of the lip and barblet group, but this is not true at the time of the appearance of the nasal group. While the nasal group lies dorsal to the maxillary group, it also represents the posterior spreading of the lip group since it lies farther back on the longitudinal axis of the body at the time of its appearance. Later, however, the nasal group probably represents functionally the extension of the lip group to the dorsal portion of the head.

Subdivision C of this group is very peculiar in that it contains but two buds up to series U. The position of these buds throughout the earlier series is so nearly constant and their separation from each other remains so nearly the same that there can be little doubt that they are the same buds in all series. The constancy of these two buds throughout so many series is still more striking when we consider the fact the area between the nasal barblets and the mid-dorsal portion of the eye of the adult is innervated according to WORKMAN ('00) by communis fibers running out through four well defined divisions of the ramus oph. sup. V and by several small twigs. Comparing group C with group A, we find practically the same stationary condition in that group, so that we shall have to consider the areas on which these buds are situated as growing slowly or else the spreading of the buds is practically wanting and does not correspond closely with the number of nerve twigs supplying these two subdivisions. The gustatory fibers evidently do not run to the surface simultaneously through nerve twigs which innervate practically the same area.

The whole group is characterized during the earlier stages of Ameiurus by its practically stationary condition. The backward movement in all the series except U can be accounted for mainly by the growth of the embryo.

Group C, while stationary in the earlier series, in the 11 mm. embryo spreads back as far as the middle of the dorsal portion of the eye and it was puzzling to know whether to include some of these buds lying over the eye in the nasal group or in a division of the post-orbital group lying behind and above the eye and innervated by the ramus max. acces. However, that group appears along with the remainder of the post-orbital and opercular group; and, while the posterior extension of the nasal group comes close to the anterior buds of the post-orbital group, still there is an area devoid of buds between the two groups. This is the only case in which two groups which later become continuous are at all difficult to separate at the time of their first appearance.

### 7. THE POST-ORBITAL AND OPERCULAR GROUP.

A fourth group comprises buds lying back of the eye mainly, and in front of the posterior edge of the operculum. The various divisions of this group arise almost simultaneously, but receive their nerves from a variety of sources. Two other groups, the cerebellar and the occipital groups, belong here as far as their position on the longitudinal axis of the body is concerned; but since they appear much later and have in addition their nerves in common with the body buds, they will be described with those of the body.

The post-orbital group can be divided into several smaller subdivisions as follows:

(A) Buds lying behind, under and above the eye and innervated by fibers from the ramus max. acces. and the ramus mand. ex. VII.

(B) Buds lying on the mandible and distributed along the mandibular lateral line canal from lateral line organs three to eight and innervated by the ramus mand. ex. VII.

(C) Buds lying on the operculum, those in the region of the pre-operculum bone being innervated by the ramus mand. ex. VII, while those lying on the posterior and dorsal portions of the operculum in the region of the post-frontal and squamosal are innervated by the ramus oticus.

(D) Buds lying on the branchiostegal rays and innervated by the ramus hyoideus.

TABLE VIII.

Table showing the number and time of appearance of buds in the post-orbital group.

| EMBRYO. | A<br>OPTIC GROUP. | B<br>POST-MAND. GROUP. | C<br>OPER. GROUP. | D<br>BRANCHIOSTEGAL GROUP. |
|---|---|---|---|---|
| 9.4 mm. | — | — | 11 | — |
| 11.0 mm. | 6 | 8 | 19 | 1 |
| 14.75 mm. | 10 | 11 | 6 | 1 |

Subdivision A does not appear until in the 11 mm. embryo, where there are six buds present, one under the eye, four on the dorsal and posterior portion of the cornea and one behind the eye. Of the ten buds present in series A in the 14¾ mm. embryo, eight lie on the upper and posterior portion of the eye and two behind the eye, none being present under the eye.

This subdivision is distinctly isolated in position from other members of the group to which it belongs. It is, however, not so sharply separated from the posterior buds of the nasal group as adjoining groups are usually separated. Even in this case, however, there is an area of 20 sections between the anterior buds of group A and most posterior buds of the nasal group. In addition, the posterior buds of the nasal groups are above the anterior half of the eye and the first buds of the orbital subdivision appear under and behind the eye.

The first buds to appear in this subdivision are situated on the border of the cornea, some of them actually lying on the transparent portions of that structure.

Without raising any question as to the relation of the accessory maxillary nerve to the ramus maxillaris, it may be of interest to note that the taste buds innervated by the ramus max. lie on the lateral portions of the upper lip, on the maxillary barblets, and on the skin of the upper lip, just anterior to the maxillary barblet at the extreme anterior end of the embryo and appear more than 130 hours sooner than those lying about the eye and supplied by the ramus max. acces.

The second subdivision B appears first in the 11 mm. embryo, where there are at least eight buds. It is not present in series U (244 hours). The whole mandible, as mentioned above in the adult (HERRICK, '01), is supplied with two nerves; first, in common with the lower lip and mental and post-mental barbules, by the ramus mand. V, external branch, and secondly, by the ramus mand. VII, a branch of the ramus hyomandibularis. This last nerve supplies the mandible from the region of the third of the main lateral line organs back to the region of the seventh, or possibly farther. In the earlier stages, however, the groups supplied by these two nerves are quite distinct. The anterior mandibular group spreads back from the lips and mental and post-mental barbules and appears much earlier, while the posterior group comes in with the remaining divisions of the post-orbital group in point of time. Even in the 11 mm. embryo there is an area of 30 sections between them quite free from buds.

The posterior mandibular group buds are distributed as follows with reference to the mandibular lateral line organs. In the 11 mm. embryo, four lie between the third and fourth organ, and four between the fourth and fifth, while in the 14¾ mm. embryo, where there are 11 buds, six lie between the third and fourth organ, and five between the fourth and fifth. In the 17½ mm. embryo, not shown in the table, there are 13 buds, six lying between the third and fourth organs, five lying between the fourth and fifth organs, and two between the fifth and sixth organs; compared with the lateral line organs, we have an evident spreading from anterior to posterior.

It is difficult, in later stages, to separate the posterior mandibular buds from the opercular groups, but since the mandible does not extend farther back than section 131 in the 9.4 mm. embryo and the first buds in the opercular group appear in section 166, which is between the seventh and eighth mandibular lateral line organs, it is altogether probable that the separation of these two groups is represented by this difference. In the 11 mm. embryo the mandible does not extend beyond section 184, and the last bud on the mandible lies in section 129 and the first of the opercular group in 160.

HERRICK ('01) describes the recurrent twig of the mandib. ex. V as supplying the skin over the dentary, articular and quadrate bones. It is possible that the first two buds of the opercular group, which lie in sections 160 and 163 behind the end of the mandible, and 30 sections in front of the remainder of the opercular group, may belong to the quadrate group, although he does not say specifically that the recurrent nerve supplies taste buds.

The posterior mandibular division at the time of its appearance is quite distinct from the anterior mandibular division anteriorly and from the posterior opercular division posteriorly. Its innervation is undoubtedly at this time solely from the ramus mand. ex. VII. It also shows, as mentioned above, a well defined progression from anterior to posterior, spreading from the second and third mandibular lateral line organs to the region between the third and fourth and later to that between the fourth and fifth. In later stages it is joined and probably overlapped by the posterior spreading of the anterior mandibular group.

The third group (C) includes buds lying on the operculum posterior to the preceding group. The buds lying in the region of the pre-operculum are innervated by the fibers arising from the main stem of the ramus hyomand. just before it divides into the ramus mand. ex. VII and ramus hyoideus. The buds lying on the dorsal and posterior portions of the operculum near the post-frontal and squamosal are innervated by the ramus oticus. This group appears somewhat earlier than those of the two preceding subdivisions, there being 11 buds in series U, 9.4 mm. Two of them are situated on the dorsal posterior portion of the operculum between the first and second organs of the main lateral line and nine along the area of the mandibular lateral line canal. Of these nine one is between the seventh and eighth mandibular lateral line organ and eight are between the last mandibular lateral line organ and the first main lateral line organ and all lie below the line of the canal.

Of the 19 buds lying on the opercle in the 11 mm. embryo, two lie between the fifth and sixth mandibular lateral line organs. These two buds have been incorporated here but they may belong to the quadrate group mentioned above. Of the remaining 17, five lie between the sixth and seventh mandibular lateral line organs, and six lie between the seventh and eighth, while two lie between the eighth mandibular and the first main lateral line organs and four lie between the first and second of the organs of the main lateral line. Of the six buds appearing in the opercular group in the 14¾ mm. embryo, four lie between the seventh and eighth mandibular organs and two between the last mandibular organ and the first main lateral line organ. There seem to be no buds on the posterior dorsal portion corresponding to those between the first and second main organs in the 11 mm. embryo. The deficiency of buds in this group in the 14¾ mm. embryo is quite striking.

In HERRICK's Ameiurus paper ('01) the ramus oticus is described as innervating the dorsal portions of the operculum and the post-frontal and squamosal bones. There seems to be no way to separate this area from that of the buds appearing on the pre-operculum, since membrane bones are not definitely formed enough to ascertain their exact boundaries and the mandibular lateral line curves dorsally in the posterior portion of the operculum and buds distributed along this line have the same general direction in spreading, so that it is not possible to give these boundaries separately. However, in the 11 mm. embryo three buds are found on what I take to be the post-frontal and squamosal regions, and in the 14¾ mm. embryo only one bud is found in this location.

A fourth division (D) of this group comprises buds lying on the branchiostegal membrane. There is only one bud in this position in the 11 and 14¾ mm. embryos. This group is innervated, as mentioned before, by ramus hyoideus.

The post-orbital and opercular group as a whole is isolated structurally, as mentioned, by well defined areas devoid of buds lying between it and the groups situated anterior to it. Its isolation in time of appearance is still more marked. Group (A) which approaches in position most nearly the nasal group can hardly be considered at the time of its appearance as continuous with that group and the remaining subdivisions are still further isolated from preceding groups. As to the homogeneity of this group functionally, in the absence of experimental evidence and apparently of the possibility of obtaining such evidence, we must fall back upon the isolation in position and in point of time as our only evidence at present.

Its innervation by communis fibers running out through five different nerves, while not different in principle from the anterior groups (notably the dorsal and ventral lip groups), still shows the greatest diversity of any of the oral or cutaneous groups.

One interesting fact in connection with this group is that it occupies practically its whole territory at the time of its appearance and of course little evidence of its spreading backward is given, although in both the mandibular and ventral opercular portions there is evidence that the group spreads posteriorly.

## 8. THE CEREBELLAR, OCCIPITAL AND BODY GROUPS.

TABLE IX.

Table showing the time of appearance and number of buds in the cerebellar, occipital and body groups.

| Embryo. | A. Cerebellar. | B. Occipital. | C. Body. |
|---|---|---|---|
| U 9.4 mm. | — | — | |
| 11 mm. | — | — | 2 |
| 14¾ mm. | — | — | 2 |
| 17½ mm. | — | — | 4 |
| 20¼ | 5 | 10 | 14 |

This group of buds includes (A) those lying on the cerebellum and innervated by the meningeal twig of the ramus. lat. acces. (B), those lying over the occipital region and innervated by the twigs of the ramus lat. acces. given off before that nerve leaves the skull; and (C) buds on the body innervated by the ramus lat. acces. There is no overlapping of this group (C) with the preceding group, the body buds being entirely separate from buds of the posterior operculum until in the 20¼ mm. embryo, when they become continuous.

It will be noticed from the table that the cerebellar and occipital groups appear simultaneously in the 20¼ mm. embryo. It is not possible to separate these two groups at this stage, the cerebellar being continuous with the occipital. Doubtless, if a series had been cut between the 17½ mm. embryo, where they are not present, and between the 20¼ mm. embryo, they would be found to be distinct groups. The separation has been made in cataloguing, by including all buds in front of the posterior portions of the cerebellum in the cerebellar group, and all those back of that point in the occipital group.

The failure of the cerebellar and occipital groups to appear simultaneously with the opercular or post-orbital group, with which they are related in position, is difficult to explain. They have the same innervation practically in Ameiurus that the body buds have and it was thought at first that possibly they followed the same rule that is so often illustrated in the groups anterior to this, of the appearance of buds on the peripheral distribution of the nerves sooner than on the proximal. However, buds on the body appear first on the anterior segments and spread from there posteriorly, and the same occurs, as we shall see later, in the case of the œsophageal buds.

It is possible that the irregularity of these two groups can be explained by the fact that they lie in close proximity to the post-orbital group which is large and appears much earlier. The functional needs of this portion of the body being thus well supplied, these two groups are not of so much importance as the body buds which occupy the regions back of the operculum alone. However, the innervation of the region under discussion is complicated and very difficult to work out, according to Professor HERRICK, so that there may be some facts about the innervation which would clear up the difficulty, and there is a slight possibility that we may have to deal with nothing more than an individual variation, since only one series of each embryo has been catalogued.

The limits of the body group were determined with reference to the lateral line organs and to the free posterior border of the operculum; that is, the point at which it was detached from the body dorsally in the section.

TABLE X.

Table showing the number and position of the buds on the body with reference to the organs of the main lateral line of the body, the free posterior border of the operculum and the distance in sections from the posterior buds of the opercular group.

| EMBRYO. | OPERCULUM DETACHED AT SECTION, | FIRST BODY BUDS APPEAR AT SECTION, | NO. OF SEC. FROM POST. OPERCULAR BUDS. | NO. OF BUDS. |
|---|---|---|---|---|
| 11 mm. | 318 between l.l. org. 3 and4 | 412 between l.l. org. 3 and 4 | 68 | 2 |
| 14 $\frac{3}{4}$ mm. | 412 between l.l. org. 3 and 4 | 427 between l.l org. 3 and 4 | 129 | 2 |
| 17 $\frac{1}{2}$ mm. | 422 between l.l. org. 2 and 3 | 461 between l.l. org. 3 and 4 | 55 ? | 4 |
| 20 .$\frac{1}{4}$ mm | 612 between l.l. org. 3 and 4 | 591 between l.l. org. 3 and 4 | 3 | 14 |

The first body buds lie in each series between the third and fourth main lateral line organs. The lateral line organs seem to be constant in position with reference to each other and to the posterior free border of the operculum, so that in locating these buds by the organs we avoid difficulties arising from the irregular growth of the head as compared with the rest of the body which might arise if they were located by sections alone.

Of the four buds found in the 17½ mm. embryo, two are found between lateral line organs three and four, as are the two found in each of the earlier series of the 11 mm. and 14¾ mm. and the other two are found behind the fourth lateral line organ.

FIG. 1. Series L, 120 hrs. *D*, dorsal lip and max. barbule group. *V*, ventral lip group which at this stage contains only one bud that could be considered as on the outer surface.

FIG. 2. Series O, 146 hrs. *V*, ventral lip buds. *M.B*, mental and post mental buds. *D′*, dorsal lip and maxillary barblet group. *B, C, D*, subdivisions of nasal group. Subdivision *A* is not represented on this chart. It is so closely related to the anterior nasal opening that it is not easy to separate it from buds lying on the nasal barblet.

FIG. 3. Series U, 244 hrs. *V.L.*, Ventral lip. *Ba*, mental and post mental barblet buds. *D. L.*, Dorsal lip and maxillary barblet group. *A, B, C, D, E*, subdivision of nasal group. *C′* and *C″*, ventral and dorsal subdivisions of the opercular group. Subdivisions *A* and *B* are not present in this stage.

FIG. 4. 20¼ mm. stage. At this stage the various subdivisions of the nasal group are continuous with each other and reach back to the eye. The dorsal lip and maxillary barblet group is continuous dorsally with the nasal group and the ventral lip and barblet group is continuous posteriorly with the posterior mand. subdivision (*B*) of the opercular group and dorsally behind the angle of the mouth with the dorsal lip group. None of these buds are shown on the chart except (*B*). *B*, the posterior mand. division of the opercular group. *C* and *C′*, the ventral and dorsal portions of the opercular division. *D*, the branchiostegal buds. Subdivision *A*, which lies behind and under the eye, is omitted. *A′*, *B′*, the cerebellar and occipital buds. *C″*, the body buds.

Fig. 1

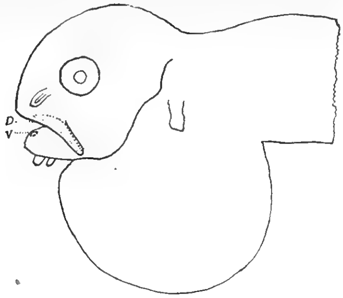


Fig. 2

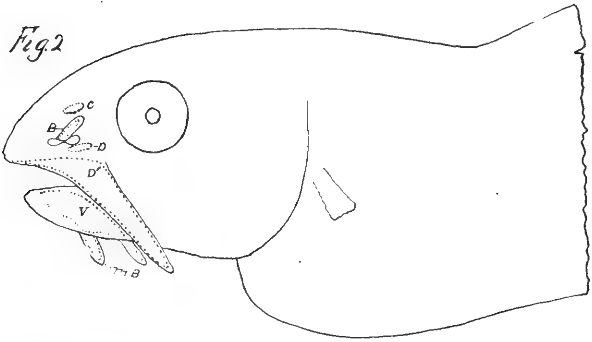


Fig. 3

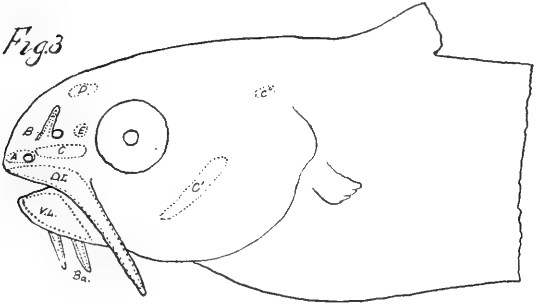
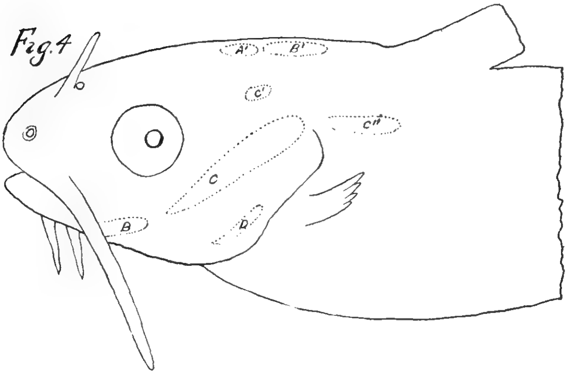


Fig. 4



Of the 14 buds found in the 20¼ mm. embryo, one is found between the third and fourth main lateral line organ, one on the skin over the fourth organ, eight are found between the fourth and fifth organ, and four between the fifth and sixth organ.

This body group shows a well defined progression posteriorly as measured by the lateral line organs, moving back from the area between the third and fourth to that between the fourth and fifth and later to that between the fifth and sixth. The nerves supplying these buds run out from the ramus lat. acces. through spinal rami, which are, of course, arranged segmentally, but no further evidence of a segmental arrangement can be detected than that noted in the table, and I am inclined, of course, from a study of the anterior oral and cutaneous buds to consider the segmental arrangement of buds here to be purely secondary; that is, they are segmental simply because they are innervated by nerves that are segmental on account of having used segmental spinal nerves as a means of reaching the surface.

The question as to whether these buds spread out from the gills or spread back from the post-orbital group will be only mentioned here, and will be discussed more fully with the pharyngeal buds. Their continuity in time of appearance is certainly with the post-orbital group, and their innervation is from the seventh nerve, along with the post-orbital group and buds lying farther forward about the anterior portions of the head. The only two ways in which continuity in distribution could be established with the pharyngeal group, would be for the pharyngeal buds to spread out from the under side of the operculum to the body or else from the bases of the gills down to the ventral surface of the isthmus and thus to the body. It will be seen later that neither of these movements takes place. We must conclude from the time of the appearance, the continuity in distribution and the innervation that they are related to other buds on the head and operculum and are part of the general spreading of buds from the anterior to the posterior portions of the body surface. They represent the posterior extension of a functionally more or less homogeneous group of buds enabling Ameiurus to ascertain the location of sapid substances when the stimulus reaches portions of the body other than the mouth and the pharynx.

The spreading of buds from the place of appearance on the body between the third and fourth lateral line organs in a posterior direction can only be interpreted as a spreading from the proximal toward the distal distribution of the nerves, since the nerves arise anterior to the areas innervated. This it will be recalled is in sharp contrast with the condition usually found in the areas lying anterior to the origin of the nerves.

The location of the cutaneous groups is shown in text figures 1 to 4, p. 37.

### 9. THE ANTERIOR PALATINE GROUP.

This group consists of buds lying on the anterior roof of the mouth. It has quite definite boundaries structurally and its mucous membrane is quite sharply differentiated anteriorly from that of the lip and breathing valve. The lip and breathing valve have a thick mucous membrane, while that of the palate is quite thin as late as series U (244 hours), so that the separation of these groups is quite easy, without considering the area devoid of buds between them, and the difference in time of appearance. In the 20¼ mm. embryo, however, the mucous membrane of the anterior roof of the mouth is quite as thick as that of the breathing valve, but usually stains lighter. Even if this histological difference were not present, it would be quite easy to determine the anterior boundaries of this group, since the breathing valve always has a free border posteriorly and medially and there is, as mentioned above, no continuity in the distribution of buds from the valve to the palate.

This group is supplied exclusively by the ramus palatinus VII, while the following group is supplied by the ramus palatinus posterior. The posterior boundaries of the anterior palatine group are not so definite as the anterior boundaries but there is always in the earlier series and even up to series U (244 hours), a well defined area devoid of buds between the anterior and posterior palatine groups.

This group appears first in series N (138 hours), when four buds are found arranged symmetrically on either side of the median line. In fact, this whole group up to the time when there are 20 buds present in U is entirely symmetrical, the same number of buds lying on either side of the median line. Up to series R (183 hours), there are only four buds. From this time on they increase, as shown in Table XI, and are very numerous in the 20¼ mm. embryo.

TABLE XI.

Table showing the number of taste buds in the anterior palatine group and the limits of their distribution expressed in sections.

| Embryo. | No. of Buds. | Extent in Sections. |
|---|---|---|
| N 138 hrs. | 4 | 55–65 |
| O 146 " | 4 | 43–73 |
| O′ 155 " | 4 | 56–67 |
| P 163 " | 4 | 58–76 |
| Q 174 " | 4 | 56–70 |
| R 183 " | 4 | 46–66 |
| S 199 " | 8 | 56–98 |
| T 213 " | 16 | 55–104 |
| U 244 " | 20 | 57–110 |

It will be seen from the table that the areas occupied as represented by sections are quite constant, ranging from sections 43 to 58 for the anterior boundary and from 65 to 110 for the posterior boundary. After the number of buds increases beyond four, the posterior limit of this group moves back slightly, but up to this time there is undoubtedly little or no spreading in this group. The posterior limit of this group in U brings it into contact with the anterior buds of the posterior palatine group.

### 10. THE POSTERIOR PALATINE GROUP.

This group consists of (A) buds lying on the posterior wide palate, (B) on the proximal parts of the hyoid arch and (C) on the suspensorium, *i. e.*, the hyomandibular, quadrate and symplectic. This group, like the preceding, is innervated by a single nerve, the ramus palatinus posterior VII.

This group is isolated when it first appears from other groups on the roof of the mouth in position, there being 40 sections between the posterior limits of the anterior palatine group and the anterior buds of this group and about ten sections between the posterior buds of this group and the buds on the roof of the pharynx in the region of the first gill arch.

TABLE XII.

Table showing time of appearance of buds and extent occupied in the posterior palatine group.

| EMBRYO. | A. PALATE. | | B. HYOID. | | C. SUSPENSORIUM. | |
|---|---|---|---|---|---|---|
| | NO. OF BUDS. | EXTENT. | NO. OF BUDS. | EXTENT. | NO. OF BUDS. | EXTENT. |
| R | 4 | 108–122 | 1 | 105 | — | — |
| S | 4 | 123-140 | 2 | 129-153 | 1 | 144 |
| T | 7 | 104–150 | 6 | 132–154 | 1 | 157 |
| U | 37 | 110–170 | 10 | 152–174 | 6 | 180–193 |

(A) From this table it will be noticed that the buds lying in the roof of the wide palate posterior to those innervated by the ramus pal. VII are found first in R at section 108. The posterior boundary of this group moves back from section 122 in R to 170 in U, which brings it into contact with the roof buds lying over the first gill arch. While the anterior boundary of this group varies slightly, still the main movement of the group is backward from the point of origin, *i. e.*, from the position of the peripheral buds innervated toward the more proximal buds.

(B) The buds on the proximal portion of the hyoid arch appear first in series R and spread from the ventralmost point of appearance back up toward the proximal. I have taken as the ventral limit of the hyoid group receiving the innervation mentioned, the point where the hyoid cartilage becomes incorporated with the operculum, as distinguished from that portion lying in the isthmus and constituting the distal or ventral portion and receiving its nerve supply from the post-trematic division of the ninth.

I have grouped the buds of the proximal hyoid supplied by the ramus pal. posterior VII with the oral group in order to show the relation of that group to those buds and because it has the same innervation; but it is altogether probable that the posterior palatine group, the hyoid and suspensorial groups with those of the distal hyoid and the floor of the pharynx form a functionally complete group, since they occupy the same area in the longitudinal axis of the embryo.

As mentioned above, the posterior palatine group undoubtedly spreads from the distal toward the proximal areas innervated, but in the case of the hyoid and suspensorial groups the evidence is not so clear. In the hyoid group the first bud is found in R at section 105 and the last in U at section 174, but the anterior limit of the group also moves back from 105 in R to 152 in U; and in the case of the suspensorial buds the same thing occurs. The one bud found in S lies in section 144, while the first bud in U lies in section 180. The only inference from this, barring the loss of buds, which is altogether improbable, is that these structures are moving bodily away from the anterior end of the embryo. In the roof buds, as mentioned above, the anterior limit is not so constant as in the anterior palatine group; still the first buds in R and the first in U are within two sections of each other while the posterior limit moves backward much more rapidly than the relative increase in length of the embryo, which is from 8.33 mm. to 9.40 mm.

## II. SUMMARY OF THE ORAL AND CUTANEOUS GROUPS.

TABLE XIII.

Table showing the relative time of appearance of the various buds in the cutaneous, oral and pharyngeal groups.

| EMBRYO. | AGE IN HOURS. | CUTANEOUS. | ORAL. | PHARYNGEAL. |
|---|---|---|---|---|
| K′ | 113 | Dorsal lip and barb. buds. | | 1, 2 and 3 gill arch buds. |
| L | 120 | Ventral lip and barb. buds. | | |
| M | 128 | | | |
| N | 138 | Nasal buds | Ant. pal. buds. | Ventral pharyng. buds. |
| O | 146 | | | 4 gill arch buds. |
| O′ | 155 | | | Dorsal pharyng. buds.<br>Dis. hyoid buds. |
| P | 163 | | | |
| Q | 174 | | | |
| R | 183 | | Post. pal. buds. | 5 gill arch buds. |
| S | 199 | | | Œsoph. buds. |
| T | 213 | | | |
| U | 244 | Post.-orb. and opercular buds. | | |
| 11 mm. | ........... | Body buds. | | |
| 14¼ mm. | | | | |
| 17½ mm. | | | | |
| 20¼ mm. | ........... | Cerebellar and occipital buds. | | |

In summarizing the result of the study of the oral and cutaneous groups two facts are patent, first, the spreading of buds is always from anterior to posterior, and second, the spreading is always by discontinuous groups. Table XIII shows the time of appearance of the cutaneous, oral and pharyngeal groups.

From Table XIII it will be seen that all the subdivisions of the pharyngeal group are present long before the cerebellar and occipital buds have appeared, and are present some hours before the body buds appear. This is to be explained probably by the homogeneous character of the pharyngeal area and by its limited extent as compared with the cutaneous area.

There are insufficient data to make a comparison of the ontogenetic order in which taste buds innervated by the various rami of the V and VII nerve appear in Ameiurus and other types. If we arrange the nerves of Ameiurus in an order corresponding to the order of appearance of the groups of taste buds it will give the following arrangement:

TABLE XIV.

Table showing the order in which the groups of taste buds appear as related to the various rami of the V and VII nerves which innervate them.

| | | |
|---|---|---|
| 113 hrs. | Dorsal lip and barb. buds innervated by | R. max. V |
| 120 " | Ventral lip and barb. buds innervated by | R. mand. V |
| 138 " | Nasal buds innervated by | R. oph. Sup. V |
| 138 " | Ant. palatine buds innervated by | R. pal. VII |
| 183 " | Post. palatine buds innervated by | R. pal. post. VII |
| 244 " | Post.-orbital and oper. buds innervated by | R. max. acces. V?<br>R. mand. ex. VII<br>R. hyomd. (prox. twigs)<br>R. oticus<br>R. hyoideus |
| 11 mm. | Body buds | R lat. acces. |
| 20¼ mm. | Cerebell. and occip. buds innervated by | Meningeal twigs and Proximal twigs of R. lat. acces. |

Whether we look upon the taste buds as appearing fortuitously and later being connected with their gustatory nerves or take just the opposite view, which seems more in accord with the evidence, and look on the nerve fiber as taking the initiative and producing the bud on reaching the surface, the order in which the nerves are arranged here would seem to indicate the relative times at which communis fibers are found in these rami of the V and VII nerves.

The spreading of buds from anterior to posterior and their appearance in detached groups have been sufficiently emphasized in the discussion of these groups. The real significance of these two facts when brought into relation with the nerve supply will be discussed later. In connection with this table, it is of interest to note that these groups are not determined solely by the nerve supply, although in some cases groups are indicated by the nerve supply, as in the two palatine groups. There are, however, enough of these groups which either have several nerves supplying the group or else branches from the same nerve supplying two groups to indicate that the fundamental fact is the anterior-posterior spreading.

The appearance of buds on the peripheral distribution of the nerve earlier than on the proximal distribution, which is of so frequent occurrence, seems to be subservient to the anterior-posterior spreading, since it is reversed in the case of the body buds which lie posterior to the origin of the nerves.

The smaller subdivisions of the units or groups are determined in almost all cases by the number of the nerves supplying these subdivisions and by the fact that they appear nearly simultaneously. They are characterized briefly by being slightly discontinuous but usually simultaneous in time of appearance. The units, on the other hand, are never continuous with adjoining groups at the time of appearance, and never simultaneous with the time of appearance of adjoining groups. They differ from the smaller subdivisions of which they are composed in the character of the nerve supply also. Some, as the anterior and posterior palatine groups, have a single nerve supply, while others, as the opercular, have as many as five nerves, some of them from the VII and some from the V. Still other groups are innervated by nerves, some of whose branches innervate other groups farther forward.

The above facts seemed to the writer to furnish a clue, not only to the origin of ectodermic from endodermic buds if such prove to be the phylogenetic method, but also to the innervation of ectodermic buds by communis fibers. The whole difficulty lies in the latter condition, for if we can explain the innervation of ectodermic buds by communis fibers the difficulty in the derivation of ectodermic from endodermic buds, if it exists, disappears.

An attempt to explain the relation of ectodermic to endodermic buds should be in harmony with the following facts.

First, buds situated in both endodermic and ectodermic areas are supplied by communis fibers. This statement is confirmed by all the workers on nerve components. Those of the oral and cutaneous areas in Ameiurus are supplied exclusively by fibers from the geniculate ganglion.

Second, the number of nerve rami through which the geniculate ganglion sends communis fibers varies greatly in various aquatic types (see historical sketch, p. 7, Table I), ranging from a few or even only one as in the larva of Petromyzon (JOHNSTON '05) to nearly every ramus of what are commonly designated as the V and VII nerves in such types as Ameiurus.

Third, the ontogenetic method of increasing gustatory areas in Ameiurus is by detached groups, spreading from anterior to posterior. This indicates that the number of nerve rami through which the geniculate ganglion sends fibers increases from the earlier stages of Ameiurus to the later, so that the total number of rami carrying gustatory fibers is not complete until more than five days after hatching. The assumption involved in the last statement, *i. e.*, that the appearance of the taste bud indicates the time at which the nerve supplying it reaches the surface needs verification for taste buds in Ameiurus, but has been shown to be true by SZYMONOWICZ for ('95) tactile corpuscles and later ('96) for GRANDRY'S and HERBST'S corpuscles. These structures, according to this author, appear as the result of the growth of the nerves to the areas where they are developed and the same is probably true for taste buds. The assumption is further strengthened by the fact that on section of the gustatory nerve in rabbits (SEMI MEYER '96), the taste buds revert into ordinary epithelium. The experiments of LEWIS ('04) in transplanting the optic cup, and producing a lens in new areas is particularly interesting in this connection. An apparent objection to the assumption is the disappearance of gustatory fibers with the loss of superficial taste buds in terrestrial vertebrates. This objection is greatly minimized, if not entirely negatived, by the results of experiments on sectioning nerves (RANSON '06, and his review of the literature), and the consequent retrograde degeneration of sensory fibers and the loss of ganglion cells. The disappearance of specialized communis fibers in terrestrial animals might be accounted for on some such basis as the above.

Fourth, the varying extent of the body covered by taste buds in different types and the varying number of nerve rami through which gustatory fibers from the geniculate ganglion run in different types indicate a very great degree of variability in this ganglion. Any variation in the number of sensory fibers must of course be traced to the variability in the ganglion from which they come. As to the variation in the number of taste buds, it seems hardly probable that they could have increased in number by varying fortuitously and later have been connected with gustatory nerves, since this would involve the origin and development of a definitely constructed sense organ, in types having a peripheral and central nervous system, that would have to exist as such without a function until connected with its appropriate nerve. Whatever may have been the phylogenetic method of origin of specialized communis fibers supplying specialized sense organs, the method in higher types seems to be that the specialized communis fiber produces its appropriate organ on reaching the surface.

As to the possibility of variations in ganglia in general, the work of HARDESTY ('05), HATAI ('02) and RANSON ('06) is interesting. RANSON, in particular, has shown that the same spinal ganglion may vary by as much as 21 per cent of the total number of cells in the smaller ganglia in white rats of the same age. All three of these authors have called attention to the fact that ganglia always contain a large excess of cells over the number of fibers coming from these ganglia, which would seem to indicate that we have here a structural basis for variation in the number of functional cells and fibers.

The explanation of the methods of increasing gustatory areas supplied by the V and VII rami mentioned above, may be stated provisionally as follows: The geniculate ganglion varies in the number of gustatory fibers it sends to the surface in various aquatic types and in different ages in the same type, as in Ameiurus. Some of these fibers on reaching the surface produce taste buds, whether in the ectoderm or endoderm. The functional needs of the organism determine the direction and manner of spreading, The various rami of the V and VII nerves which carry gustatory fibers in Ameiurus and do not in less specialized types are looked upon as routes through which these fibers reach the surface and explain to some extent the discontinuous method of spreading. Finally, the disappearance of gustatory fibers in terrestrial vertebrates from the rami of the V and VII nerves which bore such fibers in aquatic forms may be explained as a process of retrograde degeneration.

This hypothesis seems to be in accord with known facts and certainly does away with the difficulty of deriving ectodermic from endodermic buds. Spreading of buds from endoderm into ectoderm in the strict sense of the word does not occur in Ameiurus or in any other type so far as the writer is aware. Buds appear in the ectoderm in detached groups. There is a possibility that buds in ectodermic territory may actually spread into endodermic territory, as was mentioned above, in the case of the posterior palatine group. This, however, is probably peculiar to Ameiurus and has no bearing whatever on the question as to where taste buds first appeared phylogenetically. In regard to this problem, the evidence seems to be in favor of JOHNSTON's hypothesis ('05, '06) that buds in primitive forms appear first in endodermic territory, since taste buds are always supplied by communis fibers which are visceral in their relationship as far as their central nuclei are concerned. The hypothesis of COLE ('00, p. 320) that taste buds arose first in the ectoderm and spread into the endoderm seems to be negatived by the visceral character of the communis system. Neither the hypothesis of COLE nor JOHNSTON seems to the writer to be tenable, if by spreading is meant continuous spreading; for this method does not occur in Ameiurus, and, as mentioned above, probably not in other types. A more fundamental question, and one whose solution would include to a large extent that of the place of first appearance, is involved in the source of the specialized portions of the communis system. Have specialized communis or gustatory fibers innervating taste and terminal buds arisen simply through the differentiation of unspecialized communis fibers? If they have, we should expect taste buds to arise first in the endoderm, as JOHNSTON suggests.

However, before any definite conclusion is reached we must know the fate of that portion of the geniculate ganglion which is supposed to be derived from the epibranchial placode. It is conceivable that the specialized portions of the communis system may be derived from that portion of the geniculate ganglion which came from the epibranchial placode. In that case its specialized character could be traced to the fact that it was derived from a specialized sensory area before it became buried and a part of the ganglion. The question of where buds appeared first phylogenetically becomes then of secondary importance, since they might appear at any place where these specialized communis fibers reached the surface.

## 12. THE GROSS DISTRIBUTION OF THE PHARYNGEAL GROUP.

The pharyngeal group of buds, like the oral, appears on K′ (113 hours), where buds appear on the first, second and third gill arches simultaneously. The smaller number, two, on the third arch indicates, however, that if series had been taken at small intervals preceding K′, they would have been found on the first gill arch first, then on the second, and then on the third. This probability is strengthened by the fact that buds on the fourth gill arch do not appear until in O and on the fifth or posterior demi-branch until in R.

TABLE XV.

Table showing the gross distribution of the taste buds on the distal portion of the hyoid arch, the gill arches, the roof and floor of the pharynx and in the œsophagus.

| Embryo. | Hyoid. | 1 Gill. | 2 Gill. | 3 Gill. | 4 Gill. | 5 Gill. | Floor. | Roof. | Œsoph. |
|---|---|---|---|---|---|---|---|---|---|
| K′ | — | 4 | 4 | 2 | — | — | — | — | — |
| L | — | 4 | 4 | 2 | — | — | — | — | — |
| M | — | 4 | 8 | — | — | — | — | — | — |
| N | — | 14 | 15 | 4 | — | — | 14 | — | — |
| O | — | 22 | 18 | 9 | 4 | — | 16 | — | — |
| O′ | 2 | 16 | 17 | 15 | 10 | — | 16 | 4 | — |
| P | 2 | 20 | 25 | 20 | 10 | — | 17 | 8 | — |
| Q | 6 | 29 | 30 | 25 | 13 | — | 16 | 28 | — |
| R | 11 | 38 | 39 | 29 | 25 | 2 | 22 | 35 | — |
| S | 10 | 32 | 38 | 32 | 23 | 5 | 24 | 44 | 2 |
| T | 14 | 55 | 55 | 48 | 37 | 6 | 40 | 92 | 5 |
| U | 13 | 58 | 66 | 66 | 36 | 15 | 69 | 132 | 22 |

In the earlier series the first buds to appear lie on the free portions of the gill arch, that is, not on the point of attachment, although they are quite near the median ventral line, and do not reach to the dorsal portion of the gill, but appear here later, so that there is a movement of the buds from the ventral half of the gill arch dorsally toward the roof of the pharynx. The appearance of buds on the roof in series O′, where four buds are present, is due to this spreading of the gill buds to the area over the gill arches. Buds appear much earlier on the floor of the pharynx, where they are situated on a prominent ridge exactly in the median line. These mid-ventral buds appear much larger in their immature stages than any other buds in the embryo, but at their later stages are perfectly typical. Their apparently larger size is due to the fact that the ridge itself, which is segmented, may be very easily mistaken for the taste buds.

This mid-ventral series, situated as it is on a prominent ridge, is well defined in its situation and there is no difficulty in separating it from adjoining lateral areas except in the later series R, S, T and U, where the buds appear on the fifth arch. Here it is difficult to separate the two series on account of the enlargement of the copula by the appearance of the inferior pharyngeal teeth and also on account of the fact that the cartilages of the fifth arch lie parallel to the copula.

Buds appear in the œsophagus first in series S, where there are two, and increase to 22 in U. In the oldest series 20¼ mm. there are about 60.

Leaving out of consideration for the present the hyoid group and those buds on the floor of the pharynx, the most evident thing about this table is the progression from an anterior to a posterior position of buds on the gills and in the œsophagus. There is here a segmental or branchiomeric order of appearance arranged in the following manner. Buds probably appear first on the first gill, then on the second, then on the third, and then on the fourth gill arches, and finally appear in the œsophagus. The dorsal and ventral groups, as will be seen later, correspond quite closely in their segmental arrangement with the gill buds. This order probably represents not only the ontogenetic but the phylogenetic method of appearance as well. The segmental appearance of buds in the pharynx is in sharp contrast with the method by which they appear in the oral and cutaneous groups.

The apparent exception to the segmental appearance of the buds in serial order in this group is furnished by the hyoid arch and the ventral pharyngeal buds. The hyoid arch lies anterior to the gill arches but does not acquire buds until in series O′, which is much later than the time at which buds first appear on the gills, and corresponds in time with their appearance on the fourth gill arch.

In discussing the posterior palatine division it was suggested that possibly that group belonged, at least functionally, with the pharyngeal group, since its position corresponded in the longitudinal axis to the anterior gill buds. If now we compare the position of the posterior palatine group, and of the proximal and distal hyoid groups, and the mid-ventral group, we find the following relations as indicated in Table XVI, where the areas covered by these groups are given in sections. The anterior and posterior sections of each group marking its boundaries.

TABLE XVI.

Table showing extent of the anterior palatine, posterior palatine, proximal and distal hyoid, and mid-ventral floor group of the pharynx.

| EMBRYO. | ANT. PAL. | POST. PAL. | PROX. HYOID. | DIST. HYOID. | FLOOR. |
|---|---|---|---|---|---|
| N | 55–65 | — | — | — | 90–143 |
| O | 43–73 | — | — | — | 90–158 |
| O′ | 56–67 | — | — | 75–79 | 67–151 |
| P | 58–76 | — | — | 103–109 | 88–178 |
| Q | 56–70 | — | — | 76–102 | 75–157 |
| R | 46–66 | 108–122 | 105 | 86–104 | 86–206 |
| S | 56–98 | 123–140 | 129–153 | 93–126 | 93–205 |
| T | 55–104 | 104–154 | 132–154 | 105–126 | 96–217 |
| U | 57–110 | 110–170 | 152–174 | 103–150 | 93–283 |

The distal hyoid group fits in with the proximal hyoid group, the anterior and posterior palatine and the mid-ventral group, to form a structurally homogeneous group of buds on the roof, floor and sides of the area in which the hyoid lies.

The relations are somewhat different in series O′, P and Q, where the posterior palatine and proximal hyoid buds have not yet appeared, from that in series R, S, T and U, where those groups are present and serve to cover the roof, floor and sides of the pharynx completely. The condition of the buds in U will serve to explain these relations most easily.

In U the posterior palatine group extends from section 110 to 170; the distal hyoid group from 103 to 151 and the proximal hyoid from 152 to 174, making the whole extent of the hyoid group from 103 to 174, which corresponds quite closely with the area on the roof occupied by buds of the posterior palatine group, which is from section 110 to 170. On the floor of the pharynx we have the mid-ventral group, beginning at 93 and extending back to the beginning of the œsophagus. The mid-ventral buds, of course, furnish the ventral portion for the gills as well as for the hyoid arch.

Fig. 1 on Plate I will make these relations somewhat clearer. It will be seen from this diagram that the distal hyoid buds really represent a continuation of the anterior oral group rather than the beginning of the pharyngeal groups.

The distal hyoid group is a part of the posterior palatine group structurally, that is, in time of appearance, and doubtless functionally also, for it is difficult to see how buds lying on the roof, floor and sides of the pharynx could fail to be stimulated at the same time, since they lie in practically the same area measured on the longitudinal axis of the embryo. The innervation of the distal portion of the hyoid is from the ventral post-trematic branch of the ninth which enters it at the point of union with the copula and runs proximally.

The posterior palatine and proximal hyoid group, on the other hand, are innervated by the r. palatinus posterior VII and the mid-ventral buds in front of the union of the first gill arch with the copula are supplied by the same nerve as the distal hyoid group.

Probably no better illustration of what is meant by functional groups or areas in the appearance of taste buds could be given. This area is composed of four subdivisions having definite anterior and posterior boundaries and is so situated that it would seem to function as a unit. Portions of it are innervated from the seventh and other portions from the ninth nerve. The hyoid arch in particular has these two nerves supplying it, the former going to its dorsal or proximal portions and the latter to its distal or ventral portions. The distal hyoid buds represent the posterior continuation of the oral group in point of time and not at the beginning of the pharyngeal group.

In series O, P and Q the dorsal buds are represented by the anterior palatine group only, the ventral buds by the mid-ventral group and the lateral area by the distal hyoid group, there being a vacant area on the proximal hyoid which later is occupied by that group of buds. On the roof the posterior palatine is interpolated between the anterior palatine and the buds lying on the roof of the pharynx at the point where the first gill arch joins the roof.

### 13. CERATOBRANCHIAL AND ROOF GROUP.

This group consists of buds situated on the ceratobranchial bar, the pharyngeal cartilages and the roof of the pharynx.

The dorsal side of each ceratobranchial is innervated by the dorsal branch of the post-trematic division of the ninth or tenth nerve; the dorsal side of the first gill arch by the dorsal branch of the ninth and the second, third and fourth by the same branches of the second, third and fourth divisions of the tenth nerve. The posterior demi-branch behind the fourth gill slit is innervated by the ventral pharyngeal branch of the fourth division of the tenth nerve in Menidia.

As stated above, the first buds to appear on the gill are situated on the distal portions of the ceratobranchials of gills 1, 2 and 3. From this point they spread proximally, or dorsally, until in series O′ they reach the pharyngobranchials. Table XVII shows the time of appearance of buds on the pharyngobranchials and the roof of the mouth.

TABLE XVII.

Table showing time of appearance and extent of buds on the pharyngobranchials, the extent indicated by the section numbers between which buds are found.

| Embryo. | 1st Pharyngobr. | | 2d Pharyngobr. | | 3d Pharyngobr. | | 4th Pharyngobr. | |
|---|---|---|---|---|---|---|---|---|
| | No. | Extent. | No. | Extent. | No. | Extent. | No. | Extent. |
| O′ | 4 | 126–132 | 4 | 147–132 | — | — | — | — |
| P | 2 | 140–142 | 2 | 156 | 4 | 166–171 | — | — |
| Q | 5 | 132–139 | 9 | 149–158 | 2 | 164–166 | 2 | 180–185 |

In series O′ and P all buds are found on the pharyngobranchials and there is no overlapping, the groups being quite distinct; but in Q there are 28 buds present in the roof of the pharynx, only 18 of which are catalogued and shown in the table, the remaining ten being scattered between the pharyngobranchials. In Q the first, second and third pharyngobranchial groups overlap, since the cartilages do, so that in Q we have a continuous series of buds running from section 132, where they first appear, back to the œsophagus, but in the two preceding series this is not the case.

In the region of the dorsal pharyngeal teeth it is not possible to separate buds lying on the fourth and fifth pharyngobranchials (or rather epibranchials, since there is only one cartilage present for both these arches), and the mucous membrane is disarranged by the presence of numerous teeth.

From the table it will be seen, however, that the buds appear on the pharyngobranchials in the same order as on the gills; that is, on the first, then on the second, then in P on the third, and in Q on the fourth.

No buds are found on the outer sides of the gill arches on the areas occupied by the gill filaments and no buds spread from the dorsal end of the ceratobranchials or the roof of the mouth in the region of the pharyngobranchials out to the inner surface of the operculum up to a period at least as late as the 20¼ mm. embryo. In this embryo there are buds on the inner surface of the anterior portion of the operculum which belong with the mandible, and buds also extend back on the inner side of the hyoid belonging to the proximal hyoid group, but there is a wide area from this point back to the posterior free border of the operculum totally devoid of buds, so that unless they appear later than any of my series there is no evidence that buds reach the outer body surface from the gill region.

If they should prove to be found in older embryos to spread back from the mandibular and proximal hyoid groups to the inner side of the operculum beyond the point I have indicated, it would furnish no evidence that buds move from endodermic to ectodermic territory, since these areas are continuations of ectodermic groups and have their innervation from the seventh nerve and not from the ninth and tenth. It should be noted that the spreading here is from anterior to posterior, so that it would be much more likely that buds spread from ectodermic to endodermic territory, provided the anterior limit of the pharynx is cephalad of the area occupied by the proximal hyoid and suspensorium.

Buds lying on the floor of the pharynx on either side of the median line are innervated by the dorsal branches of the post-trematic branchiomeric nerves in serial order. These nerves also innervate the buds of the ceratobranchials. No buds appear on the basibranchials until in series U, 89 hours after they appear on the ceratobranchials, when two buds appear on the first basibranchials, and two also on the second basibranchials. In both cases they lie one on the right and one on the left side, respectively. The later appearance of these buds which lie on structures segmentally arranged and with segmental nerves is difficult to explain unless it is due to the minute size of the basibranchials and their late differentiation, in which case, of course, buds could not appear on them at the same time they appear on the remainder of the gill structures.

The limitations of this group even aside from its relations to the gills are quite definite. It has a definite anterior-posterior boundary which as late as series U has an area in front of it devoid of buds dorsally; laterally no buds spread from the dorsal or ventral portions of the gill out to the ectoderm. In fact, there are no buds on the ventral or lateral side of the isthmus in the 20¼ mm. embryo from the point where the first gill bar joins the isthmus back to the point where the œsophagus closes. Here one bud was found, but the whole ventral area, even in the 20¼ mm. embryo, still further back than this point, is practically devoid of buds. Those present on the body lie along the mid-lateral and dorsal portions.

There seems to be little doubt that no buds move from any portion of the pharynx out through the operculum to reach the body. All body buds in Ameiurus represent extensions backward of the surface buds lying farther forward and all are innervated by gustatory fibers from the seventh nerve. Herrick ('01) does not mention any fibers running to the posterior portion of the isthmus, but it is probably innervated by the fibers from the seventh. If by fibers from the ninth, it would be the only case in Ameiurus. However, in Menidia the ramus lat. acces. receives gustatory or communis fibers from the ninth nerve.

### 14. THE MID-VENTRAL PHARYNGEAL GROUP.

This group consists of buds lying exactly on the mid-ventral line of the floor of the pharynx. Buds appear first on the floor of the pharynx in series N somewhat later than those on the gills, and in the region where the first buds appear on the distal hyoid group. They occupy about the same position on the longitudinal axis as the middle of the mandible and distal end of the hyoid cartilage, so that they furnish the ventral buds for the regions of the posterior palatine area (see Fig. 1, Plate I). The anterior end of this group remains almost stationary, while the posterior limit moves back at almost exactly the same rate as the most posterior buds on the gills.

The innervation of these buds is segmental. Buds lying anterior to the union of the hyoid arch with the copula are innervated by the ventral division of the post-trematic portion of the ninth nerve, which runs along the copula between the union of the first gill arch and the union of the hyoid (see Professor HERRICK's note immediately below).

Buds lying in front of the union of the first, second, third and fourth gill arches, respectively, with the copula are innervated by the dorsal division and the ventral division of the post-trematic portions of the ninth and the first four branchiomeric divisions of the tenth nerves, respectively, in Ameiurus, as in Menidia, so that in each case the area in front of a gill arch and extending as far forward as the union of the next anterior gill arch is innervated by two nerves. Professor HERRICK states in his note (see below) that there is no segmentation of the buds in the adult Ameiurus, but in my earlier series there is found a well-defined segmentation of the median ventral ridge and of the buds occupying it which indicates that possibly it may be related in some way to the innervation. The segmentation of the median ventral ridge and the grouping of taste buds is shown in Table XVIII.

In discussing the taste buds of the floor of the pharynx reference was made to C. J. HERRICK's Menidia paper ('99). In view of the need of more detailed information regarding the innervation of the taste buds in this region, Professor HERRICK, in response to an inquiry of mine, has re-examined the termini of a typical branchial nerve of Menidia, as seen in the third gill, and also the distribution of the branchial nerves of the adult Ameiurus. His report upon these two points is appended in the following note:

### THE BRANCHIAL NERVES OF AMEIURUS MELAS.

The post-trematic division of the IX nerve as it passes into the first gill divides into two equal branches. One follows the dorsal (concave) side of the branchial arch and one the ventral side, the latter being accompanied by the much smaller pre-trematic branch of the vagus for the first gill. The vagal branch follows the ventro-mesial border of the ceratobranchial bone, the glosso-pharyngeal the ventro-lateral. Large taste buds are found along the whole length of the ceratobranchial bone on its mesial and dorsal surfaces and on the gill rakers which spring from it. All of these buds seem to be innervated from the dorsal IX branch. The fibers for the buds on the gill rakers are very delicate and feebly medullated and I was not able to observe their origin with certainty.

Before the distal (ventral) end of the ceratobranchial is reached the vagal nerve has disappeared, probably distributed to the gill filaments, the ventral IX branch meanwhile moving mesially to lie in the center of the gill arch. It sends twigs into the gill filaments and their muscles, but is not greatly reduced in size. The dorsal branch of the IX disappears before the first gill joins the copula. The ventral branch of the IX is the true lingual nerve. At the union of the first gill with the copula this nerve curves up to lie immediately under the mucosa just behind the union of the hyoid with the copula and then breaks up into smaller branches. One considerable branch turns backward along the dorsal surface of the hyoid (see the Ameiurus paper, HERRICK, '01, p. 193). The others distribute to the mucosa over the hyoid at its juncture with the copula, extending from the median line far laterally and cephalad as far as the basihyal bone extends. The hyoid arch is very large at its union with the copula in the adult of these fishes and this whole area is covered with large taste buds which I think are all supplied by this nerve.

As stated, the first pre-trematic branch of the vagus does not reach the copula at all, and I do not find any evidence in the adult innervation of any such segmentation of the floor of the pharynx in the glosso-pharyngeus region as you describe in the embryo.

In the other gills the relations are, *mutatis mutandis*, the same as in the first gill. On the dorsal side of each gill arch is one branch of the post-trematic division of the vagus. Below the arch is another and the pre-trematic nerve. The latter ends before the arch joins the copula. The upper, or dorsal, post-trematic nerve ends also before the copula is reached, while the ventral post-trematic nerve extends out upon the copula, where it passes upward to reach the mucosa and divides to supply buds over the basibranchial and hypo-branchial, branches turning laterally to spread over the whole dorsal surfaces of the latter.

### THIRD TRUNCUS BRANCHIALIS VAGI OF MENIDIA.

The copula in Menidia, unlike that of Ameiurus, is very slender—elongated, but narrow. The slender branchial arch follows closely parallel to the basibranchial for a considerable distance before fusing with it. The basibranchial is very slender and there is a row of very large taste buds directly over it in the median line and some similiar buds are found more laterally scattered over the hypobranchial, which for its entire length runs parallel with the basibranchial and enveloped by the fleshy copula. The pre-trematic branch of the fourth truncus branchialis vagi disappears before the third gill reaches the copula. The dorsal branch of the third r. branchialis vagiterm inates among big taste buds on the dorso-lateral aspect of the copula over its union with the branchial arch. It does not extend far forward on the copula. The sensory fibers of the ventral branch, however, terminate in part more medially than the last over both the basibranchial and the hypobranchial and in part as far cephalad as the hypobranchial extends over both it and the slender basibranchial.

The relations here are substantially as I described them in the IX nerve of Ameiurus, save for the changes produced by the elongation of the pharynx in Menidia and its widening in Ameiurus. In neither case is there any possibility of the pre-trematic nerve playing any part in the innervation of taste buds in the copula or very near it. The buds over the basihyal and basibranchial bones are innervated by the ventral branch of the post-trematic nerve; those over the hypobranchials and hypohyal have in general the same innervation, though the dorsal branch may share in their innervation laterally.

TABLE XVIII.

Table showing the extent of the attachment of the hyoid and gills to the corpula expressed in section numbers, the double segmentation of the median ventral ridge and the number of buds in each segment.

| EMBRYO. | | EXTENT OF ATTACHMENT. | EXTENT OF FIRST RIDGE. | NO. OF BUDS. | EXTENT OF SECOND RIDGE. | NO. OF BUDS. |
|---|---|---|---|---|---|---|
| N | HYOID | 83–98 | 81–99 | 4 | | |
| | 1 G. | 106–115 | 103–111 | 3 | 113–117 | 1 |
| | 2 G. | 123–135 | 119–126 | 2 | 127–134 | 2 |
| | 3 G. | 144–154 | 136–146 | 1 | 149–154 | — |
| | 4 G. | 157–178 | 157–164 | 1 | 165–169 | — |
| U | HYOID | 91–124 | 90–124 | 3 | — | — |
| | 1 G. | 127–140 | 127–146 | 3 | 146 | — |
| | 2 G. | 149–175 | 148–168 | 4 | 170–175 | 1 |
| | 3 G. | 171–205 | 177–188 | 3 | 192–197 | 1 |
| | 4 G. | 190–228 | 200–206 | 1 | 209–216 | 2 |
| | 5 G. | 213 | 219 | | | |

In Table XVIII the first double column gives the extent of the ventral attachment of the hyoid arch and gills. The second and third double columns give the extent of the two portions of the ridge for each gill arch and the single columns give the number of buds on each segment.

In front of the union of the hyoid arch the ridge is continuous and occupies the area of attachment of the hyoid, namely, 81 to 99, but between the point of attachment of the hyoid arch and the point of the attachment of the first gill arch, there are two separate portions of the mid-ventral ridge and its buds as indicated by the boundaries 103 to 111 and 113 to 117 which together are equal to the attachment of the first gill arch, namely, 106 to 115. This double arrangement of the median ventral ridge occurs between all the remaining gills and is only slightly modified up to series U, where the ridge becomes continuous between the posterior attachment of the hyoid and the attachment of the first gill arch; but even here the ridge thins out in the median portion indicating the point where the division had occurred in N, so that the disappearance of this double arrangement of the median ventral ridge begins anteriorly and extends posteriorly. In the case of the second, third and fourth gill arches, the ridge is still double in U.

A segmental appearance of the buds is indicated here in the gradually decreasing number of buds from the area in front of the first gill back to the fifth. These buds are arranged as follows in N: The area in front of the hyoid contains four buds, in front of the first gill arch 3, in front of the second 2, and in front of the third and fourth one each. The same decrease is present in this area in U.

The region of the fifth gill arch is confused by the presence of the inferior pharyngeal teeth so that it is difficult to follow the ridge in this region. It is still further complicated by the fact that the basibranchials overlap in the second, third, fourth and fifth arches. Figs. 2 and 3 (Plate I) show these relations schematically. The diagram is drawn to scale and shows not only the segmentation of the median ventral ridge in N and U, but shows the extent also to which the basibranchials overlap. For instance, in the third gill arch, the attachment of the gill extends from section 171 to 205, and the fourth basal-branchial begins at 190 (Plate I, Fig. 3). The portions of the mid-ventral ridge which belong to the third arch are those extending from section 177 to 188 and from 192 to 197. The presence of the portion of the medial ventral ridge belonging to the next gill, namely, from 200 to 206, while apparently on the chart occupying the same area as the third gill arch, really lies parallel with it on the longitudinal axis, so that no difficulty is experienced in locating buds belonging to the third arch.

It is possible that this arrangement of the buds on the ridge is correlated with the distribution of the twigs of the ninth nerve in front of the attachment of the first gill arch and similarly with the two twigs from the branchiomeric divisions of the tenth in succeeding arches. However, it would be impossible to predict which twigs of these two nerves supply the anterior and posterior divisions, respectively.

As mentioned in discussing the preceding group, no buds spread from the median ventral ridge to the exterior; in fact, the median ventral ridge is bounded on either side in the later stages by the buds described in the preceding group as lying on the median lateral portion of the copula.

## 15. THE OESOPHAGEAL GROUP.

Buds appear first in the œsophagus in series S, where there are two, and increase to five in series P and to 22 in U. In the

20¼ mm. series there are more than 60 buds present in this region. At their anterior limit they are continuous with the posterior buds situated on the roof and the floor of the pharynx and spread from this area backward. There can be little doubt that we have here an actual spreading of buds, since the area occupied by buds in the 20¼ mm. embryo is more than four times as long as that occupied in U, while the 20¼ mm. embryo is little more than twice as long as U. The œsophagus is practically a straight tube and the posterior buds are always less mature than those farther forward. It should be noted here that the distribution of buds being from anterior to posterior is also from the proximal to the distal distribution of the nerves. It will be remembered that this corresponds to the distribution of the buds on the body. The prime fact seems to be the anterior-posterior movement and the relation of buds to the proximal and distal distribution of the nerves seems to be a secondary matter.

## 16. SUMMARY OF PHARYNGEAL GROUP.

The most striking characteristic of the pharyngeal group is its complete segmental arrangement, an adaptation probably to the more fundamental segmentation of the gill region. This segmental arrangement is not confined solely to the gill, but is present in the roof and floor buds as well. The spreading of buds from anterior to posterior is almost as marked as in the case of oral and cutaneous groups, if we except the distal hyoid division. There is less evidence here that buds appear first on the distal distribution of a nerve before they appear on the proximal. In fact, the reverse occurs in the œsophageal buds and in the case of the nerves supplying the distal hyoid groups.

The œsophageal buds undoubtedly spread from the proximal toward the distal areas of distribution. It will be recalled, in the case of the body buds, that the explanation seemed to be, as indicated above, that the fundamental fact is the progression from anterior to posterior; and in case of nerves innervating areas morphologically posterior to their point of origin, the condition would be reversed as compared with nerves innervating areas anterior to their point of origin. We find no striking exceptions to the method of progression, from anterior to posterior while there are at least three well defined exceptions to the rule that buds spread along the course of any given nerve from the distal toward the proximal areas innervated. As in the case of the oral and cutaneous groups, the smaller subdivisions in which buds appear, can be isolated from each other by their nerve supply as well as by the fact that they are not continuous, structurally and that, in point of time, they do not appear simultaneously. As far as the question of the origin of ectodermic buds is concerned, it is of special interest to note that in the pharyngeal group no buds spread from endodermic to ectodermic territory. In fact, there is some evidence that the reverse process takes place in the spreading of buds from the posterior mandibular, hyoid and suspensorial groups to the anterior portions of the inner surface of the operculum. The evidence, however, is not conclusive, since we do not know the exact limit of the pharynx in vertebrates.

In Menidia (HERRICK '99) communis fibers run from the ninth nerve into the ramus lat. acces. and probably taste buds are supplied by these fibers in that type. Even this, however, does not involve an actual spreading of buds from endoderm into ectoderm, since if we may draw any conclusion from Ameiurus they probably would be found to appear in discontinuous groups.

If we are to consider the pharyngeal group as the older phylogenetically, based on the fact that its buds are in endodermic territory and innervated by visceral nerves segmentally arranged, we have a very striking difference in the extent and variety of the areas innervated by the nerves supplying this group as compared with the areas innervated by the communis fibers from the seventh nerve. We should expect to find the group which is phylogenetically older to be more stable and to adapt itself to new conditions less easily. All the evidence from Ameiurus goes to show that the gustatory fibers arising from the geniculate ganglion are more variable, that is, occupy a greater number of nerves and innervate a greater variety of areas, than those of the ninth and tenth nerves. The exceedingly specialized condition in Ameiurus must have been derived from a simpler condition in which there were fewer areas containing taste buds, fewer nerves carrying gustatory fibers and fewer fibers in any given nerve than were found in less specialized types or in Ameiurus formerly.

### 17. GENERAL SUMMARY.

1. Taste buds appear simultaneously in the extreme anterior portion of the oral cavity (ectoderm) and on the endoderm of the first three gill arches.

2. Buds always spread posteriorly from these places of origin by discontinuous groups. Those of the pharynx spread back into the œsophagus and are continuous with the buds on the last gill arch. Those of the anterior oral cavity spread back in the mouth by discontinuous groups until they reach the area occupied by the pharyngeal buds and also spread back on the outer surface of the body by discontinuous groups until they reach the posterior portions of the body.

3. No buds spread from the pharyngeal group to the outer surface of the body at least as late as the 20¼ mm. embryo when all of the main groups on the head and body are present.

4. The first buds to appear on the outer surface of the body are continuous with those just inside the lips. All the remaining buds appear in discontinuous groups determined partly by the distribution of the rami of the V and VII nerves but not entirely, since these groups may be innervated by one, two, or as many as five rami, or two closely related rami may innervate different groups, so that some factor other than the mere anatomical arrangement of nerve rami is necessary to explain the uniform anterior-posterior appearance of discontinuous groups.

5. There are six well defined groups of buds on the outer surface of the body isolated in position by the fact that there are areas devoid of buds between them at the time of their appearance, and separated in time of appearance by periods ranging from seven to more than 100 hours for groups that later become continuous. There are two well defined groups of buds in the anterior oral cavity distinct from the dorsal and ventral lip buds.

6. The pharyngeal buds are segmentally arranged and appear on the gills in order from anterior to posterior. The spreading from anterior to posterior is characteristic of œsophageal buds and they are continuous with buds on the last gill arch.

7. In the oral and cutaneous groups of buds and to a certain extent in the pharyngeal, the buds situated on the peripheral distribution of a nerve appear before those on the proximal distribution. This is reversed in the case of buds situated on areas

behind the points of origin of the nerves, as in the body buds and œsophageal buds. This indicates the extent to which the anterior-posterior spreading has dominated the developmental history.

8. The smaller divisions of which the groups are composed are usually indicated by the number of nerve rami or twigs which supply the groups. The smaller subdivisions in a group usually appear simultaneously, but, if there is any difference in time of appearance, the anterior buds appear first. The larger groups, on the other hand, are never continuous at the time of appearance with adjoining groups, and never appear simultaneously.

9. The appearance of buds in the oral and cutaneous areas in detached groups spreading from anterior to posterior seems to indicate the order in which specialized communis fibers reach the surface through rami of the V and VII nerves. A comparison of the rami bearing communis fibers in Ameiurus with other types shows a very great degree of variability in the geniculate ganglion of the VII nerve as to the number of rami through which it may send communis fibers and as to the time at which it sends them in Ameiurus. The functional needs of the organism, such as changes in the method of seeking and locating food, seem to determine the direction of spreading and also to be more important factors in determining the manner of appearance (*i. e.*, in detached groups) than the mere anatomical arrangement of trunks and rami of the nerves, so that the discontinuous groups have been designated as functional groups.

## LITERATURE.

Allis, E. P., Jr.

'89. The Anatomy and Development of the Lateral Line System in Amia calva. *Jour. Morph.*, Vol. 2, No. 3.

'97. The Cranial Muscles and Cranial and First Spinal Nerves in Amia calva. *Jour. Morph.*, Vol. 12, No. 3.

'00. The Lateral Sensory Canals of Polypterus bichir. *Anat. Anz.*, Vol. 17, No. 23.

Alcock, Miss R.

'98. The Peripheral Distribution of the Cranial Nerves of Ammocœtes. *Jour. of Anat. and Phys.*, Vol. 33 (N. S. 13), pp. 131–153.

Ayers, H.

'92. Vertebrate Cephalogenesis. II. A Contribution to the Morphology of the Vertebrate Ear with a Reconsideration of its Functions. *Jour. of Morph.*, Vol. 6, pp. 1–360.

BEARD, J.

'86. The System of Branchial Sense Organs and their Associated Ganglia in Ichthyopsida. A Contribution to the Ancestral History of Vertebrates. *Q. J. M. S.* (N. S.), Vol. 26, pp. 95–156.

BATESON, W.

'89. The Sense Organs and Perceptions of Fishes; with Remarks on the Supply of Bait. *Jour. Marine Biol. Assoc. United Kingdom,* Vol. 1 (N. S.), pp. 225–256

BOWERS, MARY A.

'00. Peripheral Distribution of the Cranial Nerves of Spelerpes bilineatus. *Proc. Acad. Arts and Sci.,* Vol. 36, No. 11.

BUNKER, F. S.

97. On the Structure of the Sense Organs of the Lateral Line of Ameiurus nebulosus. *Anat. Anz.,* Vol. 13, Nos. 8–9.

COGHILL, G. E.

'01. The Rami of the Fifth Nerve in Amphibia. *Jour. of Comp. Neur.,* Vol. 11, pp. 48–60

'02. The Cranial Nerves of Amblystoma tigrinum. *Jour. of Comp. Neur.,* Vol. 12, pp 205-289.

'06. The Cranial Nerves of Triton tæniatus. *Jour. of Comp. Neur. and Psy.,* Vol. 16, pp. 247–264.

CLAPP, CORNELIA M.

'99. The Lateral Line System of Batrachus tau. *Jour. of Morph.,* Vol. 15, No. 2.

COLE, FRANK J.

'96. On the Cranial Nerves of Chimæra monstrosa (Linn.) with a Discussion of the Lateral Line System and of the Morphology of the Chorda Tympani. *Trans. Roy. Soc. Edinburgh,* Vol. 38, part III (No. 19).

'98. Observations on the Structure and Morphology of the Cranial Nerves and Lateral Sense Organs of Fishes; with Special Reference to the Genus Gadus. *Trans. Linn. Soc. London,* 2d series, Vol. 7, part 5.

'98a. Reflections on the Cranial Nerves and Sense Organs of Fishes. *Trans. Liverpool Biol. Soc.,* Vol. 12.

'00. Notes on Professor Judson Herrick's Paper on the Cranial Nerves of the Cod Fish. *Jour. of Comp. Neur.,* Vol. 10, pp. 317–322.

COLE, FRANK J. AND JAMES JOHNSTON.

'01. Pleuronectes. *Liverpool Marine Biological Com. Memoirs, London* (Williams & Norgate).

DODDS, G. S.

'06. The Cranial Nerves of one of the Salamanders (Plethodon glutinosus). *Univ. of Col. Studies,* Vol. 3, No. 2.

DONALDSON, HENRY H.

'03. On the Law Determining the Number of Medullated Nerve Fibers Innervating the Thigh, Shank and Foot of the Frog, Rana virescens. *Jour. of Comp. Neur.,* Vol. 13, pp. 223–257.

DUNN, ELIZABETH HOPKINS.

'00. The Number and Size of the Nerve Fibers Innervating the Skin and Muscles of the Thigh of the Frog (Rana virescens brachycephala Cope). *Jour. of Comp. Neur.,* Vol. 10, pp. 218–244.

Dunn, Elizabeth Hopkins.

02. On the Number and on the Relation between Diameter and Distribution of the Nerve Fibers Innervating the Leg of the Frog (Rana virescens brachycephala). *Jour. of Comp. Neur.*, Vol. 10, pp. 297–298.

Eycleshymer, A. C.

'01. Observations on the Breeding Habits of Ameiurus nebulosus. *Amer. Nat.*, Nov., 1901.

Gaskell, W. H.

'86. On the Structure, Distribution and Functions of the Nerves which Innervate Visceral, and Vascular Systems. *Jour. of Phys.* Vol. 7.

'89. On the Relation between the Structure, Function and Distribution and Origin of the Cranial Nerves; together with a Theory of the Origin of the Nervous System of Vertebrates. *Jour. of Phys.*, Vol. 10, pp. 153–211.

Hatai, Shinkishi.

'02. Number and Size of the Spinal Ganglion Cells and Dorsal Root Fibers in the White Rat at Different Ages. *Jour. of Comp. Neur.*, Vol. 12, pp. 107–123.

Hardesty, Irving.

'05. On the Number and Relation of the Ganglion Cells and Medullated Nerve Fibers in the Spinal Nerves of Frogs of Different Ages. *Jour. of Comp. Neur. and Psy.*, Vol. 15, pp. 17-54.

Herrick, C. Judson.

'99. The Cranial and First Spinal Nerves of Menidia; a Contribution upon the Nerve Components of the Bony Fishes. *Jour. of Comp. Neur.*, Vol. 9, pp. 153–455.

'00. A Contribution upon the Cranial Nerves of the Cod Fish. *Jour. of Comp. Neur.*, Vol. 10, pp. 265–316.

'01. Cranial Nerves and Cutaneous Sense Organs of North American Siluroid Fishes. *Jour. of Comp. Neur.*, Vol. 11, pp. 177–249.

'02. A Note on the Signification of the Size of Nerve Fibers in Fishes. *Jour. of Comp. Neur.*, Vol. 12, pp. 329–334.

'03*a*. On the Phylogeny and Morphological Position of Terminal Buds in Fishes. *Jour. of Comp. Neur.*, Vol. 13, pp. 121–138.

'03*b*. The Doctrine of Nerve Components and Some of its Applications. *Jour. of Comp. Neur.*, Vol. 13, pp. 301–312.

'04. The Organ and Sense of Taste in Fishes. *U. S. Fish. Com. Bull.* for 1902, pp. 237–272.

'05. The Central Gustatory Paths in the Brains of Bony Fishes. *Jour. of Comp. Neur. and Psy.*, Vol. 15, pp. 375–454.

'06. On the Centers for Taste and Touch in the Medulla Oblongata of Fishes. *Jour. of Comp. Neur. and Psy.*, Vol. 16, pp. 403–440.

Herrick, C. L. and Coghill, G. E.

'98. The Somatic Equilibrium and the Nerve Endings in the Skin. *Jour. Comp. Neur.*, Vol. 8, pp. 32–36

Houser, Gilbert L.

'01. The Neurones and Supporting Elements in the Brain of the Selachean. *Jour. of Comp. Neur.*, Vol. 11, pp. 65–175.

Huber, G. Carl.

'00. Observations on Sensory Nerve Fibers in Visceral Nerves and on their Modes of Termination. *Jour. of Comp. Neur.*, Vol. 10, pp. 135–151.

JOHNSTON, J. B.

'98. Hind Brain and Cranial Nerves of Acipenser, *Anat. Anz.*, Bd. 14, No. 22–23.

'00. The Giant Ganglion Cells of Catostomus and Corregonus. *Jour. of Comp. Neur.*, Vol. 10, pp. 375–381.

'01a. Some Points in the Brain of Lower Vertebrates. *Biol. Bull.*, Vol. 2, No. 6, pp. 356–357.

'01b. The Brain of Acipenser; a Contribution to the Morphology of the Vertebrate Brain. *Zool. Jahrb. Abth. f. Anat. u. Ontog.*, Bd. 15.

'02a. The Brain of Petromyzon. *Jour. of Comp. Neur.*, Vol. 12, pp. 1–86.

'02b. Das Gehirn und die Cranial Nerven der Anamnier. *Merkel und Bonnet's Ergebnisse der Anat. und Entw.*, Bd. 11.

'02c. An Attempt to Define the Primitive Functional Divisions of the Central Nervous System. *Jour. of Comp. Neur.*, Vol. 12, pp. 87–106.

'05a. The Cranial Nerve Components of Petromyzon. *Morpholog. Jahrb.*, Bd. 34, Heft 2.

'05b. The Morphology of the Vertebrate Head from the View Point of the Functional Divisions of the Nervous System. *Jour. of Comp. Neur. and Psy.*, Vol 15, pp. 175–265.

'06. The Nervous System of Vertebrates. *Philadelphia, P. Blakiston's Son & Co.*

KINGSBURY, B. F.

'95a. On the Brain of Necturus maculatus. *Jour. of Comp. Neur.*, Vol. 5, No. 3.

'95b. The Lateral Line System and Sense Organs of Some American Amphibia and Comparison with Dipnoans. *Proc. Am. Soc. Mic.*, Vol. 17.

'97. The Structure and Morphology of the Oblongata in Fishes. *Jour. of Comp. Neur.*, Vol. 7, No. 1, pp. 1–36.

KINGSLEY, J. S.

The Cranial Nerves of Amphiuma. *Tuft's College Studies*, No. 7, Scientific Series, pp. 293–321.

KENDALL, W. C.

'02. Habits of Some Commercial Cat Fishes. *Bull. U. S. F. C.*, 1902, pp. 401–409.

LEWIS, LOREN HARMON.

'04. Experimental Studies on the Development of the Eye in Amphibia. *The American Journal of Anatomy*, Vol. 3, pp. 505–536.

LEYDIG, FR.

'51. Ueber die aussere Haut einiger Susswasserfische. *Zeits. wiss. Zool.*, Vol. 3.

MERKEL, FR.

'80. Ueber die Endigungen die sensiblen Nerven in der Haut der wirbelthiere. *Rostock*, 214 pp.

MEYER, SEMI.

'96. Durchschneidungsversuche am Nervus Glossopharyngeus. *Archiv mik. Anat. und Ent.*, Vol. 48.

MORRILL, A. D.

'95. Pectoral Appendages of Prionotus and their Innervation. *Jour. of Morphology*, Vol. 11.

OSBORN, H. F.

'88. A Contribution to the Internal Structure of the Amphibian Brain. *Jour. of Morphology*, Vol. 2, No. 1.

POLLARD, H. D

'95. The Oral Cirri of Siluroids and the Origin of the Head in Vertebrates. *Zool. Jhb.*, Vol. 8.

RANSON, S. W.

'04. Retrograde Degeneration in the Corpus Callosum of the White Rat. *Jour. of Comp. Neur. and Psy.*, Vol. 14, pp. 381–384.

'06. Retrograde Degeneration in the Spinal Nerves. *Jour. of Comp. Neur. and Psy.*, Vol. 16, pp. 265–293.

SCHULZE, F. E.

'63. Ueber die becherformingen Organe der Fische. *Zeits. f. wiss. Zool.*, Vol. 12.

'67. Epithel und Drusenzellen. *Arch. f. mikr. Anat.*, Vol. 3.

'70. Ueber die Sinnesorgane der Seitenlinie bei Fischen und Amphibien. *Arch. f. mikr. Anat.*

SMITH, H. M. AND HERRON, L. G.

'02. Breeding Habits of the Yellow Cat Fish (Ameiurus nebulosus). *Bull. U. S. F. C.*, Vol. 20, pp. 151–154.

STRONG, O. S.

'95. The Cranial Nerves of the Amphibia. A Contribution to the Morphology of the Vertebrate Nervous System. *Jour. Morph.*, Vol. 10.

SZYMONOWICZ, W.

'95. Beiträge zur Kenntniss der Nervenendigungen in Hautgebilden. *Archiv für mik. Anat. und Ent.*, Vol. 45, pp. 624.

'96. Ueber den Bau und die Entwicklung der Nervenendigungen im Entenschnadel. *Archiv f. mik. Anat. und. Ent.*, Vol. 48, pp. 329–358.

WEBER.

'27. Ueber das Geschmachsorgan der Karpfen. *Meckel's Archiv f. Anat.*

WHITMAN, C. O.

'84. The Segmental Sense Organs of the Leech. *The Amer. Naturalist*, Vol. 18, pp. 1104–1109.

'89. Some New Facts about the Hirudinea. *Jour. of Morph.*, Vol. 2, pp. 586–599.

'99. Animal Behavior. *Biological Lectures from the Marine Biological Laboratory, Woods Holl, Mass.*, 1898, pp. 285–338.

WORKMAN, I. S.

'00. The Ophthalmic and Eye-Muscle Nerves of the Cat Fish (Ameiurus). *Jour. of Comp. Neur.*, Vol. 10, pp. 403–410.

WRIGHT, R. RAMSEY,

'84a. On the Skin and Cutaneous Sense Organs of Ameiurus, *Proc. Canadian Institute*, N. S., Vol. 2.

'84b. On the Nervous System and Sense Organs of Ameiurus. *Proc. Canadian Institute*, N. S., Vol. 2.

Fig. 1

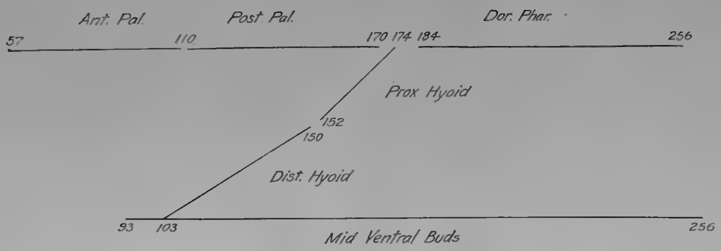


Fig. 2

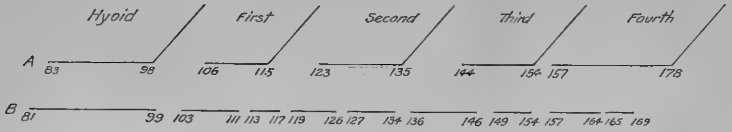


Fig. 3

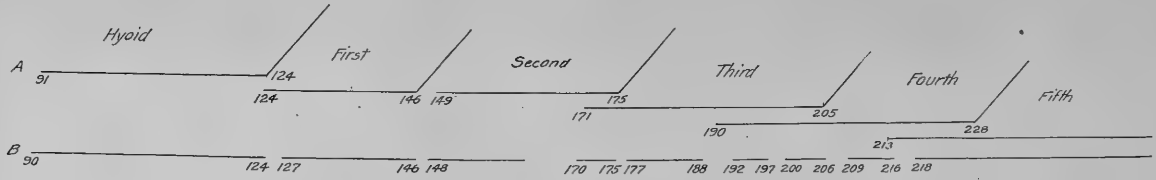


Fig. 1. Shows the relative extent measured in sections of 7 microns each of the various divisions of the anterior palatine, posterior palatine, pharyngeal, proximal and distal hyoid and mid-ventral buds on the longitudinal axis of the embryo. The numbers indicate the sections bounding of the various sub-divisions. The diagram is drawn to scale from series U.

Figs. 2 and 3 are drawn to scale also, and show the extent of attachment of the hyoid and gills to the copula and the extent of the median ventral ridge on which buds are situated and the segmentation of this ridge. Fig. 2 is plotted from series N, and Fig. 3 from series U. *A*, the extent of attachment of the hyoid and gills in each figure. *B*, the extent of the median ventral ridge and its segmentation corresponding to the areas of attachment of the gill. The numbers on the diagram represent the limits in sections.

# A STUDY OF THE VAGAL LOBES AND FUNICULAR NUCLEI OF THE BRAIN OF THE CODFISH.

By C. JUDSON HERRICK.

(*Studies from the Neurological Laboratory of Denison University, No. XX.*)

WITH EIGHT FIGURES.

## INTRODUCTION.

The peripheral and central organs of taste have received more or less careful study in three distinct groups of teleostean fishes in which taste buds are known to occur plentifully in the outer skin; viz.: the cyprinoids (carp, etc.), the siluroids (Ameiurus and other catfishes) and the gadoids (cod, tom-cod, hake). The structure of the cutaneous taste buds of the carp was described by LEYDIG in 1851 and more accurately in 1863 and 1870 by F. E. SCHULZE, who correctly inferred their function. Their gustatory function was subsequently demonstrated physiologically in Ameiurus and various gadoids (HERRICK '04), and it was shown that either tactile or gustatory stimuli alone may be correctly localized in the outer skin, though ordinarily both senses coöperate in the locating of the food. The same reaction may follow either a tactile or a gustatory stimulation of the outer skin or the simultaneous stimulation of both kinds of sense organs in the same cutaneous area.

The distribution of the nerves of touch in the skin of fishes is very accurately known and the general arrangement of these nerves is nearly constant throughout the phylum. The innervation of the cutaneous taste buds has also been studied in the three types here considered—exhaustively in Ameiurus (HERRICK '01) and less completely in Gadus (HERRICK '00) and Carassius (HERRICK '04, p. 249). The nerves for the cutaneous taste buds spring from the communis root of the facial nerve, without exception in Ameiurus and with but small exception in Gadus. The same facial root supplies also taste buds in the anterior part of the mouth.

The central gustatory paths have been investigated in cyprinoids and siluroids (HERRICK '05). In view of the demonstration, in the works cited in the preceding paragraphs, of the essential similarity in the structure, innervation and function of the cutaneous taste buds of cyprinoids, siluroids and gadoids, we should expect their central connections in the group last mentioned to resemble those described for the two former groups. But the facts seem to be quite the contrary, and the primary purpose of this inquiry was to determine the extent and if possible the functional significance of these differences. This naturally led to a study of the tactile centers also in Gadus, for the underlying problem in both this and my previous study ('06) is the central relations of those tactile and gustatory nerves which innervate the same areas of skin and have independent local signs but common pathways of motor discharge in the reaction.

## THE CENTRAL GUSTATORY PATHS OF AMEIURUS AND GADUS.

In siluroids and cyprinoids practically all the nerves supplying taste buds in the outer skin, lips and palate terminate in a single huge nucleus which forms a dorsal protuberance on the medulla oblongata, the facial lobe, while taste buds of the pharynx and gill region are innervated from the vagal lobe farther back in the oblongata.

In the gadoid fishes a facial lobe has been described and figured by several previous authors; but my examination of the brain of the cod shows that the facial lobe does not exist in the form described by these authors. Nevertheless I find the peripheral distribution of the gustatory root of the facial nerve of Gadus is practically the same as in Ameiurus. What, then, are the central connections of the cutaneous taste buds in Gadus?

Taste buds are scattered over the whole body of Ameiurus but most abundantly on the barblets, and experiment shows that these are very sensitive to both tactile and gustatory stimulation. They are constantly used for the exploration of the bottom and the maxillary barblets are actively waved about whenever a savor diffuses through the water. In the gadoids, particularly the tom-cod and the hake, the free filiform rays of the pelvic fin function in a similar fashion and are likewise richly supplied with end-organs of both taste and touch.

In Ameiurus the facial lobe, which receives all the gustatory nerves from the outer skin, gives rise to two chief secondary tracts. One passes upward into the mid-brain and one downward toward the spinal cord. The first of these accompanies the ascending cerebral tract for taste from the vagal lobes and is feebly developed or absent in the cod. It will therefore receive no further consideration here. The descending path terminates, as shown in Fig. 1, in the primary tactile correlation center of the brain, the funicular nuclei, and farther caudad in the spinal cord. From this correlation center a common motor pathway runs out by way of the funiculus ventralis for the innervation of all the somatic muscles of the body.

Now remembering that the body, considered as a reflex mechanism comprises two primary systems (the somatic system for reaction of the body as a whole to external stimuli, and the visceral system for correlation of the internal parts by reaction to visceral stimuli), we may summarize the reflex connections of the taste buds of Ameiurus as follows: The primary gustatory center is differentiated into a visceral region (vagal lobe) for taste buds lying in mucous membranes and a somatic region (facial lobe) for taste buds lying in the outer skin. The somatic character of this latter region has been secondarily acquired. It was without question phylogenetically derived from the visceral center. Both centers send an ascending tract to a common mid-brain nucleus. Their descending paths are strikingly different. The visceral center (vagal lobe) makes reflex connections only with the visceral musculature of the jaws, gills, œsophagus, etc. The somatic center (facial lobe) connects broadly with the funicular nuclei and there the gustatory stimuli from the skin are correlated with tactile stimuli from the same cutaneous areas and from this common sensory correlation station the motor pathways go out to the somatic muscles. There is also a direct path from the facial lobe to the motor V nucleus which innervates the muscles of the barblets, these being waved about when stimulated either by taste or touch. The preceding description applies with but slight modification also to the carp and other cyprinoid fishes.

Now, in the cod there is no well defined facial lobe. Gustatory fibers from the mouth and from the outer skin terminate in the vagal lobe, a condition which was entirely inexplicable to me after my demonstration physiologically that the taste buds on the fins of the gadoids and on the barblets of Ameiurus function similarly as organs of taste, that the fishes can localize pure gustatory stimuli applied to these organs and that ordinarily both taste and touch coöperate in finding food by means of them, though the two sensation factors may be experimentally isolated by training.

Accordingly, I have reëxamined the vagal lobes and their connections in the cod and find that the gustatory nerves of the somatic type, those from the outer skin, and the gustatory nerves of the visceral type, from the mucous membranes, do have distinct central connections, though in quite a different way from that found in the catfish. The facts are these (*cf.* Fig. 2).

The vagal lobe of the cod is internally divided by a longitudinal septum into median and lateral lobules of about equal extent (Figs. 3 and 4). The median lobule is primarily visceral and receives the gustatory roots of the IX and X nerves, as in other fishes. The gustatory root of the facial nerve, which carries practically all of the fibers from taste buds in the outer skin and a smaller number of fibers from the mucous membrane of the anterior part of the mouth (ramus palatinus VII, etc.), terminates in both lobules, but chiefly in the lateral one. While I have not been able to demonstrate that the facial fibers which reach the median lobule are from visceral buds within the mouth, yet this is very probable. In any case, it is clear that the lateral lobule is primarily, if not exclusively, the terminal nucleus for the gustatory fibers of the somatic type; that is, it is the physiological, if not the morphological, equivalent of the facial lobe of siluroids and cyprinoids.

The two important papers on the brains of teleosts published in the Gegenbaur *Festschrift* (Goronowitsch '96, and Haller '96) give figures of the medulla oblongata of Lota vulgaris, a form closely allied to Gadus. Both of these authors were so dominated by the endeavor to reduce all cranial nerves to segmental units of the spinal type as to vitiate to some degree their observation. Their two figures of the brain of Lota bear very little resemblance to one another, or to the brain of Gadus, which is somewhat remarkable in view of the fact that both authors were studying the internal courses of the nerve roots microscopically. Haller shows (Plate I, Fig. 6) a series of four pairs of enlargements in the vagal region, the first belonging to the IX nerve, the others to the vagus. The figure of Goronowitsch (Plate I, Fig. 3) is evidently much more accurate as to externals, but is in part incorrectly interpreted. He figures a lobus facialis (my lobus vagi lateralis), to which he correctly traces the communis VII root; a lobus glossopharyngei (my lobus vagi medialis), to which he correctly traces the IX and X nerves; a lobus vagi impar (my visceral commissural nucleus), to which he traces vagus fibers; and a lobus vagi which corresponds to my somatic commissural nucleus. The error in the latter point is due to his failure to recognize the distinction between the somatic and visceral regions of the oblongata. With this point in mind it is impossible to confuse the vagal lobes with the somatic commissural nucleus.

The subdivision of the vagal lobe of Gadus into median and lateral lobules is mentioned in the catalogue of the Museum of the Royal College of Surgeons of London (BURNE '02, p. 93) but unfortunately in the absence of a knowledge of the internal structure Mr. BURNE here was led by external appearances and by the previous figures of Lota by GORONOWITSCH ('96) into error in the interpretation of this region In the two dissections of the brain of the codfish there figured and in the accompanying text the true vagal lobes are termed facial lobes and the somatic commissural and funicular nucleus complex of my descriptions is termed lobus vagi and is said to give rise to the sensory roots of the vagus nerve. Examination of the internal courses of these nerves at once corrects this mistake. The dissections of the codfish brain figured in T. J. PARKER's Zoötomy ('00, p. 125) show the vagal lobes very small with no designation. The "lobi posteriores," which might be mistaken for the vagal lobes, are the tubercula acustica. The excellent series of transections of the codfish brain given by KAPPERS ('06) extends back only to the cephalic end of the vagal lobe. Fig. 4 of the present paper is from a section taken a short distance caudad of Fig. xcix of Plate VII of KAPPERS' memoir.

In Fig. 3 I present a photograph of this region of the brain of a large codfish (Gadus morrhua), whose internal connections are as shown in Fig. 2. From the figure and description of GORONOWITSCH, I have no doubt that the relations are essentially similar in Lota.

The central tracts leading from the median lobule are the same as those from the vagal lobe in other fishes; and caudad this lobe merges into the visceral commissural nucleus of CAJAL in the typical way. The lateral lobule, which receives only facialis fibers, is wholly unlike the facial lobe of the siluroid and cyprinoid fishes in its secondary connections. It contributes few, if any, fibers to the long ascending secondary gustatory tract, this tract being derived from the median lobule (Fig. 4). Moreover, there does not arise from any part of the vagal lobe a large, clearly defined descending secondary gustatory tract, like that from the facial lobe in Ameiurus and Cyprinus, entering the dorso-lateral fasciculus for the funicular nucleus region and spinal cord. The lateral lobule is directly continuous caudad with the funicular nucleus region. A considerable tract of delicately medullated fibers accumulates on the ventro-lateral border of the lateral lobule and passes directly back to enter the cephalic end of the funicular nucleus where it joins the substantia gelatinosa Rolandi. My Wiegert sections do not show positively whether these fibers are ascending or descending, but I assume the latter by analogy; for this tract seems to correspond with the descending secondary gustatory tract from the facial lobe of Ameiurus. But in the cod this is a small and unimportant tract.

The chief secondary connection of the lateral lobule is by a very strong and heavily medullated tract which passes from its entire extent into the ventral commissure and enters the ventral funiculi of the same and the opposite side. These appear to be descending fibers. Some of them may pass over into the opposite tractus bulbo-tectalis (lemniscus), but it is not possible to be certain on account of the confusion in the ventral commissure of the internal arcuate fibers from the lateral vagal lobule with those from the tuberculum acusticum. This connection through the ventral commissure puts the lateral vagal lobule into connection with the long conduction paths of the somatic system, and thus directly connects the primary center for cutaneous taste buds and the ventral cornua of the spinal cord, from which the muscles of the fins and body are innervated. These relations are shown diagrammatically in Fig. 2.

The representatives of the Ostariophysi which I have studied (Ameiurus, Cyprinius, Catostomus, etc.) agree in possessing a distinct center (the facial lobe) for all of the fibers from cutaneous taste buds, the secondary connections of this center being partly with visceral motor and partly with somatic motor centers via the funicular nuclei. The fact that Gadus accomplishes a somewhat similar result by the different and more direct method of separating at the start the facialis root fibers into those for visceral and somatic centers is another illustration of the distinctness of the Ostariophysi from other teleostean fishes.

The end result is similar in the case of the cod and the catfish. Peripheral areas of skin may receive both tactile and gustatory stimulation simultaneously. The fish reacts to the composite stimulus by a single movement of the body adapted to reach and seize the food object. The *tactile* path in both cases leads to the funicular nuclei, and thence to the somatic muscles. The somatic gustatory path in the catfish leads to the tactile correlation center (funicular nuclei), whence it reaches the somatic muscles by the same tracts as the tactile. In the cod the somatic gustatory path passes directly from the primary center to the somatic motor centers in the ventral cornu without interruption in the tactile centers.

In searching for the explanation of this difference two lines of inquiry are at once suggested. First, are there any mechanical necessities of cerebral structure sufficient to account for them; and, second, do the habitual modes of reaction to external stimuli, *i. e.*, the habits of the animals, suggest an explanation. I believe that both of these factors have operated.

In the first place, why do the somatic gustatory nerves of the cod end in a specialized part of the vagal lobe and those of Ameiurus in a separate lobe in front, the lobus facialis ? Why should not the cutaneous gustatory nerves of Ameiurus end likewise in the vagal region ? That there is no mechanical impediment to the necessary enlargement of the vagal lobe is evident from the fact that in the carp the vagal lobe suffers much greater enlargement to provide a terminal nucleus for an increased number of taste buds within the mouth.

In Ameiurus many, though by no means all, of the cutaneous taste buds are in the head. These areas of skin receive their tactile innervation from the trigeminus nerve. Now, I have found in this fish two centers of correlation between the nerves of touch and taste from the skin of the head. One is the funicular nuclei, already referred to. The other is in the facial lobe, in whose deeper layers trigeminus root fibers have been found to end. The demand for a correlation center in front of the vagal lobe is probably the motive which in Ameiurus has drawn the facialis gustatory center cephalad of the vagal lobe, thus providing also an immediate path from end organs of both touch and taste to the motor centers of the barblets and jaws. In the gadoids, on the other hand, some of the most important areas of distribution of cutaneous taste buds are on the fins, which are freely moved about in the exploration of food objects. These receive their tactile innervation from spinal nerves which enter behind the vagal lobes and, therefore, the motive for a forward movement of the somatic gustatory center to correlate with the corresponding tactile nerves does not exist to so high a degree, or possibly has been counteracted by stronger spinal tactile impulses associated with gustatory stimuli on the fins.

But this explanation still leaves unaccounted for the short-circuiting of the somatic gustatory path in the cod by which it passes under the tactile centers without connection with them and reaches the motor centers directly. The peculiar feeding habits of the cod may explain this arrangement (HERRICK '04).

The body taste buds of Gadus and its allies are most abundant on the filiform pelvic fins, and these are the organs most used in the detection of food, serving a purpose closely similar to that of the barblets of Ameiurus. In Ameiurus the somatic reaction consequent upon contact of a barblet with food is a lateral turning of the whole body by a single movement to reach the food object.

But in Gadus the movement is quite different, since the food stimulus is under the center of the body when it is detected. Before the food can be taken, the fish must check the forward movement and back up until the mouth has reached the object. This involves a very precise movement of the pectoral fins in particular, and if the prey be living it must be very rapidly done. These features, taken in connection with the more active life of the gadoids in general, are sufficient to account for the short-circuiting of the reflex path between the gustatory root of the facial nerve and the ventral cornu of the spinal cord, so that a gustatory stimulus on the fins alone may cause the reaction promptly without the coöperation of the tactile centers.

We have then, in summary, the following striking series of structural adapations correlated with the appearance of taste buds in the outer skin of fishes. Such buds occur in fishes generally in the mouth and on the lips, the latter being innervated by the facial nerve. LANDACRE has shown in a recent embryological research ('07) that in Ameiurus the cutaneous buds appear first in the region of the lips and then progressively farther caudad. It is probable that this was also the order of their appearance phylogenetically, a supposition which is supported by the course of the branches of the facial nerve which supply these cutaneous buds in the adult. As these facial gustatory nerves increased in importance, especially those from the barblets, central correlation was required with the tactile and motor centers for the barblets in the region of the trigeminus. This anatomical connection finally caused the cutaneous gustatory center to move forward from the vagus region into the facial, and a further correlation was effected between the gustatory and tactile centers by means of the descending secondary gustatory tract from the facial lobe to the funicular nuclei.

In the gadoids the fins, particularly the free pelvic fin rays, serve as motile organs of tactile-gustatory sensation. The gustatory innervation is as before through the facial nerve, but the tactile through spinal nerves which enter the brain behind the vagal lobes. Accordingly, the somatic gustatory center does not migrate forward, but remains stationary, and the secondary gustatory path passes from it directly to the motor centers of the spinal cord instead of first to the tactile correlation center. This provides a shorter path from taste buds on the fins to the muscles which move the fins and the body as a whole.

## THE COMMISSURA INFIMA AND FUNICULAR NUCLEI OF GADUS.

The analysis of the region of the commissura infima Halleri and funicular nuclei is much more difficult in Gadus than in some other types where the visceral and somatic elements of this complex are more highly differentiated, as in Ameiurus. For the typical arrangement and nomenclature of these parts the reader is referred to my recent paper ('06) on the centers for taste and touch in Ameiurus and to Fig. 1 of the present article, which summarizes the chief conclusions reached in that inquiry.

The somatic division of the commissura infima of Gadus is large and heavily medullated; the visceral division is unmedullated. The commissural nucleus is large and the somatic part is more extensive than the visceral.

The median lobule of the vagal lobe passes directly back into the visceral commissural nucleus, which occupies the mid-dorsal line caudad of the vagal lobes (Figs. 3 and 5). This nucleus contains no medullated fibers; it does, however, contain many small cells and a dense neuropil of unmedullated fibers, many of which cross the median line, forming the most cephalic part of the commissura infima. The nucleus ambiguus lies below it and gives rise to motor roots of the vagus. The most caudal sensory root of the vagus is seen in Fig. 5 entering the caudal tip of the vagal lobe laterally of the commissural nucleus. In the Weigert sections of young fish here examined (the specimens were about 7 cm. long) no vagus root fibers are seen to enter the commissura infima. In this, I confirm the statements made for Gadus by KAPPERS ('06), who also worked with Weigert preparations. It is, however, by no means clear from my preparations that no unmedullated termini of these root fibers cross in the commissure. In fact, the appearance of the sections strongly suggests that this is the case, as I have also found it in both Ameiurus and Cyprinus.

Immediately behind the last sensory root of the vagus the somatic commissural nucleus fills the wide space embraced between the spinal V tracts and their nuclei of the two sides, and is composed of dense neuropil, large cells and medullated fibers in very complex formation (Figs. 3 and 6). Just cephalad of the level of this figure there is a large transverse band of thick medullated fibers which connects the substantia gelatinosa of one side with that of the other or possibly with the opposite commissural nucleus. There is shown in this figure a broad medullated connection between the commissural nucleus and the homolateral spinal V nucleus and formatio reticularis, and also fascicles of commissural fibers in the commissural nucleus.

A very short distance caudad of the level of Fig. 6 the commissural nucleus greatly expands and merges laterally with the spinal V nucleus and funicular nucleus and ventrally with the formatio reticularis (Fig. 7). This complex area may also contain a portion of the visceral sensory commissure and nucleus, though no part of it can be recognized as such. It is not possible to analyze this area into its component parts on the basis of microscopical appearances in Weigert sections, as I have done in Ameiurus. Short tracts of medullated and unmedullated fibers pass through it in all directions, many crossing the median line. A vestige of the nucleus ambiguus extends as far back as the level here figured under the commissural nucleus. The relations shown in this figure continue essentially unchanged far back into the spinal cord, where the area in question gradually shrinks in size and passes over into the dorsal cornua.

The first spinal nerve is a fusion of two or more nerves. The dorsal roots enter the complex area just mentioned, which at the level shown in Fig. 8 is designated cornu dorsalis. At the level of the origin of the second spinal nerve (which joins the first in the brachial plexus) the relations are similar, though the dorsal cornu complex is much smaller and in its dorsal portion the true dorsal cornu is structurally well defined, with a small but distinct funiculus dorsalis laterally of it. At the level of the dorsal root of the third spinal nerve the dorsal area of gray matter is still further reduced, the dorsal cornu and funiculus are still more distinct and the other portions of the dorsal gray complex are reduced to a small median vestige. The ventral ramus of this nerve also effects connection with the brachial plexus for the innervation of the pectoral fin. The fourth spinal does not enter the brachial plexus. The pelvic fin is innervated chiefly from the ramus ventralis of this nerve and by a smaller twig from the fifth spinal.

The dorsal cornua at the levels of the fourth and fifth spinals are reduced to the meager dimensions commonly seen in teleosts. The cross-section of the spinal cord at this level is almost completely filled with very large medullated fibers, showing that long conduction paths are here more important than short reflex connections. The dorso-lateral fasciculi, in particular, are large and heavily medullated. In this respect the cod resembles the eel and other fishes with highly developed body musculature, in striking contrast with the sluggish catfish. Even the cyprinoids, like the carp and the gold-fish, have far smaller longitudinal spinal tracts. At the cephalic end of the spinal cord (third spinals to vagal lobes) the same compact formation of the long tracts is evident as farther caudad, save in the dorsal cornu and funicular nucleus region. The dorsal funiculi disappear in the most caudal part of these nuclei and the dorso-lateral fasciculus sends large tracts into them for their entire extent, suffering corresponding reduction in size cephalad. A considerable proportion of this fasciculus, however, passes farther cephalad to terminate in the oblongata. The ventro-lateral fasciculi also decrease greatly in size in the funicular nucleus region, or more properly expressed, they increase as they pass caudad under the funicular nuclei by accretions from this region. The lateral fasciculi (tracts midway between dorsal and ventral funiculi) also suffer considerable diminution in this region; but some strong bundles of these fibers pass directly cephalad from the spinal cord into the brain as the tractus spino-tectalis, to be greatly augmented in the region of the tuberculum acusticum by the tractus bulbo-tectalis.

We conclude, then, that in Gadus the region of the funicular and commissural nuclei is, as in other types of fishes, a correlation center for all tactile impressions from the skin and their motor responses. The pectoral and pelvic fins of the gadoids are particularly delicate tactile organs and the dorsal cornua of the anterior end of the spinal cord have been enlarged and intimately related to the funicular nuclei and somatic commissural nucleus to serve these sense organs. This process has been carried to a much greater extreme in the gurnards (Trigla, Prionotus, etc.). But the taste buds located on these fins in the gadoids, as we have seen above, are not centrally connected with this tactile correlation center, as they are in the siluroids and cyprinoids, but effect an independent and more direct connection with the ventral horn cells and other motor centers by way of the ventral funiculi. For summary of these connections, see p. 74.

Finally it is a pleasure to acknowledge my indebtedness to the U. S. Bureau of Fisheries for the specimens of young codfish upon which the histological part of this paper is based, and to my colleague, Professor Frank Carney, for assistance in the preparation of the illustrations.

Denison University,
December 22, 1906.

## LITERATURE CITED.

BURNE, R. H.

'02. Descriptive and illustrated catalogue of the physiological series of comparative anatomy contained in the museum of the Royal College of Surgeons of England. Second Edition. *London*, Vol. 2, pp. 90–93.

GORONOWITSCH, N.

'96. Der Trigeminofacialis-Complex von Lota vulgaris. *Festschr. f. Gegenbaur*, Vol. 3.

HALLER, B.

'96. Der Ursprung der Vagusgruppe bei den Teliostiern. *Festschr. f. Gegenbaur*, Vol, 3.

HERRICK, C. JUDSON.

'99. The cranial and first spinal nerves of Menidia. *Journ. Comp. Neur.*, Vol. 9.

'00. A contribution upon the cranial nerves of the codfish. *Journ. Comp. Neur.*, Vol. 10.

'01. The cranial nerves and cutaneous sense organs of the North American siluroid fishes. *Journ. Comp. Neur.*, Vol. 11.

'04. The organ and sense of taste in fishes. *Bulletin of the U. S. Fish Commission for* 1902.

'05. The central gustatory paths in the brains of bony fishes. *Journ. Comp. Neur. and Psych.*, Vol. 15.

'06. On the centers for taste and touch in the medulla oblongata of fishes. *Journ. Comp. Neur. and Psych.*, Vol. 16.

JOHNSTON, J. B.

'06. The nervous system of vertebrates. *Philadelphia, P. Blakiston's Son & Co.*

KAPPERS, C. U. ARIENS,

'06. The structure of the teleostean and selachian brain. *Journ. Comp. Neur. and Psychol.*, Vol. 16.

LANDACRE, F. L.

'07. On the place of origin and method of distribution of taste buds in Ameiurus Melas. *Journ. Comp. Neur. and Psychol.*, Vol. 17, No. 1.

LEYDIG, FR.

'51. Ueber die äussere Haut einiger Süsswasserfische. *Zeits. wiss. Zool.*, Vol. 3.

PARKER, T. JEFFERY.

'00. A course of instruction in zoötomy (Vertebrata). *New York, The Macmillan Co.*

SCHULZE, F. E.

'63. Ueber die becherförmigen Organe der Fische. *Zeits. wiss. Zool.*, Vol. 12.

'70. Ueber die Sinnesorgane der Seitenlinie bei Fischen und Amphibien. *Arch. f. mik. Anat.*, Vol. 6.

Fig. 1. Diagram of the gustatory and tactile paths in the medulla oblongata of Ameiurus, as seen from above. The gustatory connections are shown on the lower (left) side of the figure, the tactile on the upper (right) side. The gustatory centers are bounded by the fine dotted lines, the tactile centers by the broken lines (short dashes). The neurones of the commissural nuclei are not shown in the diagram. The position of the visceral commissura infima and its nucleus is indicated by two vertical crosses (‡) behind the vagal lobes; that of the somatic commissure and its nucleus by a single oblique cross (×) farther caudad between the two median funicular nuclei. Only the long secondary tracts are indicated. The short secondary and tertiary tracts from both visceral and somatic centers to the formatio reticularis, etc., are omitted.

The data from which the diagram is constructed will be found in two previous papers (Herrick, '05 and '06), where cross sections and other figures of the oblongata of Ameiurus are given.

Fig. 2. Diagram of the gustatory and tactile paths in the medulla oblongata of Gadus morrhua, as seen from above. The plan of the diagram is the same as that of Fig. 1, both gustatory and tactile centers being bounded by fine dotted lines. As before, the position of the visceral commissura infima and its nucleus are indicated by two vertical crosses (‡) and that of the somatic commissure and its nucleus by oblique crosses (× × ×).

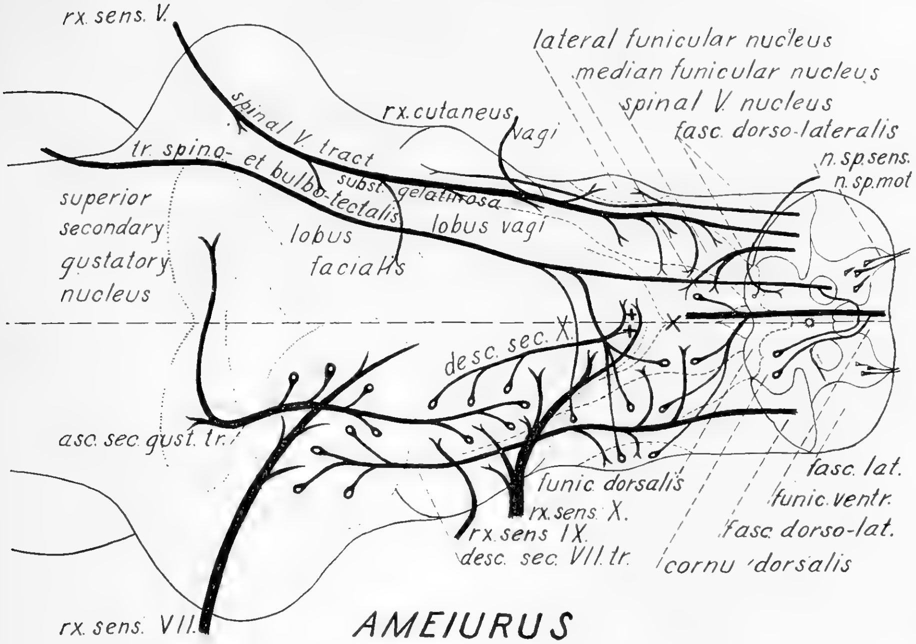

rx. sens. V.
lateral funicular nucleus
median funicular nucleus
spinal V. nucleus
fasc. dorso-lateralis
n. sp. sens.
n. sp. mot
rx. cutaneus vagi
spinal V. tract
tr. spino- et bulbo-tectalis
subst. gelatinosa
superior secondary gustatory nucleus
lobus facialis
lobus vagi
desc. sec. X.
asc. sec. gust. tr.
funic. dorsalis
rx. sens. X.
rx. sens. IX.
desc. sec. VII. tr.
fasc. lat.
funic. ventr.
fasc. dorso-lat.
cornu dorsalis
rx. sens. VII.
AMEIURUS

FIG. 1.

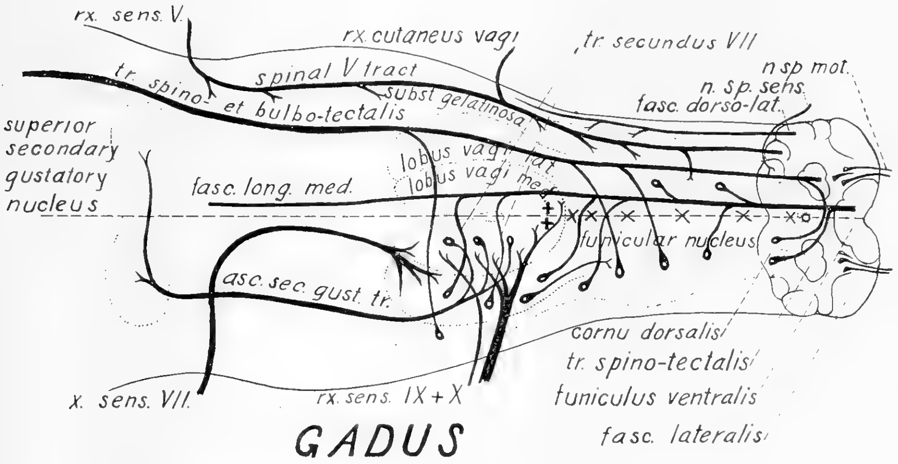

rx. sens. V.
rx. cutaneus vagi
tr. secundus VII
n. sp. mot.
n. sp. sens.
spinal V tract
fasc. dorso-lat.
tr. spino- et bulbo-tectalis
subst. gelatinosa
superior secondary gustatory nucleus
lobus vagi lat.
lobus vagi med.
fasc. long. med.
funicular nucleus
asc. sec. gust. tr.
cornu dorsalis
tr. spino-tectalis
funiculus ventralis
fasc. lateralis
x. sens. VII.
rx. sens. IX + X
GADUS

FIG. 2.

Fig. 3. A photograph of a dissection of a brain of a large specimen of Gadus morrhua. × 1.3.

The cerebellum and a portion of the tubercula acustica have been dissected away, the cut surfaces being indicated by parallel shading on the accompanying outline. The dissection exhibits the relations of the lateral and median vagal lobes and the commissural nuclei. For the internal connections of these structures compare Fig. 2 and the following figures of cross sections.

Fig. 4. Transverse section through the medulla oblongata of Gadus morrhua. × 35.

The section is taken through the middle of the vagal lobes and illustrates the relations of their median (visceral) and lateral (somatic) lobules. Vagus root fibers are seen entering the median lobule on its lower border. Secondary facialis tracts pass from the lateral lobule to the ventral funiculi and from the median lobule to the ascending secondary gustatory tract. Dorsally of the latter is the fasciculus dorso-lateralis, containing the spinal V tract, tracts between the oblongata and the spinal cord and probably the tr. spino-cerebellaris.

Figs. 4 to 8 are taken from a single series of transverse sections of an entire fish 7 cm. long, fixed in Flemming's stronger fluid and stained by the method of Weigert. The external form of this young brain does not differ materially from that of the very large adult shown in Fig. 3.

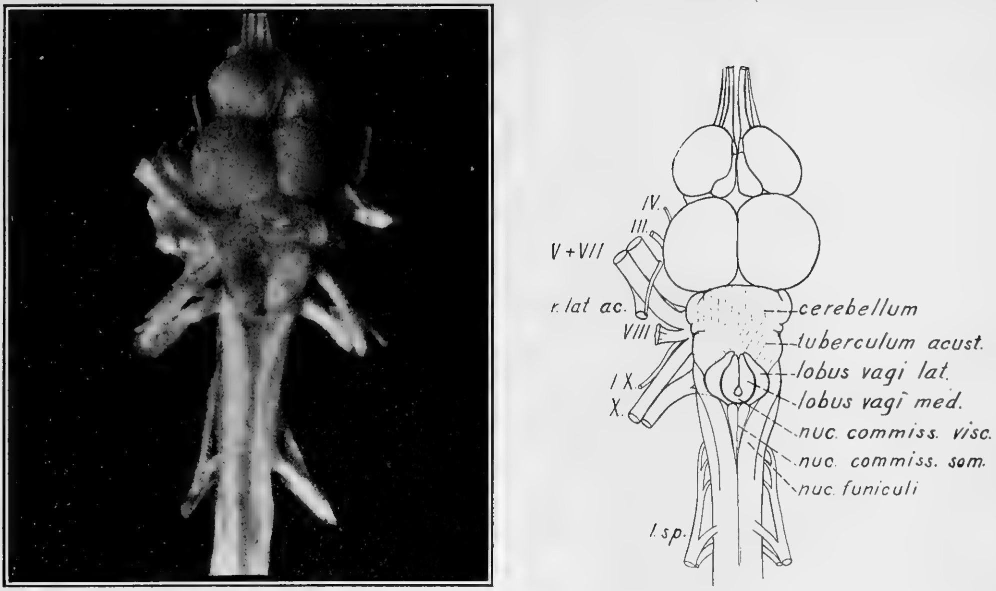

IV.
III.
V+VII
r. lat ac.
VIII
IX.
X.
I sp.
cerebellum
tuberculum acust.
lobus vagi lat.
lobus vagi med.
nuc. commiss. visc.
nuc. commiss. som.
nuc. funiculi

FIG. 3.

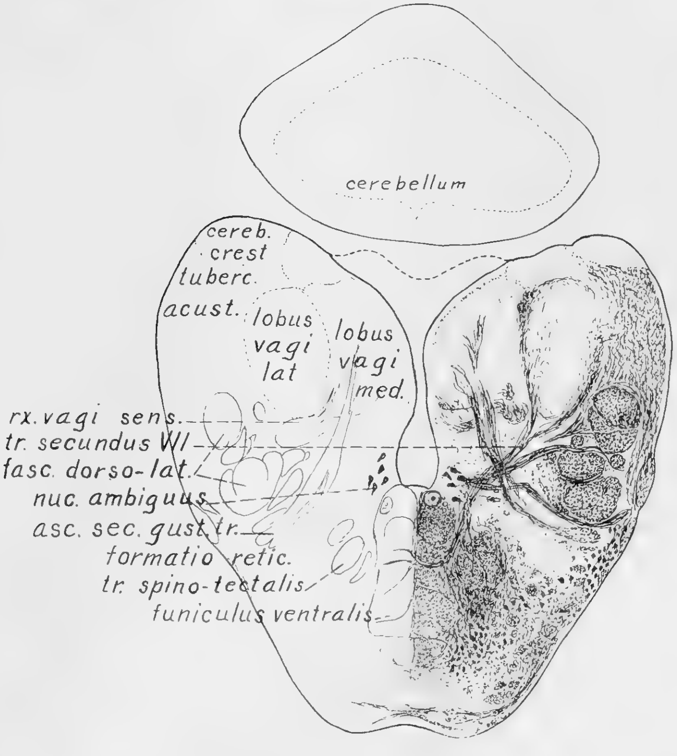

cerebellum
cereb. crest
tuberc. acust.
lobus vagi lat
lobus vagi med.
rx. vagi sens.
tr. secundus VII
fasc. dorso-lat.
nuc. ambiguus
asc. sec. gust. tr.
formatio retic.
tr. spino-tectalis
funiculus ventralis

FIG 4

FIG. 5. Transverse section 0.4 mm. caudad of the last, passing through the caudal tip of the median division of the vagal lobe at the point where it passes over into the cephalic end of the visceral commissural nucleus. The caudal end of the lateral division of the vagal lobe may be seen two sections farther cephalad in the area here designated *substantia gelatinosa.* × 35.

FIG. 6. Transection a little farther caudad through the beginning of the somatic portion of the commissura infima. The vagal lobes and visceral commissural nucleus lie farther cephalad and the corresponding region is here occupied by the somatic commissural nucleus (*cf.* Fig. 3). The substantia gelatinosa has begun to enlarge and a little farther caudad (Fig. 7) has expanded into the spinal V nucleus. Short tracts pass between the commissural nucleus and the substantia gelatinosa and formatio reticularis, and secondary tactile paths pass from all of these regions to the ventral cornu and, as internal arcuate fibers, into the ventral commissure. × 35.


lobus vagi med.
visc. commissural nuc.
substantia gelatinosa
asc. sec. gust. tr.
rx. vagi sensor.
rx. vagi motor.
fasc. dorso-lat.
nuc. ambiguus
formatio reticularis
tr. spino-tectalis
funiculus ventralis

FIG. 5.

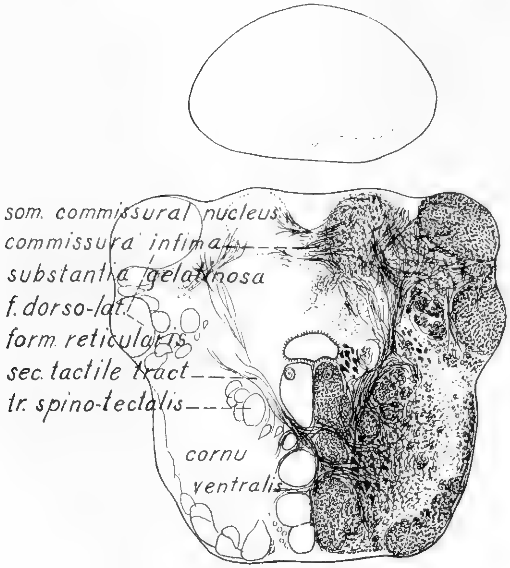

som. commissural nucleus
commissura infima
substantia gelatinosa
f. dorso-lat.
form. reticularis
sec. tactile tract
tr. spino-tectalis
cornu ventralis

FIG. 6.

Fig. 7. Transection a short distance farther caudad. The area designated *funicular nucleus* contains in addition to that structure the somatic commissural nucleus and probably also a spinal prolongation of the visceral sensory column, though the latter cannot be separately distinguished. The spinal V nucleus is so intimately related to the same area that no line of demarcation can be found between them. The whole area seems to function as a unit. The lateral funicular nucleus is not separately developed. The most cephalic ventral root fibers of the first spinal nerve appear in this section. × 35.

Fig. 8. Transection farther caudad which passes through a dorsal and a ventral rootlet of the first spinal nerve. The cornu dorsalis is considerably larger than in the remainder of the spinal cord and still includes a vestige of the funicular nucleus complex and commissura infima. × 35.

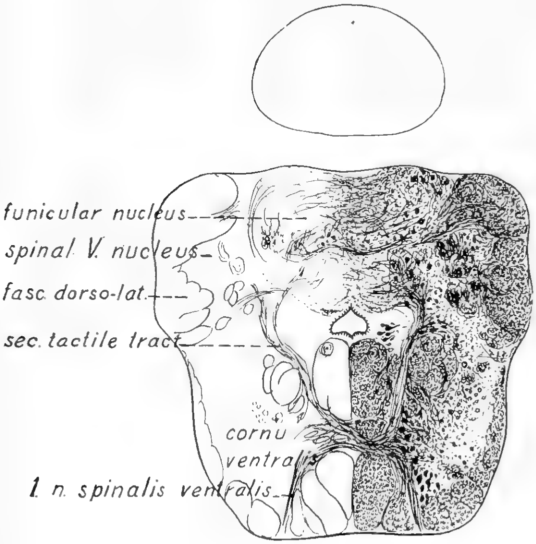

funicular nucleus
spinal V. nucleus
fasc. dorso-lat.
sec. tactile tract
cornu ventralis
1. n. spinalis ventralis

FIG. 7.

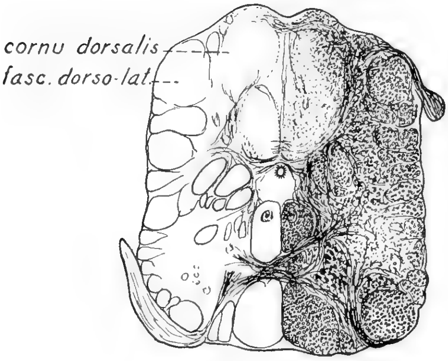

cornu dorsalis
fasc. dorso-lat.

FIG. 8.

# CHROMOTROPISM AND PHOTOTROPISM.

Because of the obvious importance of the facts which MINKIEWICZ claims to have discovered and of the stimulating value of his statements it has seemed worth while to print in this *Journal* a translation of the two brief notes on responses to chromatic stimulation which he has recently published.[1] The whole of the first note appears below; in the case of the second note the introductory paragraph is omitted in the translation.—THE EDITORS.

Because of striking contradictions in the generally accepted theory of SACHS and LOEB, to the effect that the most refrangible rays of the spectrum are alone active in the phototropism of animals and plants and that their action is the same as that of white light, and certain facts well established by P. BERT and LUBBOCK for Daphnia, which is attracted especially by the yellow-green, and by WIESNER for plants, which present two extremes of tropic action (first to the blue-violet, second to the infra-red, the action of the yellow being nil), I have given special attention in the course of my researches upon the tropisms and instinct to the tropic action of the chromatic rays. Some of my results follow:

1. The larvæ of Maia squinado (zoea) recently hatched present, as is well known, a strongly marked positive photo- and heliotropism. I have shown that they are at the same time very sensitive to chromatic rays, that they are directed constantly toward the rays of the shortest wave length, that is toward the violet, and in its absence toward the blue. They distinguish thus all the visible rays. The reaction is almost instantaneous; all the larvæ dash like a flock of birds toward the most refrangible rays as soon as they are placed under their influence.

This phenomenon has taken place not only in horizontal glass tubes but also in vertical ones no matter what the distance of the most tropic region from the surface of the water.

2. Nemerteans of the specias Lineus ruber behave in an entirely different manner. They are strongly negative in the presence of diffuse white light and at the same time they all direct themselves toward the rays of the greatest wave light, that is, toward the red, and in its absence, toward the yellow, etc.

Thus far everything seems to agree with the theory of LOEB. The positive phototropism of the larvæ coincides with the strongest positive action (attractive) of the violet part of the spectrum; the negative phototropism of Lineus with the strongest negative action (repellent) of the violet part. And yet these phenomena are not necessarily bound together.

---

[1] MINKIEWICZ, ROMAULD. Sur le chromotropisme et son inversion artificielle. *Comptes rendus de l'académie des sciences, Paris.* Nov. 19, 1906. Le rôle des phénomènes chromotropiques dans l'étude des problemes biologiques et psycho-physiologiques. *Comptes rendus de l'académie des sciences, Paris.* Dec. 3, 1906.

3. One may bring about artificially with the nemerteans the inversion of the tropisms in the presence of chromatic rays while preserving the negative sense of their phototropism with reference to white light.

*a.* Placing Lineus in a solution composed of from 25 to 80 cc. of distilled water to 100 cc. of sea water, I obtained on the following day this inversion with absolute certainty. Lineus while remaining negative with reference to white light now directs itself toward the most refrangible rays of the spectrum, just as it had previously directed itself away from them.

The result of the inversion is that the phototropism, which remains negative, is here absolutely separated from the chromotropism, of which the sense is changed. Every chromatic ray has a specific action and at the same time the action of white light is not a simple resultant of a mechanical fusion of the actions of all the possible rays of the spectrum.

I must remark further, that I have not as yet found, in spite of long continued researches, a single means of transforming the negative phototropism of Lineus into positive phototropism by agents either chemical, osmotic or thermic. Thus, for example, the animal remains negative until its death in the presence of white light whatever the concentration of the sea water.

*b.* The inversion of the chromotropism of the nemerteans appears the second day, continues in general two days and disappears the fourth, the animal becoming again normally erythrotropic. This seems to me to prove that the nature of chromotropism is not an absolute function of such or such vital medium but a function of the physiological state of the organism, a fact which agrees with the observations of LOEB concerning the changes in heliotropism at different periods of life.

*c.* There is one fact which confirms further this point of view, namely, that my Lineus after having lived for two or three weeks in my solutions and presenting consequently their normal chromotropism (erythrotropism) change anew when one transfers them into pure sea water and become purpurotropic (direct themselves toward the violet).

But this is not all.

*d.* The inversion of the chromotropism is not produced immediately and it also does not disappear all at once. There are stages when the animal still erythrotropic (normal) ceases to distinguish green from yellow. There are others when though indifferent to green and yellow it is already purpurotropic. These stages of tropic blindness with reference to the middle parts of the spectrum last several hours and thus one can easily observe them on the second and the fourth day. There should exist still two stages in the passage from erythrotropism to purpurotropism and inversely, during which the animal is completely indifferent in the presence of colored rays, that is, is achromotropic—either because it is equally influenced by all the chromatic rays or because it is entirely insensitive. This I have not yet been able to observe, for these stages are of very short duration.

In a second note the author points out the following bearings of his discovery upon the problems of general biology and of the psycho-physiology of vision.

## A. GENERAL BIOLOGY.

1. One may find animals chromotropic with reference to the middle rays of the spectrum, each ray having its own specific action. Indeed Daphnia, according to PAUL BERT and J. LUBBOCK, is xantho-chlorotropic, a fact which is absolutely incompatible with the theory of LOEB ('90).

2. Purpurotropism is not necessarily connected with positive phototropism nor erythrotropism with negative phototropism. One may find animals which behave in the reverse manner. This is proved by the excellent experiments of ENGELMANN upon unicellular organisms (1882 and 1883). According to him Paramecium bursaria, which is positively phototropic, avoided the green and the blue and directed itself toward the red. Likewise Navicula (a diatom) ceased movement in darkness and in the green.

3. Organisms should exist which, while being positively or negatively phototropic are not at all chromotropic (total tropic blindness; that is achromotropy), as Lineus is during the transitory stages of inversion.

4. There are organisms like the plants studied by J. WIESNER ('79) which are insensitive to certain rays of the spectrum (partial tropic blindness; that is, the axanthotropy of Vicia sativa).

5. It follows from the vertical tube experiments upon the zoea larvæ that the chromatic rays may have a certain influence upon the vertical distribution of aquatic animals, granting the unequal absorption of the different rays of the spectrum, the greatest for the red, the least for the blue (W. SPRING, H. FOL, E. SARASIN, FOREL).

## B. PSYCHO-PHYSIOLOGY.

The experiments which I described in my preceding note lead me to believe that in studying the biology of the lower animals one should seek the indices which may point the way to an explanation of the complex and difficult phenomena of vision.

1. Chromotropism being independent of phototropism, it seems to me that the perception of white light may be a primitive phenomenon, much more simple than it is generally believed to be and independent of chromatic perception (this is corroborated by the well known experiments of A. CHARPENTIER, and also by the historic fact that in the best theory of vision, HERING was forced to admit the existence of a special white-black substance).

2. It seems superfluous and futile to seek for the solution of the problems of chromatic vision in the hypothetical creation of different nerve fibers (YOUNG-HELMHOLTZ), of various pigment granules (A. PIZON), or of different chemical substances (HERING), endowed with specific sensitiveness for different rays of the spectrum. One should rather ask whether there are not different physiological states in the same living substance which give rise to these complex phenomena of chromatic vision, as in Lineus the different states artificially induced bring about all the successive and transitory stages of chromotropism. [Experiments of PERGENS and further of LODATO ('00) upon the chemical phenomena in the retina, the intensity of which varies according to the action of different rays of the spectrum.]

3. Thus is it not possible and profitable to compare color-blindness (Daltonism), in general, and the different cases of achromotropy, partial or total, of the xanthotropic blindness of plants (Wiesner) and of the indifference $\frac{\text{chloro-}}{\text{xantho-}}$ tropic of Lineus in certain stages of the artificial inversion of its chromotropism? [Personal experiments of W. Nagel ('01) upon the artificial transitory blindness for red induced by santonin.]

4. Finally, is it not in this direction that one should look for the explanation of the consecutive colored images (six according to C. Hess ('00) or even more) after a short chromatic stimulation, if one bears in mind the succession of stages in the artificial inversion of chromotropism in my Lineus?

# LITERARY NOTICES.

**Jennings, H. S.** Behavior of the Lower Organisms. Columbia University Biological Series, X. *New York, The Macmillan Company.* 1906. pp. xiv and 366. Price $3.00.

The custom which the zoölogical faculty of Columbia University has followed for some years of having an annual series of special lectures on some particular topic in biology, given either by one of its own members or by some distinguished biologist from elsewhere, has indirectly resulted in the production of a very notable series of books. With a single exception these books have been written by men who by birth or adoption are American workers. The series as a whole is unquestionably representative of the best in American biological work. This being the case, it is altogether fitting that the volume here under consideration should have a place in the series. The author's brilliant investigations on the behavior of lower organisms, begun about ten years ago, have attracted wide attention, both here and abroad, and further can truly be said to have distinctly influenced the trend of American biological work in the period during which they have been appearing. In no small degree is the present activity in the field of animal behavior in this country a result of the stimulus of Dr. JENNINGS' pioneer work.

To characterize the present book in a single sentence it may be said to be a carefully condensed statement from a unified standpoint of the important objective results which have been obtained by students of the behavior of lower organisms, together with a critical analysis and discussion of the significance of these results and their bearing on certain specific and general problems of biology. Roughly two-thirds of the space is given to the descriptive account of behavior, and the other third to discussion. The descriptive portion of the work is not encyclopedic in character. Much which might have been inserted, and which doubtless would have been by a less careful and critical author, has been omitted. The reader is spared the mass of unimportant and trivial detail which is usually supposed to be the necessary accompaniment of the thorough and systematic development of a scientific subject. From this statement, however, it is not to be concluded that the treatment of behavior in the descriptive portion of JENNINGS' book is in any way sketchy or lacking in thoroughness. Rather, the fact is that it is an unusually nice sense on the author's part of what really *is* important both in his own work and the work of others, for a thorough general survey of the subject, which has kept the book so free of irrelevant and trivial detail. At the outstart it should be said that the scope of the work is not precisely indicated by the title. To have been exactly indicative of the contents the title should have read, "The Behavior of *Certain* Lower Organisms." The descriptive portions of the book include full and connected accounts of behavior of representatives of only two large groups of organisms; namely, (1) unicellular animals and plants (especially the bacteria), and (2) cœlenterates. A brief account is given of certain features of the behavior in representatives of other invertebrate groups, notably the Echinodermata, Platyhelminthes (Planaria) and the Rotifera. We are told in the preface that: "As originally written, this descriptive portion of the work was more extensive, including, besides the behavior of the Protozoa and Cœlenterata, systematic accounts of behavior in Echinoderms, Rotifera, and the lower worms, together with a general chapter on the behavior of other invertebrates. The work was planned to serve as a reference manual for the behavior of the groups treated. But the exigencies of space compelled the substitution of a chapter on some of the important features of behavior in other invertebrates for the systematic accounts of the three groups mentioned." Every student of behavior will regret the necessity for this omission.

The descriptive portion of the book is subdivided as follows: Chapter I deals with the behavior of Amœba and Chapter II with the behavior of bacteria. The next eight chapters are devoted to the infusoria, the forms on which the greater part of the author's own investigations have been made. The behavior of Paramecium is taken as the type and described in considerable detail. Chapter III includes a description of the normal movements of Paramecium, special emphasis being laid on the adaptive characters of the spiral path followed in the swimming. The mechanism of the "avoiding reaction," by which term is designated the reaction originally called by the author the "motor reflex," is fully described. A final section describes the method by which "positive" reactions are brought about. From this chapter as a foundation the author proceeds to a more detailed discussion of special features in the reactions of Paramecium to different stimuli, Chapter IV including the account of reactions to mechanical, chemical, thermal and photic stimuli and the orienting reactions to water currents, to gravity and to centrifugal force. Chapter V is devoted mainly to an excellent account of the reactions of Paramecium to electricity. It also includes a short section on the subject of trichocyst discharge. Chapter VI concludes the account of the behavior of Paramecium, and deals with some of the more general features. The first section treats of the behavior under two or more stimuli, especial attention being paid to the interference of the contact reaction (thigmotaxis) with the reactions to other stimuli. Variability and modifiability of reactions are next considered. It is clearly demonstrated that the behavior is not of a fixed character, but subject to relatively wide modifications under certain circumstances. The behavior during fission and conjugation is briefly described. Following this there is given a very interesting "composite reconstruction" of the daily life of Paramecium. Finally we have a brief discussion of certain general features of the behavior in this organism. The next four chapters deal with behavior of other infusoria according to the same general plan as is followed in the account of Paramecium, but of course with less detail as to individual organisms. An account of the "action systems" of flagellates, holotrichous, hypotrichous and heterotrichous ciliates is followed by descriptions of the reactions of representatives of these groups to mechanical, chemical and thermal stimuli. The reactions of infusoria to light receive very full treatment. The general conclusion is that "reactions to light occur in the infusoria in essentially the same way as do the reactions to most other stimuli through the avoiding reaction; that is, by the method of trying movements in different directions. The cause of reaction is a change in the intensity of light, primarily that affecting the sensitive anterior end." There is a brief account of the reactions of infusoria to gravity and centrifugal force. Chapter IX is devoted to an account of reactions to the electric current, and a critical discussion of the various theories of the electrotactic reaction which have been proposed. None of these is found to be entirely satisfactory. Chapter X completes the account of the behavior of infusoria: the topics discussed in it are modifiability of behavior, behavior under natural conditions and food habits. The next two chapters are given to the behavior of lower Metazoa. The behavior of cœlenterates receives very full treatment. Summing up his conclusions from the study of behavior in these relatively simple multicellular organisms the author says: "Comparing the behavior of this low group of multicellular animals with that of the protozoa, we find no radical difference between the two. In the cœlenterates there are certain cells—the nerve cells—in which the physiological changes accompanying and conditioning behavior are specially pronounced, but this produces no essential difference in the character of the behavior itself." The treatment of other metazoan forms occupies but a single chapter and is topical rather than systematic in form. This brings us to the end of the descriptive portion of the book.

The objective point of view is very carefully and consistently maintained in these descriptive chapters. Though treating of a variety of topics, they have nevertheless a very definite unity. This comes about through the marked emphasis which the author puts upon certain features which he has found to be common to the behavior of all the lower organisms so far investigated. Of these common features the following are the ones on which greatest stress is laid:

1. Organisms change their behavior (*i. e.*, react) in response to changes in external conditions. "The most general external cause of a reaction is a *change* in the conditions affecting the organism."

2. The character of the behavior of an organism under any particular set of external conditions is not determined solely by those external conditions but to as great or even to a greater degree by internal conditions (the "physiological state" of the organism).

3. The behavior of all organisms is, generally speaking, of a markedly adaptive character.

4. The most usual mechanism by which this adaptiveness in behavior is brought about is that of the "trial and error" method of response to stimuli. "We find behavior largely based on the process of performing continued or varied movements which subject the organism to different conditions of the environment, with selection of some and rejection of others."

5. Behavior is in general not a fixed or stereotyped character, but instead is capable of varying degrees of modification under different circumstances. On the whole modifications so induced are of an adaptive character.

In the opinion of the reviewer the clear and conclusive demonstration that the features enumerated *are* common to the behavior of all the lower organisms hitherto investigated in detail is a great achievement of the book. The thing most lacking in animal behavior work hitherto, has been a unified standpoint leading to the elucidation of the features of behavior which were general (that is, common to a wide range of organisms).

Turning now to the theoretical portion of the book, we have first a short chapter (XIII) comparing the behavior of unicellular and multicellular organisms. The author's general conclusion is that there are no differences of fundamental character in the behavior of the Protozoa and Metazoa. He is strongly inclined towards the view as to the function of the nervous system which has been upheld by LOEB; namely, that it has no exclusive functions not primitively common to all protoplasm. The next chapter is devoted to a convincing destructive criticism of the "tropism theory." The author's views on this subject are so well known that special comment regarding them is unnecessary. How any person of a scientific habit of mind can still uphold the general validity of the local action theory of tropisms in the face of the facts which have been brought out by JENNINGS showing just how unicellular organisms actually *do* react to "directive" stimuli, passes all understanding. In this chapter a brief section is given to a discussion of the various systems of terminology and nomenclature which have been devised for use in animal behavior work. The following sentences demand quotation: "To the present writer, after a long continued attempt to use some of the systems of nomenclature devised, descriptions of the facts of behavior in the simplest language possible seems a great gain for clear thinking and unambiguous expression. If investigators on the lower organisms would for a considerable time devote themselves to giving in such simple terms a full account of behavior in all its details, paying special attention to the effect of the movements performed on the relation of the organism to the stimulating agent, this would be a great gain for our understanding of the real nature of behavior and some theories now maintained would quickly disappear. Less attention to nomenclature and definitions, and more to the study of organisms as units, in their relation to the environment, is at the present time the great need in the study of behavior in lower organisms." Who does not heartily agree?

Chapter XV asks the question: "Is the behavior of lower organisms composed of reflexes?" The answer may be gathered from the following sentences: "The behavior of Paramecium and the sea-urchin is reflex if the behavior of the dog and of man is reflex; objective evidence does not indicate that there is from this point of view any fundamental difference in the cases." The next three chapters contain a searching analysis of the phenomena of behavior in lower organisms. The general result of this analysis is summed up by the author as follows: "The three most significant features of behavior appear to be (1) the determination of the nature of reactions by the relation of external conditions to the internal physiological processes, and particularly the general principle that interference with these processes causes a change in behavior; (2) reaction by varied and overproduced movements, with selection from the varied conditions resulting from these movements—or, in brief, reaction by selection of overproduced movements; (3) the law of the readier resolution of physiological states after repetition. The first of these phenomena produces the regulatory character of behavior. The second and third furnish the mainsprings for the development of behavior, the second being constructive, the third conservative."

In Chapter XIX are set forth the author's views regarding the development of behavior. Space is lacking for a full consideration of the argument on this subject. The principal factors which make for progressive development of more effective (*i.e.*, adaptive) behavior in the individual are held to be (1) the selection of varied movements as a general method of behavior, and (2) "the law in accordance with which the resolution of one physiological state into another becomes readier and more rapid through repetition." It is shown in detail how these factors might lead in several ways to progressive development in behavior. To account for progressive evolution of the race in respect to behavior the author, after rejecting the inheritance of acquired characters as unproven, falls back on the principle of natural selection operating according to the method which has been called "organic selection." In reading over this section one cannot escape the feeling that the author only adopts natural selection to account for race progress in behavior because there is no other general principle even formally adequate at hand, and further that he is quite cognizant of the fact that in our present state of knowledge of the phenomena of behavior the explanation of evolution in this field given by natural selection is a purely formal and artificial one.

Chapter XX deals with the question of consciousness in lower organisms in a highly interesting way. The conclusion reached is that: "All that experiment and observation can do is to show us whether the behavior of lower organisms is objectively similar to the behavior that in man is accompanied by consciousness. If this question is answered in the affirmative as the facts seem to require, and if we further hold, as is commonly held, that man and the lower organisms are subdivisions of the same substance, then it may perhaps be said that objective investigation is as favorable to the view of the general distribution of consciousness throughout animals as it could well be. But the problem as to the actual existence of consciousness outside of the self is an indeterminate one; no increase of objective knowledge can ever solve it."

The final chapter has for its heading "Behavior as regulation, and regulation in other fields." The importance as a general regulatory principle of the selection from a variety of activities, those lines of activity which lead to a minimum interference with the physiological processes of the organism, together with the preservation or fixation of adaptive activities through the law of the readier resolution of physiological states, is emphasized. This chapter has been published elsewhere in essentially its present form.

A bibliography and index complete the volume. The book is very completely and well illustrated.

On the whole, one finds very little in the book to criticise. Undoubtedly there are many who will not fully agree with JENNINGS in some of his interpretations and conclusions, but technical discussion of views opposed to those of an author falls properly within the scope of the special memoir, not that of the review. He who searches this book for errors in statement of fact or of principle, or for evidence of deficient knowledge of what has previously been done in the field covered, or for slips in logic or diction, will spend his time fruitlessly. One fault of omission should be corrected in a later edition. Throughout the book there is no indication of the scale to which the figures are drawn, and hence there is no way for one not already familiar with the organism discussed to know anything about their relative sizes. Of course this matters not at all to the biologist, but as things stand at present, the "lay" reader of the book must inevitably go away with the impression that *Chilomonas* is a veritable giant among Protozoa altogether surpassing in size the mediocre, not to say diminutive, *Bursaria.* This, however, is a matter of detail. In general one has only praise for the book. It is a contribution of a high order of merit to biological literature. It is valuable to the specialist as a careful and thorough summary and digest of the present state of knowledge in the field of which it treats, and as a unified setting forth of the author's matured opinions regarding the broader aspects of the problems of animal behavior. To the general reader it presents an authoritative, clear and most interestingly written account of a side of natural history which has hitherto, for the most part, lain entirely outside his ken. We heartily wish for it the large circulation which it certainly deserves.

RAYMOND PEARL.

## BOOKS AND PAMPHLETS RECEIVED.

**Baldwin, James Mark.** Mental development in the child and the race. Methods and processes. Third Edition, Revised. *New York, The Macmillan Co.* 1906.

**Grasset, J.** Demifous et demiresponsables. *Paris, F. Alcan, Editeur.* 298 pp. 1907.

**Ingegnieros, J.** Le langage musical et ses troubles hystériques. Études de psychologie clinique. *Paris, F. Alcan, Editeur.* 208 pp. 1907.

**Guyer, Michael F.** Animal micrology. Practical exercises in microscopical methods. *The University of Chicago Press.* 240 pp. 1906.

**Maxwell, S. S.** Chemical stimulation of the motor areas of the cerebral hemispheres. Reprinted from the *Journal of Biological Chemistry,* Vol. 2, No. 3. 1906.

**Yagita, K.** Ueber die Veränderung der Medulla oblongata nach einseitiger Zerstörung des Strickkörpers nebst einem Beitrag zur Anatomie des Seitenstrangkernes. Reprinted from *Okayama-Igakkwai-Zasshi* (*Mitteilungen der medizinischen Gesellschaft zu Okayama*), No. 201. 1906.

**Hrdlicka, A.** Anatomical observations on a collection of orang skulls from western Borneo; with a bibliography. Reprinted from the *Proc. U. S. Nat. Mus., Washington,* Vol. 31. 1906.

**Weysse, A. W. and Burgess, W. S.** Histogenesis of the retina. Reprinted from the *Am. Nat.,* Vol. 40, No. 477. 1906.

**Smith, Grant.** The eyes of certain pulmonate gasteropods, with special reference to the neurofibrillæ of Limax maximus. From the *Bul. Mus. Comp. Zool., Harvard College,* Vol. 48, No. 3. 1906.

**Harrison, Ross Granville.** Further experiments on the development of peripheral nerves. Reprinted from *Am. Journ. Anat.,* Vol. 5, No. 2. 1906.

**Dean, Bashford.** Chimæroid fishes and their development. *Publications of the Carnegie Institution,* No. 32. 1906.

**Drew, G. A.** The habits, anatomy and embryology of the giant scallop (Pecten tenuicostatus Mighels). *University of Maine Studies,* No. 6. 1906.

**Metcalf, M. M.** Salpa and the phylogeny of the eyes of vertebrates. Reprinted from *Anat. Anz.,* Vol. 29. 1906.

**Carpenter, F. W.** An astronomical determination of the heights of birds during nocturnal migration. From *The Auk,* Vol. 23, No. 2. 1906.

**Montgomery, Thos. H.** The æsthetic element in scientific thought. Reprinted from the *Academy of Science,* Vol. 8. 1905.

**Bell, J. Carleton.** Reactions of the crayfish. Reprinted from *Harvard Psychological Studies,* Vol. 2. 1906.

**Smallwood, W. M.** Notes on Branchiobdella. Reprinted from the *Biol. Bul.,* Vol. 11, No. 2. 1906.

**Wilder, B. G.** Some linguistic principles and questions involved in the simplification of the nomenclature of the brain. Reprinted from the *Proc. Am. Physiological Assoc.,* Vol. 36. 1905.

**Weysse, Arthur W.** Notes on Animal behavior. *Science,* N. S., Vol. 19, No. 495. 1904.

**Lindsay and Blakiston.** The physician's visiting list for 1907. *Philadelphia, P. Blakiston's Son & Co.*

Thirteenth Annual Report of the Craig Colony for Epileptics at Soneya, N. Y.

The Journal of
Comparative Neurology and Psychology

VOLUME XVII MARCH, 1907 NUMBER 2

# LIGHT REACTIONS IN LOWER ORGANISMS.

## II. VOLVOX GLOBATOR.

BY

S. O. MAST.

*Professor of Biological Science at Hope College, Holland, Michigan.*

WITH FIFTEEN FIGURES.

CONTENTS.

### I. INTRODUCTION.

Since the discovery of Volvox by LEEUWENHOEK, over two hundred years ago, it has been studied in detail by many investigators. Nearly all noted the effect of light on the direction of

smaller ones, especially such as were still within the mother colonies, appeared quite normal in color. Intense light evidently causes some change in the chlorophyl.

The specimens used in the experiments performed at Harvard University were collected in various small ponds located some little distance west of Cambridge. Some of these ponds are artificial, having formed in clay pits; others are apparently natural, being located in low, swampy land. All of the ponds contained numerous aquatic plants, and the water in them was stagnant but clear and not foul. The material used in the work done at Hope College was collected in ponds connected with a very sluggish river which runs through a marsh directly north of the city of Holland. Colonies of Volvox were found sparsely scattered here and there along almost the entire shore line of nearly all the ponds. In a few spots, however, they were so numerous that the water appeared green, and in these places they could readily be collected in great numbers.

There are two well defined species of Volvox, globator and aureus (EHRENBERG = minor STEIN). In the ponds near Cambridge practically all the colonies belonged to the species globator; but in the ponds north of Holland the two species were found about equal in number. They were usually found intermingled, but in a few places I found only globator and in one place nothing but minor.

After colonies of Volvox have been in the laboratory from 12 to 24 hours they become inactive, and no longer respond readily to stimuli, and are therefore not satisfactory for experimental work. This makes it necessary to collect frequently. An abundance of material close at hand is consequently almost a requisite for experimental work on this form. In the following experiments, the specimens usually were collected early in the morning and used the same day.

## 3. STRUCTURE.

Since the discovery of Volvox by LEEUWENHOEK nearly every naturalist has had something to do with the study of this exceedingly interesting organism. Most of these investigators laid greatest stress on the structure, but in spite of all this work there are still two questions with regard to structure, concerning which there is some doubt. One is the location of the eye-spot with reference to the colony as a whole, the other, the variation in form of the vital portion of the individuals composing the colony. Since these structures are of considerable importance in the study of light reactions, I shall take up the structure of Volvox rather more in detail than otherwise would be necessary. The following description is the result of a review of the literature on this subject, supplemented by my own observations.

Volvox varies in form from approximately spherical to ovoid. The smallest free swimming colonies can scarcely be seen with the naked eye, while the largest are nearly, if not quite, one millimeter in diameter; KLEIN ('89, p. 143) gives 850$\mu$, HANSGIRG ('88, p. 101) 800$\mu$, KIRSCHNER ('79) 700$\mu$, and FOCKE ('47) 1100$\mu$. Some of the investigators found Volvox globator to be larger than Volvox minor, while others found the opposite to be true. KLEIN gives 800$\mu$ as the diameter of the largest colonies of V. globator and 850$\mu$ as that of the largest V. minor. HANSGIRG gives 800$\mu$ as the diameter of the former and 460$\mu$ as that of the latter. In my own collections I found V. globator in general much larger than V. minor. I did not, however, make any accurate measurements with reference to this point.

The colonies of both species are composed of numerous individuals, each of which consists of one cell. KLEIN ('88, p. 146) found from 200 to 4400 individuals in various colonies of V. minor and from 1500 to 22,000 in V. globator. The individuals consist of a central portion, composed largely of protoplasm, and a thick hyaline layer which surrounds the central portion. The central portion will be referred to as the zooid in the future description. The hyaline layers of contiguous cells usually appear continuous, one with the other, but WILLIAMS ('53) demonstrated that they are limited by cell walls. I was not able to see these in living colonies of V. minor, but could see them very distinctly in a few spore-bearing colonies of V. globator, especially at the anterior end. The hyaline layer is much thicker in V. minor than in V. globator and the zooids are much more nearly spherical in the former than in the latter, in which they are in general quite angular. The difference in the shape of the zooids forms the chief distinguishing characteristic of the two species. The cells in the colonies are arranged side by side so as to form a wall enclosing a cavity. In V. minor the hyaline layer is figured by MEYER ('95, p. 227) as extending nearly to the middle of the colony, thus leaving only a very small central

the surface, and a conical portion which projects from near the middle of the flattened portion into the hyaline layer almost to the surface of the colony. At a point about halfway between the anterior pole and the equator of the colony, the altitude of the projection is about twice as great as the diameter of its base. The ratio between these dimensions becomes gradually greater as one proceeds farther from the anterior end, until at the posterior end the altitude is four to five times as great as the diameter. It will thus be seen that the distal end of the conical projections gradually extends farther out as one proceeds from the anterior end to the posterior (see Fig. 2). The only reference to the variation in form of zooids in the same colony is found in Overton's article ('89, p. 70), and he states only that the projection (Schnabel) is longer in the neighborhood of injured places ("In der Nähe von verletzten Stellen verlanget sich der Schnabel").

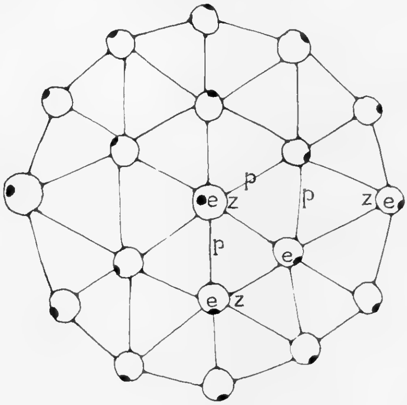


Fig. 3. View of the anterior end of a colony of Volvox minor, showing the location of the eye-spots. *Z*, zooids; *e*, eye-spots; *p*, protoplasmic fibers connecting the zooids.

The projection is nearly circular in outline at the base, but it becomes considerably flattened toward the distal end, so that a cross section near this end is elliptical in outline. The zooids are so arranged in the colony that one of the flattened surfaces of the projections faces the anterior end and the other the posterior. Viewed from either of the flattened surfaces, the outline of the distal end forms nearly a straight line, at either end of which is found the attachment of a flagellum. The flagella are five or six times as long as the diameter of the zooids. Overton ('89, p. 72) says they are about $\frac{1}{2}\mu$ apart and $25\mu$ long. The eye-spot is situated on the surface of the projection which faces the posterior end of the colony. It is found but a short distance from the free end, between the points of attachment of the flagella.

If the projections are short or absent and the zooids nearly spherical the eye-spots are still located in the same relative position as they are in zooids containing long projections, *i. e.*, they face the posterior end of the colony. This becomes very evident in viewing a colony from the anterior end. Under such conditions it is clearly seen that the eye-spots are situated on the surface of the zooids farthest from the middle of the anterior end, as represented in Fig. 3.

Nearly all the investigators, who have worked on the structure of Volvox, figure the eye-spot as situated on one side of the zooids near the outer surface, but only one, OVERTON, describes and figures it in such a way that its position with reference to the colony as a whole is made clear. OVERTON ('89) in Taf. 4, Fig. 26, and Taf. 1, Fig. 3, clearly represents the eye-spot as being located near the outer anterior surface of the zooids and says, p. 114: "Sehr bemerkenswerth erscheint, dass, wie bei einstellung auf einen Meridiankreis des Volvox Stockes sich ergibt, die Augen flecke (wenigstens bei V. minor) bei allen Zellen derjenigen Seite anliegen, die dem vorderen Pole am nähsten liegt."

During the first few days in August, 1905, I examined 30 specimens of V. globator and 50 of V. minor, with special reference to the location of the eye-spots and found that in all but one of these, they were unquestionably located on the outer posterior surface of the zooids. Furthermore, I gave the problem of locating this structure to three of my students in October, 1905. These students had never seen Volvox before and knew nothing about any work done on it. All of them concluded that the eye-spots face the posterior end of the colony. When they took up the problem they knew that these organisms are usually positive in their light reactions. I had given them the term, eye-spot, and it was clearly evident that they assumed that this structure functioned in directing the organisms toward the light, and consequently expected to find it on the anterior surface of the zooids, for they were all much surprised to find it on the opposite surface. It is, therefore, safe to conclude that OVERTON's observation was wrong.

The eye-spots in Volvox are brownish in color and lenticular in

all phototactic under others. Davenport ('97, p. 188) proved certain species of Amœba to be negative to light, and it is well known that Stentor cœruleus responds very definitely to stimulation by light. It is said that the Chytridium swarm spores have an orange colored oil globule at the base of the flagellum which may function as an eye-spot, but in the four organisms mentioned last there are no structures which appear as though they could take the place of these organs. It is, therefore, evident that we have organisms without eye-spots which are sensitive to light but as far as I know there are none with these structures that are not sensitive.

4. Wager ('00, Pl. 32, Fig. 2) represents the flagellum in Euglena viridis as indirectly connected with the eye-spot, in that it has an enlargement which lies immediately over the concave surface of this structure as represented in Fig. 4. The eye-spot is supposed to absorb the blue of the spectrum and in some way to stimulate the enlargement on the flagellum.

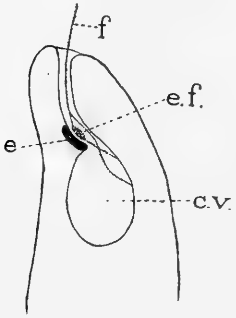


Fig. 4. Side view of anterior end of Euglena viridis, after Wager; *e*, eye-spot; *f*, flagellum; *e. f.*, enlargement in flagellum; *c.v.*, contractile vacuole.

5. The fact that the eye-spots are larger and more highly colored at the anterior end of Volvox than at the posterior, that they lose their color and become smaller in the absence of light, and that they are situated near the distal end of projections which become longer as one proceeds from the anterior end toward the posterior, and thus expose the eye-spots to more light, indicates that these structures function in light reactions.

In view of the evidences presented above in favor of considering the eye-spot as a light recipient organ, and in view of the fact that there is nothing in the structure or location which indicates that it could not function in light reactions or that it has any other function, it appears safe to conclude that Ehrenberg's idea with reference to the function of the eye-spot is correct.

Wager ('00) suggests three ways in which the eye-spot in Euglena viridis may function in light reactions: (1) It may absorb light and thus produce a change in the movement of the flagellum; (2) it may merely prevent the light rays from reaching one side of the enlargement in the flagellum, while the other side is exposed, and thus produce a difference in light intensity on opposite sides of the enlargement; or (3) it may cut off the light from one side of the sensitive portion of the anterior end of the organism when it is not oriented, and thus produce unequal illumination on opposite sides of this end.

It seems impossible to test the suggestions of WAGER experimentally, but it may be possible to arrive at a tentative conclusion concerning the matter, from what we know about the structures and reactions of these organisms. JENNINGS ('04, p. 54) shows that Euglena swims in a spiral course with the larger lip constantly farthest from the center of the spiral. In thus swimming the longitudinal axis never points toward the source of greatest illumination, so that when the organism is oriented the side of the anterior end containing the larger lip is always more shaded by the eye-spot than that containing the smaller lip (see Fig. 4). From this it seems evident that the eye-spot in Euglena does not function in accordance with WAGER'S third suggestion. That it does not function in accordance with this suggestion in Volvox is still more clearly evident, for here the eye-spots are located near the posterior surface in the projection of the zooid, so that if this projection is sensitive to light there certainly is no possibility of opposite sides being equally stimulated when the organism is oriented, for under such conditions the shadow of the pigment granule falls on the posterior surfaces while the anterior surface is fully exposed to the light. With reference to the second suggestion, it is probably true that the eye-spot does prevent the light from reaching one side of the enlargement in the flagellum in Euglena, but by referring to Fig. 4 it will be seen that the difference in light intensity thus produced on opposite sides of the enlargement must be practically the same when the light strikes the organism nearly parallel with the longitudinal axis, as it is when it strikes it an at angle from the side containing the smaller lip. If this be true, there is no change in stimulation when the organism is slightly thrown out of orientation. It therefore does not seem probable that the eye-spot in Euglena functions in accordance with the second suggestion of WAGER. In Volvox we know of no enlargement in the flagellum such as that found in Euglena, and if there were one, or some other similar structure, the criticism offered above with reference to Euglena would hold here also.

in the direction of rotation is caused by contact stimuli at all it must be by contact stimuli along the sides of the colonies.

Volvox colonies were subjected to such stimuli by laying a glass slide into an aquarium containing filtered water about 3 mm. deep, so that the edge of the slide made an angle of about 45 degrees with the rays of light. When the colonies moved toward the source of light and came in contact with the slide, the point of contact was not at the anterior end but some little distance from it. After being thus stimulated they immediately turned from the slide making an angle of about 95 degrees with their previous course. Then they gradually turned toward the source of light again and thus continued along the edge of the slide making a zigzag path. In following along the edge in this way they frequently came in contact with the slide before they were perfectly oriented and were consequently stimulated at a point further from the anterior end than usual, sometimes about midway between the two ends. In all these reactions the direction of rotation was seldom changed. It is therefore clear that a single contact stimulus on the side of a colony, which does not obstruct forward progress, does not cause reversal in the direction of rotation. In the experiment just referred to a small portion of one of the upper corners of the slide was slivered off, making an incline on which the water became gradually more shallow until, at the upper end, it was not deep enough for the larger colonies to swim without difficulty. As the colonies worked up this incline, they came in close contact with the glass and the direction of rotation was frequently changed.

It may then be concluded that continuous contact stimulation on the sides causes reversal in the direction of rotation, providing the contact is such that considerable resistance is offered to forward motion.

But why should contact stimuli on the anterior end, which prevents forward motion, not cause reversal as well as similar stimuli along the sides? Considering the structure of the organism in question, it seems probable that rotation is brought about largely by an oblique stroke of the cilia along the side and that those at the ends have little if anything to do with it. Now it seems reasonable to assume that when a certain proportion of these cilia on the sides meet considerable resistance they all strike in the opposite direction and thus produce reversal of rotation. When the anterior end is in contact with an object the cilia along the sides are of course free, and if it is the action of these cilia which causes rotation we should not expect a change in the direction of rotation when the anterior end is stimulated.

As stated above, we find reversal in the direction of rotation frequent in water containing numerous small particles. What is the cause of this? This is probably due to particles becoming entangled in the cilia and obstructing their free movement, thus causing a change in the direction of rotation.

While we have thus found that reversal of rotation is largely caused by external agents, it is unquestionably true that it depends to some extent upon the condition of the organism itself, for under similar external conditions difference in the frequency of reversal was repeatedly noted.

### 6. ORIENTATION—GENERAL DISCUSSION.

It is well known that if Volvox is subjected to light of moderate intensity, it swims toward the source of light; but if the light intensity is high, as *e. g.*, direct sunlight, it travels in the opposite direction. In casually studying such movements it appears as if the course of the colonies in either direction were nearly parallel with the light rays, and investigators have, in general, assumed this to be true. HOLMES ('03, p. 320), writes: "It is easy to determine that *Volvox* orients itself, and that very accurately, to the direction of the rays of light. If specimens of *Volvox* are taken into a dark room and exposed to the light from an arc lamp they travel towards the light in almost a straight course, swerving remarkably little to the one side or the other. They will often travel a foot without deviating as much as a quarter of an inch from a perfectly straight course."

In studying the effect on the direction of movement, of difference in light intensity on opposite sides of a Volvox colony, I accidentally discovered that, contrary to HOLMES' conclusion, Volvox very seldom orients "accurately to the direction of the rays." The colonies do, of course, swim toward or from the source of light in a general way; but movement parallel with the rays is quite the exception. In swimming toward a source of light the colonies may deflect not only to the right or left but also up or down. Deflection up or down will be discussed under the effect of gravitation on orientation (p. 122); deflection to either side will be taken up in connection with the description of the following experiments.

Most of these experiments were performed in an apparatus which I have called a "light grader." I have given a detailed description of this apparatus in another paper (Mast '06, p. 364). The important features of the apparatus will be readily understood, however, by referring to the accompanying figure.

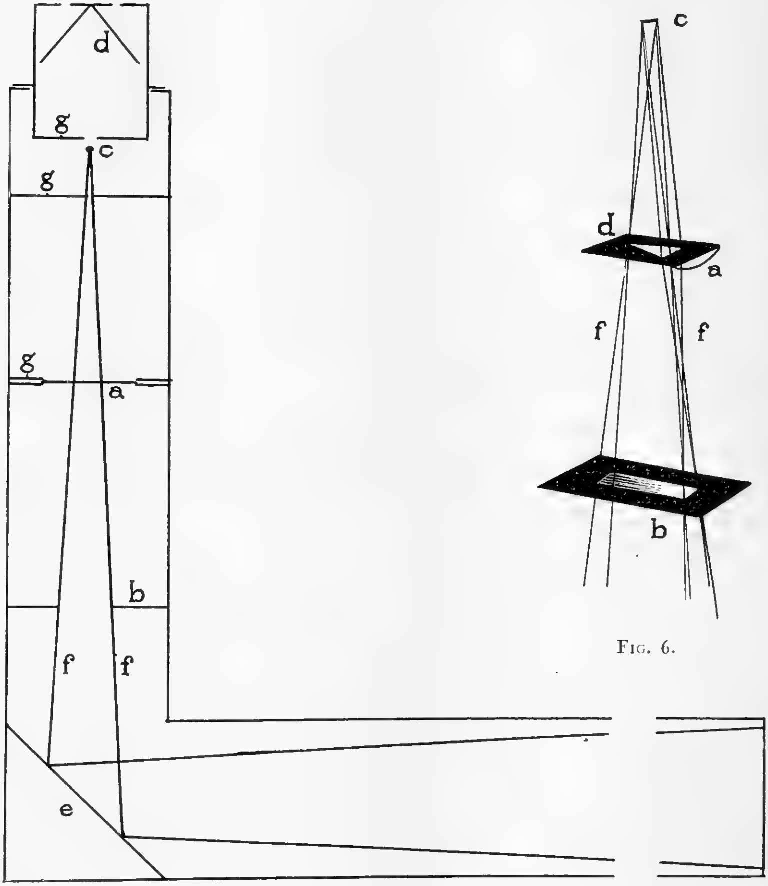


Fig. 6.

Fig. 5.

Fig. 5. A vertical section of the light grader. The lens (*a*) which is a segment of a cylinder has its longitudinal axis lying in the plane of the section; *b*, stage; *c*, Nernst glower; *d*, non-reflecting background; *e*, mirror; *f*, light rays; *g*, opaque screens. Distance from glower of lamp to stage, one meter.

Fig. 6. Stereographic view of light, lens, and image; *a*, lens; *b*, field of light produced by the image of the glower (*c*); *d*, opaque screen which lies flat on lens and contains a triangular opening which causes a gradation in the light intensity of the field (*b*).

An aquarium[1] 15 cm. long, 8 cm. wide and 8 cm. deep inside was placed at one of the principal foci in the light grader, which was in a horizontal position and so arranged that the Nernst glower at the other principal focal point was vertical. The light rays passed through the aquarium practically parallel with each other and the bottom of the aquarium and perpendicular to the sides. An opaque light screen, containing a rectangular slit 10 mm. wide and 13 cm. long, was fastened to the side of the aquarium nearest the light, so that the lower edge of the slit was on a level with the bottom and the ends of the slit were 1 cm. from either end of the aquarium. Filtered water was poured into the aquarium to such a depth that its surface was above the upper edge of the slit and was consequently in darkness. Since the rays were practically parallel with the bottom and perpendicular to the sides of the aquarium, it is evident that reflection from the water surfaces was practically eliminated. The light which passed through the aquarium was largely absorbed by the wall of the dark room which was over seven meters from the light grader, and since this was the only light which entered the room it is safe to conclude that the direction of movement of Volvox in the aquarium was influenced only by rays direct from the Nernst glower.

By placing an opaque screen containing a triangular opening over the cylindrical lens in the light grader, a field of light is produced which becomes gradually less intense from one end to the other (MAST '06, p. 364). If Volvox is allowed to swim toward the source of light in such a field it is evident that one side of the colonies will be more strongly illuminated than the opposite, and if difference in light intensity on the two sides, regardless of ray-direction, determines the direction of movement we should expect the organisms to move at an angle with the direction of the rays of light. This was found to be true, as will be shown later (pp. 136-141).

The first series of experiments made to ascertain the effect of difference in intensity on orientation was performed in the light grader, arranged as described above, by carefully introducing about one hundred colonies into the aquarium at a fixed point

---

[1] The aquarium was made of the best plate glass obtainable, accurately cut and ground, and cemented with Canada balsam boiled in sufficient linseed oil to give it the desired consistency. This cement proved very satisfactory, much more so than any other of several tried. Balsam in xylol is good but it becomes so brittle on drying that it breaks readily. Linseed oil prevents this.

near the side farthest from the light. In some conditions, the colonies thus introduced, proceed across the aquarium nearly parallel with each other, spreading but little, frequently not more than five or six millimeters. In other conditions, however, they spread out as much as three or four centimeters. By laying a straight wire on the aquarium and constantly keeping it over the middle of the group of colonies as they proceeded on their way, the average course was quite accurately ascertained. The course under most conditions, although at a decided angle with the rays, was remarkably straight; but under some conditions it curved considerably as the organisms approached the side of the aquarium nearest the light. The paths produced and the direction of the rays were transferred to paper by means of a miter square; and thus the angle of deflection was recorded for future reference.

Between August 20 and 30, 1904, seventy-three paths observed under the conditions described above were recorded, and many more were observed. In nearly all of these cases the colonies deflected strongly to the left, frequently making an angle of 45 degrees with the light rays, and rarely less than 5 degrees. This deflection to the left was brought out in a striking way, by putting the Volvox colonies into the aquarium a few centimeters to the right of the left edge of the light area. When introduced at this point, they soon reached the plane between light and shadow and passed into the dark area without any apparent change in their course. After they had traveled in the dark region some little distance they rose, deflected more sharply to the left, and frequently made a small circle or spiral and entered the light region again.

This deflection to the left in the light area was, of course, thought to be due to the fact that the light was graded in intensity, the more intense end of the field being to the right. It was accidentally discovered, however, that similar deflections were produced when no lens was used, and later it was found that when the screen over the lens was inverted so as to make the left end of the field the more intense instead of the right as in the previous experiment, the Volvox colonies still deflected to the left. It was therefore clear that this deflection was not due to difference in light intensity on opposite sides of the organisms.

One hundred and one additional paths were observed and recorded between July 18 and August 3, 1905. Some of these observations were made in the light grader; others outside. In many cases a single colony was selected and its course studied, in place of that of a number of colonies in a group. To my surprise, I found that whereas during the preceding season, 1904, Volvox colonies deflected, with scarcely an exception, to the left, they now deflected to the right more often than to the left. We shall consider the cause of this somewhat in detail later. In all I have records of 174 paths, only a few of which were observed in light of uniform intensity. Seventy-eight of them deflect to the left from 2 to 45 degrees; seventy-five deflect to the right from 2 to 45 degrees; and only twenty-one are found in the area between 2 degrees to the right and 2 degrees to the left, and very few of these are parallel with the rays.

In these experiments, however, only deflections to the sides were recorded; it is important to note that marked deflection up or down was also to be observed. It becomes clear then, that the colonies which appeared to be moving nearly parallel with the rays when seen from above, were in all probability slowly ascending or descending as they proceeded toward the source of light.

The cause of deflection—the inability to orient accurately—is complicated. The direction of movement in Volvox is affected by internal as well as by external factors. The effect of some of these factors on orientation or deflection will be discussed under the following headings: (*a*) Effect of internal factors on orientation; (*b*) Effect of light intensity on orientation; (*c*) Effect of gravitation on orientation; (*d*) Effect of contact stimulation and rotation on orientation.

### *a. Effect of Internal Factors on Orientation.*

If a number of Volvox colonies, varying in size, are put into the aquarium at the same time and allowed to swim horizontally toward any concentrated source of light, it will be seen that the larger colonies, especially such as contain numerous daughter-colonies, soon collect along the right side of the group, and the smaller ones, and such as contain only very small daughter-colonies along the left side. In some experiments there was such striking difference between the deflection of different colonies in a group that two distinct columns were formed, which moved across the aquarium at quite a definite angle with each other. The right column in such cases invariably contained most of the larger colonies, and the left most of the smaller ones.

On July 26, 1905, the paths of two such diverging columns, observed in light of uniform intensity, were recorded. The one containing the larger colonies deflected to the right, making an angle of nine degrees with the light rays, while the one containing the smaller colonies deflected to the left, making an angle of fifteen degrees. Both columns, however, sometimes deflect to the right or to the left of the light rays.

Deflection then varies with different periods in the life of the colonies; but it also depends upon the physiological state of the organisms, as is shown by the following observations.

In the morning, after being in the aquarium all night, Volvox colonies were repeatedly found lying on the bottom, apparently perfectly quiet. They were in a state which may be termed dark rigor. When light is thrown on them while they are in this condition, they do not respond at once. After a time, however, they begin to swim about, slowly at first, without orienting; but soon, more rapidly, until they become normally active, and move toward the light. Apparently there is a certain chemical change necessary to bring the organisms out of the state of dark rigor into such a condition that they can respond readily to light; and this change appears to be induced by light. The production of carbon dioxid in darkness suggests itself as the probable cause of dark rigor.

When a colony, after having been in darkness all night, first begins to respond to light, it moves toward the surface of the water and deflects strongly either to the right or left as it proceeds toward the source of light. But if it be made to cross the aquarium several times in succession, it is found that the deflection gradually decreases until it has traveled 25 to 30 cm. Then it reaches an apparently stable condition; and on the following trips it takes a fixed course which may be at almost any angle with the light rays, but is usually at an angle of from 5 to 10 degrees. Such reactions were observed many times, mostly in experiments performed for other purposes. The following detailed experiment is typical.

On August 7, 1905, Volvox was collected at 6.15 a. m. and left in total darkness until 8.30 a. m., at which time the colonies were still moving about, but very slowly. One of them was put into the aquarium in the light grader in a light intensity of nearly 400 candle meters. This colony moved about irregularly at first and deflected strongly to the right, but it soon became more active and moved quite rapidly toward the light. On its first trip across the aquarium it deflected to the right 17 degrees, on its second trip 15 degrees, and on its third trip 11.5 degrees. The following thirty trips were made with so little deviation from 11 degrees that it could not be measured. The experiment was closed at 10.45 a. m., two hours and fifteen minutes after it was begun.

It appears, then, that when the internal factors have become stable, and the external factors are not changed, the angle of deflection remains constant.

### *b. Effect of Change in Light Intensity on Orientation.*

In general a decided increase or decrease in light intensity causes an increase in deflection. This seems to be connected with the fact, pointed out by HOLMES ('03, p. 321), that in low or high light intensity the colonies are not strongly positive.

On August 3, 1905, the relation between the course of a given colony and the ray direction was obtained in a light intensity of 400 candle meters and also in an intensity of 20 candle meters. In the higher intensity, the deflection to the left was found to be 1 degree; in the lower intensity 11 degrees. The course was ascertained by letting the colony across the aquarium three times in succession in the lower intensity, then three times in the higher, then twice in the lower, and finally twice in the higher. The light intensity was reduced by cutting off part of the light with a screen, which contained a narrow slit, placed close to the Nernst glower, and so arranged that the slit was perpendicular to the glower. Neither the light nor the aquarium had to be touched in decreasing or increasing the light intensity, so the ray direction was unquestionably the same under both conditions. There was remarkably little variation in the angle of deflection in all the trips made across the aquarium in either light intensity. There can thus be no question about the accuracy of these observations. This experiment was repeated a few days later with similar results. The colony selected, however, deflected to the right instead of to the left, as the one in the first experiment had done. The deflection in the second experiment was studied in three different light intensities: 20 candle meters, 400 candle meters and nearly 2000 candle meters. The highest intensity was produced by a carbon arc. The angle between the light rays and the course taken by the colony was found to be 12 degrees in 20 candle meters intensity; 2 degrees in 400, and 40 degrees in 2000.

Moderate increase or decrease in light intensity does not appear to affect the degree of deflection, *e. g.*, the path of a given colony in a light intensity of 400 candle meters was found to be so nearly the same as that of the same colony in an intensity of 100 candle meters that the difference could not be measured. From numerous experiments, it appears that in order to influence deflection, the increase or decrease in intensity must be great enough to affect the positiveness of the organism; that is, the intensity must be decreased to somewhere near the threshold or increased to near the optimum. Now the threshold and optimum in different colonies, and in the same colony under different conditions, vary extremely. It is therefore to be expected that the effect of variation in intensity on deflection varies much. This was found to be true experimentally.

The above discussion on the effect of change in light intensity on deflection might lead one to assume that all Volvox colonies could be made to move parallel with the rays, if the proper light intensity were used. This, however, was not found to be true. To bring about such a reaction, not only the proper light intensity is necessary, but the organisms must also be in a certain physiological state. Immediately after taking colonies from darkness or very intense light in which they have been for some time, they are in such a condition that no light intensity was found in which they travel parallel with the rays. And many colonies under various other conditions could not be made to swim parallel with the rays. In the above discussion deflection up or down is not considered; by parallel we mean merely without lateral deflection.

### *c. Effect of Gravitation on Orientation.*

If Volvox is killed in formol and then transferred to water, it gradually sinks to the bottom, showing that its specific gravity is greater than one. When first dropped into the water there is, of course, no indication of orientation; the longitudinal axis of the different colonies point in all directions, but as they sink, it is soon found that their axis becomes approximately perpendicular, *i. e.*, the colonies become oriented with the anterior end up. Such orientation is especially marked in organisms which contain numerous daughter-colonies, but it is apparently accidental or absent in those without. Since the colonies are dead this orientation can be brought about only by a difference in the specific gravity of the anterior and the posterior half of the body, and since this orientation to gravity is definite only in specimens containing daughter-colonies it is evident that the daughter-colonies, located as they are mostly in the posterior half of the body, render it heavier than the anterior half.

The specific gravity of living Volvox is also greater than one. If the colonies become inactive they sink to the bottom, and it is undoubtedly due to this that they are frequently found lying quietly on the bottom of the aquarium after being in darkness all night. The fact that the specific gravity of living colonies is greater than one and that the posterior end of those which contain daughter-colonies or spores is heavier than the anterior end, has an important bearing on orientation to light and the direction of motion.

It is owing to the difference in weight of the two ends, that the anterior end turns up, if for any reason the forward motion of a colony ceases. In this position the colonies are frequently found in very dim light, apparently hanging in the water motionless. If they become active while in this position, they swim upward. Such activity may be induced by light so dim that the organisms do not orient. The degree of activity in light of low intensity, without doubt, depends upon the physiological state of the organism, for it was frequently noticed that many colonies did not become quiet in darkness, and several times after exposure to darkness for as long as four or five hours, a large majority was found at the surface of the water, apparently clinging to the surface film.

If horizontal movement of Volvox colonies toward a given source of light is observed from the side instead of from above, as was customary in the experiments described in the preceding pages, it can be clearly seen that the longitudinal axis of most of the specimens forms a decided angle with the bottom of the aquarium, that is, the posterior end is lower than the anterior. This angle varies from zero to 90 degrees. Contrary to the observations of KLEIN ('89, p. 169), it was found to be larger in organisms which contain numerous daughter-colonies and spores than in those which do not contain these structures. It is therefore in all probability caused by the difference in weight of the two ends.

The angle which the axis makes with the bottom of the aquarium varies also with the light intensity. The more strongly positive a given colony is, the smaller the angle; but the positiveness of

Volvox depends upon the light intensity, as was shown above (p. 121). Light, therefore, under the seconditions, tends to keep the axis horizontal, while gravitation tends to keep it vertical.

In traveling horizontally toward a source of light, then, the axis of Volvox is not parallel with its course, but if the light is suddenly decreased in intensity, as was repeatedly done, the colonies change their course and start in the direction in which the axis points. This seems to indicate clearly that they *tend* to travel in a direction parallel with the longitudinal axis. Now when they are strongly positive the axis becomes nearly horizontal and they consequently tend to move horizontally toward the source of light, but the force of gravity keeps pulling them down so that when the colonies are strongly positive they move toward the light very near the bottom of the aquarium. This was observed many times. If they are oriented in a beam of light thrown through the aquarium at some distance from the bottom, they soon sink out of the region of light into the darkness, but as soon as they get into the dark region gravity causes their longitudinal axis to take a vertical position and they swim upward again, unless darkness produces inactivity and thus causes them to sink slowly to the bottom. Thus they were frequently seen, while swimming across the aquarium, to pass from light down into darkness and back into the light again several times. If the specimens are not strongly positive the inclination of the axis toward the horizontal is not great, and they therefore tend to swim toward the surface. This upward tendency may be just sufficient to compensate the effect of gravity, and if so, the colonies appear to be moving parallel with the rays when viewed from the side. Under these conditions specimens were frequently seen to swim across the aquarium with very little deflection upward or downward.

In summing up, we find that when the colonies are strongly positive to light, the deflection to the side is reduced to a minimum, but owing to the effect of gravitation the downward deflection is marked; and when they are not strongly positive the deflection to the side is marked, while the vertical deflection may be practically zero. Thus it becomes evident that accurate orientation in horizontal movement is indeed exceptional.

If gravitation tends to keep the longitudinal axis of Volvox vertical with the anterior end directed upward, and light tends to keep it parallel with the rays with the anterior end directed toward the source of light, and if the colonies tend to travel parallel with the axis, we should expect them to move parallel with the rays, when the rays are vertical and the source of light is above. This was found to be approximately true, as is shown by the following experiment.

On August 8, 1905, the plate glass aquarium was nearly filled with filtered water and put upon the stage of the light grader which was so arranged that the rays were vertical (see Fig. 5). A number of colonies were then put into the aquarium with a pipette and set free near the bottom in a beam of light, which was uniform in intensity and two and one-half centimeters square in cross section. After swimming upward to the surface of the water, some of the colonies wandered out into the shaded region. These could readily be forced to swim down again by reflecting the beam of light upward through the aquarium slightly to one side of the illuminated area produced by the light direct from the glower. The reflected beam could be made vertical by tipping the light grader so that the direct beam of the light made an angle of about 10 degrees with the vertical. In this way movements both upward and downward were studied.

In swimming up Volvox was found to travel very nearly parallel with the light rays, taking a spiral course, which was in some instances at least 2 mm. wide. In thus traveling upward, it could be clearly seen that the anterior end described a larger circle than the posterior, which in many colonies appeared to go almost in a straight line. The anterior end appeared to swing about the posterior as a pivot. While a large majority of the colonies traveled nearly parallel with the rays, there were a few which deflected considerably, some to such an extent that they passed out of the beam of light before reaching the surface of the water. That the movement parallel with the rays was due to the harmonious interaction of gravitation and light, and not to especially favorable conditions of light intensity, was demonstrated by the course of a certain colony in traveling upward toward the source of light parallel with the direction of the force of gravity, and then again in movement perpendicular to this force. When moving parallel with the direction of the force of gravity, the colony observed did not deflect more than one degree in making several trips up through the water in the aquarium, but in moving perpendicular to this force in the same aquarium and in the same light intensity, this same colony deflected 30 degrees to the right.

In swimming downward there is no evidence of a spiral course, the path, however, is much more irregular than in swimming upward; colonies on their way down were frequently seen to swerve to one side as if about to turn and go in the opposite direction. Gravitation, as has been stated, tends to keep the longitudinal axis vertical with the anterior end up, but the light from below, under the conditions of the experiment, tends to orient the organisms with the anterior end down. It is the interaction of these two opposing directive forces which brings about the swerving reaction and the irregularity in the downward course. If the light is weak its directive influence is not as strong as that of gravitation, and many colonies may be seen oriented with the anterior end up. The downward movement of specimens in this position is very slow compared with that of those with the anterior end directed down. This is evidently the result of the effect of gravity and a tendency to swim upward, *i. e.*, in the direction which the anterior end faces.

The rate of movement varies greatly in different colonies under the same external conditions. It is, however, in general, much faster toward a source of light with the force of gravitation than against it. This is shown by the following results. The time required for each of three specimens to swim downward 8 cm. toward a source of light, in a given intensity, was found to be 40 seconds for one, 32 seconds for another, and 30 seconds for the third. That required to swim up toward the light in the same intensity, was 100 seconds, 80 seconds, and 66 seconds, respectively, an average of 48 seconds longer to swim upward 8 cm. than to swim the same distance downward. It is very probable that the activity of Volvox in swimming upward is just as great as it is in swimming downward and that the difference in rate is entirely due to its specific gravity.

In summing up this whole matter we find: (1) That Volvox tends to move in a direction parallel with its longitudinal axis; (2) that gravity tends to keep this axis vertical, with the anterior end up, but owing to stimulation by light the organisms tend to orient with the anterior end facing in the direction of strongest illumination; (3) that Volvox travels very nearly parallel with the rays in moving up toward a compact source of light, but that it very rarely moves parallel with the rays in swimming downward or horizontally toward a source of light; (4) that in reacting to light it almost always deflects upward or downward, or to the right or left, and that these deflections depend upon the light intensity and the physiological conditions of the organisms; (5) that it deflects most in moving horizontally when its axis is most nearly vertical and that the axis becomes most nearly vertical when the organism is not strongly positive.

In swimming downward toward a source of light, the deflections are clearly due to a tendency of the organism to orient in the direction of the force of gravity with the anterior end directed upward. In swimming horizontally it is clear that the downward deflection is due to the specific gravity of the organism, and the upward deflection to the tendency to swim parallel with the axis. The cause of lateral deflection in such movement is, however, not so evident.

Colonies swimming horizontally toward a single source of light, tend, as stated, to take a position such that the axis is parallel with the rays and the zooids on all sides are equally illuminated. If the organisms are strongly positive, the axis is nearly horizontal, so that if they turn to the right or left, one side immediately becomes shaded and thus causes a reaction which tends to keep the direction of movement parallel with the rays. But if the colonies are not strongly positive, the axis is more nearly vertical, and while they are in this position there is already a difference in light intensity on opposite sides, so that if the organism now turns to the right or to the left, this intensity difference is only slightly changed. There is consequently but little cause for reaction and therefore nothing to prevent movement at an angle with the rays. Since lateral deflection has been observed to be greater the more nearly vertical the axis, it seems probable that this is a valid explanation of the cause of such deflection. But how is it that a colony can repeatedly travel across an aquarium, making the same angle with the light rays each time; or that when the position of the source of light is changed, after it has started on a course at a given angle with the rays, it changes its course until the new one has the same angle? The only explanation I have to offer is the following: If colonies in water only a few millimeters deep, are simultaneously and equally illuminated from above and from below, they do not move in straight lines but in curves, frequently making continuous complete circles to the right or to the left. They therefore seem to have a tendency to swim in curves. I am unable to account for this. But if it is true, their path (as seen from above) in traveling horizontally toward a source of light, must be the resultant of the directive force of the light and the tendency to swim in curves. This would necessarily result in movement at an angle with the light rays. The size of this angle would depend upon the relative efficiency of the directive force of the light and the tendency to swim in circles. If the organisms are strongly positive, the directive force of the light is strong compared with the tendency to move in curves and the angle becomes small. But if they are not strongly positive, the directive force of the light is relatively weak and the angle becomes large. The theoretic results thus formulated are in accord with the experimental results described in the preceding pages.

### *d. Effect of Contact Stimulation and Rotation on Orientation.*

When colonies of Volvox come in contact with the side of the aquarium nearest the light and the rays are perpendicular to this side, many of them soon begin to drift to the right along the glass wall, and in a short time a large majority are found in the right hand corner of the aquarium nearest the source of light. This movement to the right takes place in a field of graded light as well as in light of uniform intensity, and it is apparently as marked if the intense end of the field is to the left as it is if this end is to the right. Thus the organisms were frequently seen to move along the wall toward the right, on the one hand, into regions gradually decreasing in intensity until they passed into darkness and, on the other, into regions gradually increasing in intensity until they became negative. The movement to the right along the wall takes place, with much greater regularity, however, in specimens containing large daughter-colonies or spores than in young colonies. Indeed it is doubtful whether more of the young colonies turn to the right than to the left after they reach the wall of the aquarium. At any rate shortly after the introduction of a group containing both large and small colonies, practically all the large colonies, together with some small ones, have gathered in the right hand corner, some small ones have collected in the left hand corner, and a few of both kinds usually remain scattered along the entire side. What is the cause of this movement to the right along the wall?

After reaching the wall the colonies ordinarily remain with the anterior end in contact with it for some little time, but sooner or later the posterior end begins to settle, the longitudinal axis becomes nearly vertical, and the organism begins to swim upward along the wall, deflecting to the right. The angle of deflection varies greatly. Some colonies travel nearly parallel with the bottom at once; others swim nearly straight upward. During the time that the anterior end is in contact with the wall, the colonies usually rotate counter-clockwise without reversal, and rotation in this direction frequently continues during the whole process of turning and moving to the right. It is, therefore, clear that the drifting to the right along the wall is not due to change in the direction of rotation.

After the axis becomes nearly vertical the colonies sometimes remain in close contact with the wall but continue to rotate counter-clockwise without moving forward, and thus roll along the wall to the left. Frequently after thus moving along the wall a short distance, the anterior end turns to the left and the organism begins to swim forward, but still continues to roll on the wall. This rolling along the wall, together with the effect of gravity, soon carries it to the bottom of the aquarium, where it apparently becomes lodged in the angle between the bottom and the side. Here it remains for a time, but sooner or later works its way out, usually by swimming back from the wall a short distance, after which it turns and soon comes in contact with the wall again. A colony may, as is clear from what has just been said, turn either to the left or to the right after reaching the wall, but many of those which turn to the left are prevented from continuing on their course by the effects of rotation and gravitation, as explained above; and since those which turn toward the right are not thus prevented from continuing, the result is, of course, a general drifting of the colonies in this direction. But as a matter of observation a much larger proportion of colonies turn to the right than to the left shortly after they reach the wall, so that general movement to the right cannot be primarily brought about by the prevention of continuous movement to the left. Neither can it be due primarily to the direction of rotation, for many colonies were repeatedly seen to deflect to the left in swimming across the aquarium toward the source of light, and then to the right, after coming in contact with the wall, without changing the direction of rotation. It seems then that the tendency to turn to the right after reaching the wall must be due primarily to contact stimuli. As evidence in support of this view I present the following experiments:

On August 10, 1905, between 20 and 30 colonies were put into the aquarium into an intensity of 21 candle meters. When the rays were parallel with the bottom the group spread very little and swam across the aquarium nearly parallel with the rays. But when the glower was lowered so that the rays passed up through the glass bottom of the aquarium, making an angle of 25 degrees with it, the group spread out considerably and the majority deflected quite sharply to the right. The largest colonies were found along the right side of the column and the smallest along the left, under both conditions. It is doubtful whether the smaller colonies changed their course after the position of the glower was changed, but the larger ones certainly did. Later more definite results were obtained by experimenting with a single colony. The specimen selected was of medium size and contained quite a number of rather small daughter-colonies. When the rays were parallel with the bottom this colony deflected three degrees to the right, but when the light was below the level of the bottom and came up through it so that the rays made an angle of 25 degrees with it, the organism deflected 19 degrees in the same direction.

In ascertaining these deflections the colony was allowed to cross the aquarium a few times first with the rays parallel with the bottom, then with the rays at an angle of 25 degrees with it, then again with the rays parallel with it, and finally, with the rays at an angle of 25 degrees. The deflection during the various trips under each condition, was nearly constant. It is therefore certain that the increase in deflection was not due to a possible change in the physiological condition of the organism. Neither was it due to difference in light intensity, for the strength of illumination was nearly the same under the two conditions of the experiment, and deflection is not much affected unless there is very marked change in the intensity of the light (see p. 122).

In moving toward the light in rays parallel with the bottom, the axis of this colony was at an angle of about 12 degrees with the bottom. The organism moved near the bottom of the aquarium so that the posterior end appeared to be slightly in contact with it. But when the light came from beneath at an angle of 25 degrees the axis of the colony was nearly horizontal and the organism moved so near the bottom that the cilia must have come in close contact with it. As the specimen thus swam across the aquarium the axis could be clearly seen to swing at short intervals, from a position nearly parallel with the general direction of motion to a position nearly perpendicular to it. This swinging of the axis, it is thought, was due to contact with the bottom and counter-clockwise rotation, owing to which the posterior end seemed to roll to the left more rapidly than the anterior. This appeared to turn the anterior end of the axis sharply to the right, and since the colonies tend to move parallel with their axis, it would cause deflection to the right. Some such reaction must be at the basis of the deflection to the right when the organism is in contact with the vertical wall nearest the light. It may also explain why the larger colonies are found to deflect more to the right than the smaller, since the specific gravity of the two is different.

I have discussed the cause of the movement of Volvox to the right along a vertical wall at some length because of its importance in the study of the reactions of the colonies in aggregating in regions of optimum intensity in graded light, which will be taken up later.

### 7. ORIENTATION TO LIGHT FROM TWO SOURCES.

In the preceding pages we have conclusively demonstrated that while Volvox moves in general toward a given source of light, it seldom travels parallel with the rays, excepting when they are vertical, and it swims upward. But while the colonies do not usually swim parallel with the rays they still orient in a definite way. That is, if a colony is swimming at a given angle with the rays and the source of light is moved, it so changes the direction of motion that its course again makes the same angle with the rays that it did before the position of the source of light was changed. What is the cause of orientation?

OLTMANNS, as has been stated (p. 100), came to the conclusion that difference in light intensity is the principal cause of orientation of Volvox, but he presented no direct evidence in favor of this view, and his indirect evidence is based upon experiments which have since been proved to be defective. HOLMES was not able to explain orientation by assuming difference in light intensity on opposite sides of the organism to be the cause, and he is inclined to believe that it is due to the direction of the rays. He writes ('03, p. 324): "It seems not altogether improbable that light in passing through a nearly transparent organism like *Volvox* exercises a directive effect upon its movements, in a similar way, whatever it may be, to that produced by the current of electricity.

The direction of the ray may be the important factor in orientation irrespective of difference of intensity of light upon different parts of the organism, as has been maintained by SACHS for the phototropic movements of plants. I am not ready to adopt the theory of SACHS, but I feel that it is a view that is not entirely out of court."

The following experiments on the movement of Volvox when exposed to light from two different sources, and on the orientation of Volvox in light graded in intensity seem to me to settle this question conclusively.

On August 18, 1904, a single 222 volt Nernst glower was fixed in a vertical position 70 cm. from the middle of the plate glass aquarium, so that the lower end of the glower was level with the bottom of the aquarium and the rays perpendicular to the side at a point 4 cm. from one end. A single 110 volt glower was arranged like the 222 volt glower, but in such a position that the light rays were perpendicular to the end of the aquarium at the middle and, therefore, perpendicular to the rays from the 222 volt glower at a point 4 cm. from the end, and half way between the two sides, as represented in Fig. 7. The 222 volt glower was stationary, but the 110 volt glower could be moved to any desired distance from the aquarium. These glowers were both carefully screened so that the only light which escaped passed through a rectangular slit a trifle larger than the glower. The side and end of the aquarium facing the glowers was also screened, with the exception of an opening one centimeter wide and six centimeters long, at the bottom of the aquarium, as indicated in Fig. 7. The aquarium contained thoroughly filtered water 1.5 cm. deep. Thus, practically all reflection from the sides of the aquarium and the surface of the water was eliminated.

The direction of movement of Volvox was ascertained, first with the 222 volt glower exposed alone, then with both glowers exposed, the 222 volt glower 66 cm. from the side, and the 110 volt glower 24, 49, 99, and 199 cm. from the end of the aquarium. In order to ascertain the direction of motion under the various light conditions, a considerable number of colonies were carefully dropped into the corner of the light area farthest from the glowers. Among the specimens used in this experiment there were about as many that deflected to the right as to the left, so that when one glower only was exposed the center of the group of colonies moved across the aquarium practically parallel with the light rays. Several trials were made under each light condition and each path, as recorded in the table below and in Fig. 7, is the average of several such trials. There was, however, surprisingly little variation in the direction of motion of different groups when subjected to the same light condition. The light intensity was measured with care. Both glowers were on the same circuit so that variation in voltage could not have affected markedly the relative intensity of the light from the two sources. There can thus be no question about the approximate accuracy of the experiments, the results of which will be readily understood by referring to Table I, in connection with Fig. 7.

TABLE I.

| I. | II. | III. |
|---|---|---|
| 82.4 candle meters. | .0 candle meters. | 0 degrees. |
| 82.4 candle meters. | 6.0 candle meters. | 9 degrees. |
| 82.4 candle meters. | 23.5 candle meters. | 25 degrees. |
| 82.4 candle meters. | 89.0 candle meters. | 47 degrees. |
| 82.4 candle meters. | 318.8 candle meters. | 59 degrees. |

Table I represents the effect of light from two sources on the direction of movement of Volvox. Column I gives the light intensities at the middle of the light area in the aquarium, which were produced by the 222 volt glower under the five different conditions. Column II gives light intensities produced by the 110 volt glower, and column III the angles between the rays produced by the 222 volt glower and the course taken by the organisms under the different light conditions.

In these five experiments the direction of the rays from the two sources of light was practically constant, but the direction of movement of the Volvox colonies varied 50 degrees. This variation was certainly not primarily due to any influence of the ray direction; for when the relative intensity of light affecting different sides of the organism was changed the orientation changed, though the direction of the rays remained the same. It can, therefore, be considered fully demonstrated that *difference in light intensity on different sides of the colonies may determine orientation independently of the direction of the rays.* Additional proof of this conclusion will be given later, in experiments of a different character.

This conclusion is not in harmony with the dictum of LOEB, repeatedly expressed in a recent work (1905), in which he writes, "It is explicitly stated in this and the following papers that if there are several sources of light of unequal intensity, the light with the strongest intensity determines the orientation and direction of motion of the animal. Other possible complications are covered by the unequivocal statement, made and emphasized in this and the following papers on the same subject, that the main feature in all phenomena of heliotropism is the fact that symmetrical points of the photosensitive surface of the animal must be struck by the rays of light at the same angle. It is in full harmony with this fact that if two sources of light of equal intensity and distance act simultaneously upon a heliotropic animal, the animal puts its median plane at right angles to the line connecting the two sources of light. This fact was not only known to me but

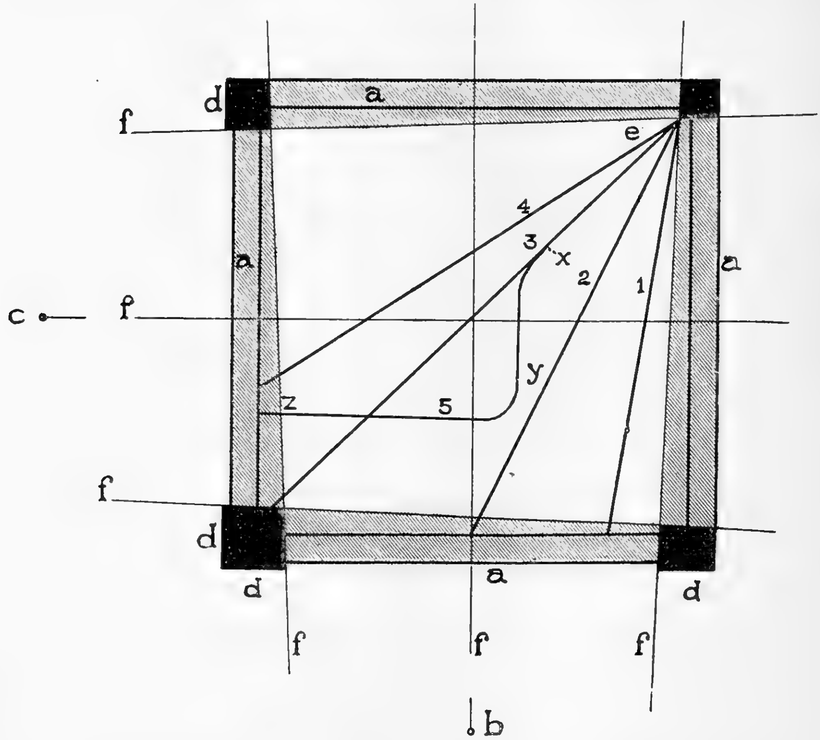


Fig. 7. Representation of the direction of movement of Volvox when subjected to light from two sources. *a*, plate glass aquarium 8 cm. long and 8 cm. wide; *b*, 222 volt Nernst glower, 66 cm. from aquarium (distance from aquarium constant); *c*, 110 volt glower, (distance from aquarium variable); *d*, screen; *e*, point of introduction of Volvox; *f*, direction of light rays; 1, 2, 3, and 4, courses of Volvox exposed to light from both glowers: 1, with 110 volt glower 199 cm. from aquarium; 2, with 110 volt glower 99 cm. from aquarium; 3, with 110 volt glower 49 cm. from aquarium; 4, with 110 volt glower 24 cm. from aquarium; *xy*, course of Volvox when exposed to light from glower *b* only; *y—z*, course when exposed to light from glower *c* only.

had been demonstrated by me on the larvæ of flies as early as 1887, in Würzburg, and often enough since. These facts seem to have escaped several of my critics" [p. 2]. "When the diffuse daylight which struck the larvæ [Musca larvæ] came from two windows, the planes of which were at an angle of 90° with each other, the paths taken by the larvæ lay diagonally between the two planes. This experiment was recently published by an American physiologist as a new discovery to prove that I had overlooked the importance of the intensity of light!" (p. 61-62). "The direction of the median plane or the direction of the progressive movements of an animal coincides with the direction of the rays of light, if there is only a single source of light. If there are two sources of light of different intensities, the animal is oriented by the stronger of the two lights. If their intensities be equal, the animal is oriented in such a way as to have symmetrical points of its body struck by the rays at the same angle" (p. 82). "Attention need scarcely be called to the fact that if rays of light strike the animal [larvæ of Limulus polyphemus] simultaneously from various directions, and the animal is able to move freely in all directions, the more intense rays will determine the direction of the progressive movements" (p. 268).

It is evident without further discussion that the reactions of Volvox do not fit the statements by LOEB, given in the above quotations. Upon what experimental evidence does he base these statements? Those with reference to orientation when the animals are subjected to light from two or more sources are based largely, if not entirely, upon the following observations: (1) "When the diffuse daylight which struck the larvæ (Musca larvæ) came from two windows, the planes of which were at an angle of 90° with each other, the path taken by the larvæ lay diagonally between the two planes." (2) "Hawk moths were brought into a room with the single window at one end, and a petroleum lamp at the opposite end. It was found that, as twilight came on, the moth flew to the window, or to the light, according to the relative intensity of the one or the other at the point where the moth was liberated."

In the first place I am unable to understand how the direction of rays can be ascertained in diffuse daylight coming through a window; and in the second place, it is certainly not difficult to see that an object placed between two windows, or between a window and a petroleum lamp, in an ordinary room, is illuminated by light rays striking it from every conceivable direction, for light under such conditions is reflected from practically all surfaces in the room as well as from those outside. Under the conditions of the experiments cited above, then, the larvæ and moths were not exposed to light from two sources but to light from an infinite number of sources, and the direction of the rays was not known. How then, can it be concluded from the results of these and similar experiments (1) "That if there are several sources of light of unequal intensity, the light with the strongest intensity determines the orientation and direction of movement of the animals;" (2) "that symmetrical points of the photosensitive surface of the animal must be struck by the rays of light at the same angle;" and (3) "that if two sources of light at the same intensity and distance act simultaneously upon a heliotropic animal, the animal puts its median plane at right angles to the line connecting the two sources of light?"

Let it be clearly understood that in the criticism of Loeb's conclusions, I do not wish to intimate, that because the reactions of Volvox or any other organism do not take place in accord with those conclusions, they necessarily cannot hold for the organisms Loeb worked with. I do, however, wish to state and emphasize that in my opinion his experimental results as quoted above, do not warrant his conclusions, even for the animals worked on, much less for all organisms which orient in light.

The experiments upon which Loeb bases his theory of orientation to a single source of light will be discused later (see p. 142).

## 8. ORIENTATION IN LIGHT GRADED IN INTENSITY.

The reaction of Volvox to light from two sources varying in relative intensity seems to me to prove conclusively that orientation is determined by the relative intensity of the light on opposite sides of the organism, while there is no evidence that the direction of the rays has anything to do with orientation in this organism except in so far as it may affect the relative light intensity on opposite sides. If, however, difference in light intensity on opposite sides of a colony can be produced with the rays of light approximately parallel, and such intensity difference affects the direction of motion, the verdict must be considered final.

By means of the light grader referred to several times in the preceding pages, I was able to subject colonies to rays which were nearly parallel but decreased in intensity from one end of the field to the other, so that when the longitudinal axes of the colonies were parallel with the rays, one side was more strongly illuminated than the other; and I found that this intensity difference did affect the direction of motion, as will be shown in the following detailed account of the experiment.

The light grader was so arranged that the Nernst glower was vertical and the rays and the long axis of the lens horizontal. The plate glass aquarium was so placed that the rays were parallel with the bottom. Now by fastening over the lens a screen, which contained an opening in the form of two truncated triangles with their apices in contact, a field of light was produced which was of high intensity at either end and gradually became lower toward the middle. Two methods were used in ascertaining the direction of movement in such a field of light.

In the first method a large number of colonies were taken up in a pipette and half of them introduced into the aquarium near the side farthest from the glower at a fixed point some distance from one end of the field, and the other half in a similar place near the opposite end. Thus the organisms in one group as they swam across the field were more intensely illuminated on the right side, while those in the other group were more intensely illuminated on the left side.

In the second method a single colony was selected and allowed to cross the aquarium toward the source of light several times, first near the right end of the field so that the lower light intensity was to the left and then near the left end of the field so that the lower light intensity was to the right. This alternating process was continued until the path in the two different positions was definitely established. The angles of deflection were read and recorded as described on p. 117. Those obtained by the first method may be found in Table II and those by the second method in Table III. The negative numbers indicate deflection to the left of the ray direction and the positive to the right.

Table IV represents the effect of difference in light intensity on deflection in graded light. The course taken by the colonies was obtained by studying the reactions of single colonies, just as in the experiments of Table III. This table shows that an increase

## TABLE II.

Light Intensity 333± candle meters.

| Angle of deflection with strongest illumination to the left. | Angle of deflection with strongest illumination to the right. | Difference in angle of deflection |
|---|---|---|
| 6° | 11° | 5° |
| 7 | 11 | 4 |
| 8 | 13 | 5 |
| 8.5 | 15 | 6.5 |
| 11 | 13 | 2 |
| 14 | 16.5 | 2.5 |
| 15 | 15 | 0 |
| 19 | 25 | 6 |
| 19 | 23 | 4 |
| 21 | 27 | 6 |
| 7.5 | 10 | 2.5 |
| 7.5 | 10 | 2.5 |
| 9 | 9 | 0 |
| 9 | 10 | 1 |
| −17.5 | −15 | 2.5 |
| −13 | −12 | 1 |
| 10 | 12 | 2 |
| 10 | 15.5 | 5.5 |
| 11 | 15.5 | 4.5 |
| 13.5 | 18.5 | 5 |
| 13.5 | 20 | 6.5 |
| 16.5 | 20 | 3.5 |
|  | Average difference | 3.6 degrees. |

## TABLE III.

Light Intensity 333± candle meters.

| Angle of deflection with strongest illumination to the left. | Angle of deflection with strongest illumination to the right. | Difference in angle of deflection |
|---|---|---|
| 3° | 5° | 2° |
| 7 | 9.5 | 2.5 |
| 0 | 2 | 2 |
| − 1 | 4 | 5 |
| − 5.5 | − 1.5 | 4 |
| 3 | 6.5 | 3.5 |
| 13.5 | 16.5 | 3 |
|  | Average difference | 3.1 degrees. |

## TABLE IV.

| Angle of deflection in 142 candle meters of light. Strongest illumination to the left. | Angle of deflection in 380 candle meters of light. Strongest illumination to the left. | Difference in angle of deflection |
|---|---|---|
| 6.5° | 4° | 2.5° |
| 8 | 9 | − 1 |
| 10 | 10 | 0 |
| 10 | 6 | 4 |
| 14.5 | 11.5 | 3 |
| −20.5 | −18 | 2.5 |
|  | Average difference | 1⅚ degrees. |

in light intensity from 142 candle meters to 380 candle meters causes an average decrease in deflection of 1⅚ degrees.

By referring to the above tables and text figures it will be noted: (1) that Volvox, in swimming horizontally toward a source of light, seldom moves parallel with the rays. There is striking individual variation in the angle of deflection, the variation in these experiments being from 16 degrees to the left to 24 degrees to the right; (2) that in a field of light graded in intensity there is a tendency to deflect toward the brighter end of the field, an average of over 1½ degrees under the conditions of these experiments; (3) that the degree of deflection in a field of light graded in intensity depends upon the strength of illumination, it being greater in a low light intensity than in a high one. A decrease in intensity from 380 candle meters to 142 candle meters without

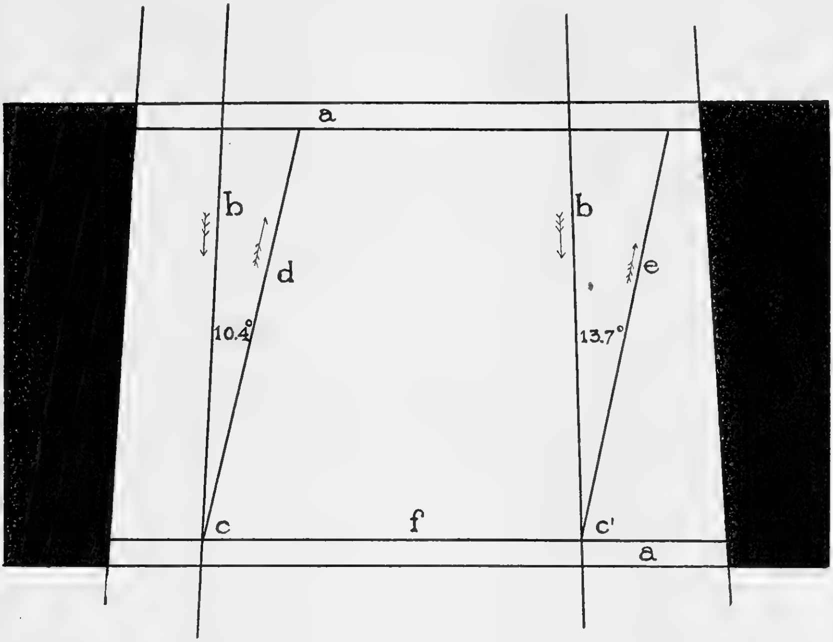


FIG. 8. Graphic representation of the total average difference in deflection due to difference in light intensity on opposite sides of the colonies, as indicated in Tables II and III. *a*, plate glass aquarium 8 cm. wide and 15 cm. long; *b*, light rays; *c*, *c'* points where the colonies were introduced; *d*, average course with the region of highest light intensity to left; *e*, average course with strongest illumination to the right. Light intensity at (*f*) the middle of field 57.12 candle meters. From the middle the intensity gradually increased toward either end where it was 442.68 candle meters. Intensity at *c*, 327 candle meters, at *c'*, 263 candle meters.

change in the grade of intensity caused an average increase in deflection of $1\frac{5}{6}$ degrees.

*Cause of Deflection Toward the More Strongly Illuminated Side in Graded Light.*—If a colony of Volvox deflects to the right in light of uniform intensity it will deflect more in a field of light graded in intensity, provided the more highly illuminated end of the field is to the right, but not as much if this end is to the left. This fact is clearly expressed in Fig. 8. Under the conditions of the experiments described above, this difference in deflection must have been primarily due to one of three factors: (1) difference in total light intensity under the two conditions; namely, with the more highly illuminated end of the field to the right and with this end to the left; (2) refraction or reflection as the light passes through the aquarium; (3) difference in light intensity on opposite sides of the colony. A discussion of these three factors follows.

1. We have demonstrated (see Table IV) that an increase in light intensity, without change of grade, causes a decrease in deflection. Now, as represented in Fig. 8, the colonies, as they deflect in crossing the aquarium with the brighter end of the field to the right, gradually pass into regions of higher light intensity, but when the brighter end of the field is to the left, they gradually pass into regions of lower intensity. This consequently tends to cause a decrease in deflection under the former conditions and an increase under the latter, but the angle of deflection is greater under the former condition than under the latter. The difference in deflection under the two conditions, therefore, cannot be due to the higher light intensity to which the organisms are exposed when the more strongly illuminated end of the field is to the right than when it is to the left.

2. As the light passes through the glass wall of the aquarium and the water in it, some is reflected and some refracted thus producing lateral rays. This reflection and refraction cannot be entirely eliminated even with the utmost precaution. May not these lateral rays have been of sufficient intensity to cause deflection toward the brighter end of the field as was found to be true in case of OLTMANNS' apparatus ?[2]

---

[2] OLTMANNS ('92) produced a field of light graded in intensity by placing a hollow prism filled with a mixture of gelatine and India ink between the source of light and the aquarium. He assumed that the rays in the aquarium were all perpendicular to the wall facing the source of illumination. This, however, is not true, for the particles of ink in the prism disperse the light before it gets into the aquarium.

The field of light in which the colonies were exposed in the above experiments was high in intensity at either end and low in the middle. In such a field of light it is clear that an organism swimming toward the light in the middle is stimulated alike on both sides, since the lateral rays necessarily come in equal numbers from both ends of the field. Consequently the direction of motion cannot be influenced by these rays. But if the organism in traveling toward the light swims nearer one end of the field than the others, the lateral rays might influence the direction of motion. If, however, the lateral rays do affect the direction of motion under such conditions, we should certainly expect to be able to detect it when all lateral rays on one side of a colony swimming toward the source of light are eliminated by shading the entire portion of the field either to the right or to the left of the colony. I repeated the above experiments many times with a portion of the field thus shaded, but was unable to detect any effect on the angle of deflection. It must therefore be concluded that the difference in deflection, represented in columns I and II of Tables II and III, was not caused by lateral rays.

THE DIRECTION OF MOTION IN VOLVOX EXPOSED TO LIGHT IS CONSEQUENTLY REGULATED BY THE RELATIVE INTENSITY OF THE LIGHT ON OPPOSITE SIDES OF THE COLONIES REGARDLESS OF THE DIRECTION OF THE RAYS.

*Cause of the Effect of Change in Intensity Upon the Degree of Deflection in Graded Light.*—The difference in intensity of illumination on opposite sides of the colonies exposed in the light grader under the conditions of the experiments just discussed, can readily be calculated. The light intensity was 442.6 candle meters at either end of the field, from which it gradually decreased toward the middle, where it was 57 candle meters. The distance from the middle to either end was 60 millimeters. We have therefore a change of 385+ candle meters in 60 millimeters or 6.4 candle meters per millimeter. The largest colonies are nearly a millimeter in diameter and the average light intensity to which they were exposed was about 333 candle meters. In the largest specimens, then, one side was exposed to an intensity of about 330 and the other to an intensity of about 336 candle meters.

If WEBER'S law holds true, as we have good reason to believe, (see p. 171), we should expect this difference in intensity on opposite sides to be more effective in weak light than in strong and we should consequently expect a greater deflection in regions in the field where the light intensity is low than in those where it is high. As is clear from Table IV this was found to be true. But since we have demonstrated (p. 121) that deflection in light of uniform intensity can be increased either by decreasing or increasing the intensity, it may be maintained that the difference in deflection recorded in Table IV is due to the difference in light intensity in the field regardless of difference in intensity on opposite sides of the organisms. It must be remembered, however, that deflection in a field uniformly illuminated, is increased only if the intensity is decreased to a point near the threshold or increased to a point near the optimum. In the experiments just referred to, the intensity, in all probability, was far below the optimum and above the threshold, so that it is not likely that mere reduction in illumination affected the deflection to any considerable extent. The difference between the degree of deflection in 142 candle meters and 380 candle meters of light, graded in intensity, must, therefore, have been due to the greater effect of the differences in light intensity on opposite sides of the organism when exposed to weak light than when exposed to strong. The experimental results recorded in Table IV therefore support our previous conclusion, that the direction of motion in Volvox is regulated by the relative intensity of light on opposite sides of the colonies.

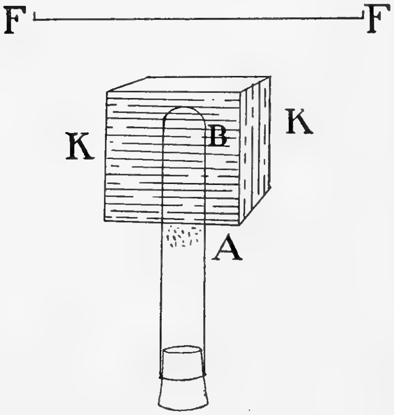


Fig. 9. After Loeb, 1905, p. 25, Fig. 1.

Loeb, however, as is well known, asserts that orientation is caused by the direction of the rays regardless of the difference in light intensity. He bases his assertion largely on the results in the three following experiments on Porthesia larvæ (Loeb '05, p. 25–28).

"*Experiment 3.*—The test tube is placed perpendicular to the plane *F* of the window, and at the beginning of the experiment the animals are collected at the window side *B* of the test tube." Now if the half near the window is covered, the animals soon collect at *A*. "As soon as they emerge from the box *K* into *A* they turn about, direct their heads toward the window, move to the edge of the pasteboard and remain at the boundary between the covered and uncovered portions of the tube at *A*, and especially at the top of the test tube. The remarkable thing is that they are not distributed evenly over the whole brightly illuminated part of the test tube. The explanation is as follows: As soon as the animals near the window at *B* are covered by the pasteboard, the weak rays of light reflected from the walls of the room fall upon them. *The animals follow the paths of these rays and arrive at the uncovered portion of the tube*" [Italics ours].

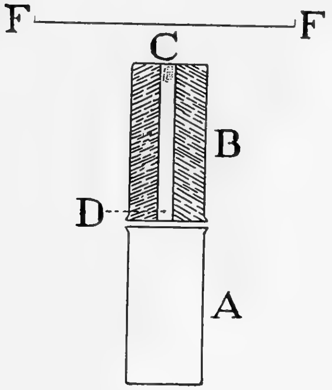


Fig. 10. After Loeb, 1905, p. 27, Fig. 2.

*Experiment 4.*—The larvæ were found to move to *C*, toward the window *F—F*. In the test tube *B*, shaded as represented in the figure, the light intensity is lower than in the test tube *A*, not shaded, but the larvæ go to *C*.

*Experiment 5.*—The animals move from direct sunlight at *A* to *B* into the diffuse daylight. They pass from the direct sunlight into diffuse daylight without even attempting to return into the sunlight.

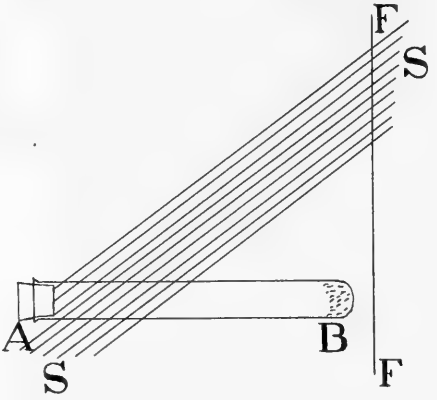


Fig. 11. After Loeb, 1905, p. 28, Fig. 3.

In these, as in other experiments of Loeb referred to on p. 135, the animals were exposed to light, the ray direction of which must have been exceedingly complicated, since the light was diffused before it reached the tube in which the animals were. Moreover, the walls of the tube caused still further diffusion by refraction and reflection. How, then, could it be ascertained in any of these experiments whether the animals moved in the direction of the rays or not?

In Experiments 4 and 5, the animals moved from a region of higher light intensity to one of lower. Now from this the author concluded that difference in intensity does not cause orientation, for if it did, the animals, being positive, would remain in the region most highly illuminated.

In discussing the effect of difference in light intensity it is necessary to define the sense in which this is meant. There is a vast difference between the difference in light intensity in a given field and the difference in intensity on different areas of the surface of a particle in the field. For example, hold an opaque piece of paper in direct sunlight so that the rays strike it at right angles and you will find almost an infinite difference in the light intensity on the two sides, but remove the paper and you will find that the intensity difference in the field is actually infinitesimal. It is evident then that an organism can move from regions of higher to regions of lower light intensity in a field produced by apparatus arranged as represented in Figs. 10 and 11, and still have the anterior end constantly more highly illuminated than the posterior. LOEB evidently did not recognize this in the experiments cited above, for he accepts the theory of SACHS, who ('87, p. 695) defines his position very clearly, as follows: "I came to the conclusion that in heliotropic curvatures, the important point is not at all that the one side of the part of the plant is illuminated more strongly than the other, but that it is rather the direction in which the rays pass through the substance of the plant."

In moving toward the window in the test tubes arranged as represented in Figs. 10 and 11, the anterior end of the animal was very likely more highly illuminated than the posterior. On the assumption that difference in intensity on the surface of the organism causes orientation, the larvæ would consequently be expected to move toward the window. I can, therefore, see nothing in these experiments which in any way indicates that difference in light intensity on the surface of the body, regardless of the direction of the light rays, is not the cause of orientation.

## 9. ORIENTATION OF SEGMENTS.

In working on Volvox it was noticed that colonies with various portions missing still appeared to respond to stimulation by light. Such colonies were most frequently found after heavy rain storms or other rather violent disturbances. On July 28, 1905, a colony was found, in which the anterior end and a narrow portion of the side extending nearly to the posterior end, were missing. This segment oriented quite definitely. In swimming horizontally toward a source of light it moved approximately parallel with the rays, deflecting but little. When exposed to light from two sources of equal intensity, it took a course about midway between them. If the light from one of the sources was cut off after the segment had thus oriented, it continued on its original course for a few millimeters, then changed the direction of motion until it was oriented once more. Its light reactions in general were like those of intact colonies, but the path of this segment instead of being straight as is true in case of entire colonies, was in the form of a spiral. This was evidently the result of the mechanical effect of the gap in the side and rotation on the longitudinal axis.

The reactions of many other segments of colonies were studied later. Most of these segments were made by cutting the colonies in pieces. In performing these operations a considerable number were put under a cover glass which was then carefully pressed down until the colonies split open. Under these conditions they usually split at the posterior end, but sometimes at the side. By inserting a needle ground to a knife-edge, the wall could be cut in any direction desired without much difficulty.

It was found that segments of practically all forms and sizes responded to stimulation by light, but owing to their form and the effect of gravitation, many could move only in small circles, and were unable to orient.

It can be stated definitely, however, that among segments of various forms and sizes, such as are produced by cutting the colonies in half, either parallel or perpendicular to the longitudinal axis, respond in general like whole colonies, with the exception that most of the segments take a spiral course, the width of which depends upon the form of the segment. It is thus clear that a colony of Volvox can orient when the anterior or the posterior end or one side is missing. A theory of orientation must be broad enough to explain not only the reactions of entire colonies but also those of any segments.

## 10. MECHANICS OF ORIENTATION.

JENNINGS ('04, p. 32–62) found that Stentor cœruleus and Euglena viridis orient by means of motor reactions when exposed to light. If stimulated they turn toward a structurally defined side regardless of the direction of the rays or difference in light intensity on opposite sides of the organisms. If they fail to become oriented by a single motor reaction they repeat the reaction, turning successively in different directions, until they turn in the right direction; this direction they hold and thus become oriented. The process of orienting in these organisms is, therefore, strictly on the trial and error basis.

In Volvox, taking a colony as a whole, there is no evidence of motor reactions, nor is there any hit or miss method about its orientation. It makes no mistakes in the process. If exposed to light it turns toward the source of light without error. What sort of mechanism has this organism, by means of which it can thus regulate the direction of its motion?

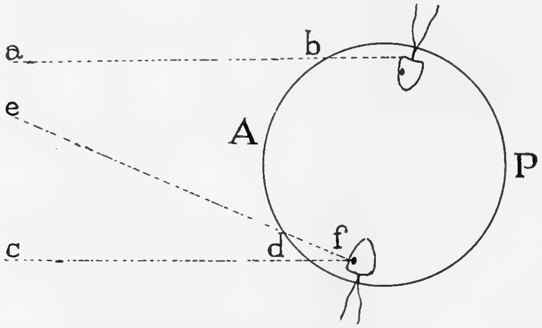


Fig. 12. After Holmes, 1903, p. 325.

A colony of Volvox may be conceived to turn in its course by decreasing or increasing the backward stroke of the flagella on one side or the other, or by using the flagella on either or both ends as rudders, or even by directing the stroke of these flagella in such a way as to turn the organism. But since the organisms orient when either the posterior or the anterior end is missing, and probably also when both ends are missing, it is clear that the flagella on the ends do not function primarily in changing the direction of motion. Such changes must, therefore, be the results of inequality of the strokes of the flagella on opposite sides. What then is it that causes the strokes on opposite sides to become unequal?

Holmes ('03, p. 325) after concluding that it cannot be caused by difference in light intensity on opposite sides, suggests the following explanation. "The orientation of the colony may be accounted for, if we suppose that the eye-spots are most sensitive to light striking them at a certain angle such as is indicated in the diagram by the lines *a—b* and *e—f*. If rays of light enter the colony in the direction of the lines *a—b* and *c—d* somewhat obliquely to the long axis, *A—P*, the flagella of the cells represented on the upper side of the diagram would beat more vigorously and accelerate the motion of that side of the organism. The opposite cell being struck by rays in the direction *c—d* would be less stimulated, and, as the flagella would beat less strongly than those on the other side of the colony, the organism would swing about until its long axis is brought parallel with the rays when, being equally stimulated on both sides, it would move in a straight course towards the light. We do not have to suppose that each cell makes a special effort to orient itself at a particular angle to the rays, but that it is so organized that the effective beat of the flagella is most accelerated by light striking the cell at a certain angle. If the cells were most stimulated by light falling upon them at such an angle as would result if the rays diverged from a spot in front of the colony and in line with its long axis the conditions for orientation would be fulfilled. Since the eye-spots in all the cells face the anterior end of the colony this supposition appears very probable. The foregoing explanation of the orientation of *Volvox* may or may not be the true one, but it enables us to see a significance in the peculiar arrangement of the eye-spots in this form and is consistent with the results of the experiments we have described." Is it also consistent with the results of the experiments described in the preceding pages?

In the first place the eye-spots, upon the arrangement of which HOLMES places considerable importance in his theory, are not so situated that they all face the anterior end; quite the contrary, they face the posterior end of the colony, as pointed out on p. 107; and in the accompanying diagram by HOLMES they should be on the side of the zooids nearest the end *P*, instead of on that nearest the end *A*. They do, however, probably function as light recipient organs, as already stated (p. 108). Let us then assume that the zooids are influenced by the direction of the rays as HOLMES suggests, even if the eye-spots do face the posterior end of the colony, and see if the theory fits our experimental results.

1. It was clearly demonstrated (p. 139) that if specimens of

Volvox be exposed to parallel rays of light so that there is a difference in intensity on opposite sides of the organisms when the longitudinal axis is parallel with the rays, they do not move directly toward the source of light but deflect toward the side most highly illuminated. In accordance with HOLMES' theory we should expect them to move parallel with the rays under these conditions.

2. HOLMES states that the condition for orientation, according to his theory, would be fulfilled "if the rays diverge from a spot in front of the colony in line with its long axis." If this be true, we should certainly expect the conditions for orientation also to be fulfilled, if the rays converge from two luminous points in front of the organism and if "the eye-spots are most sensitive to light striking them at a certain angle" we should expect the organisms to move toward a point nearly, if not exactly, midway between the two sources of light regardless of their relative intensity. But it has been demonstrated (p. 133) that if Volvox colonies be exposed to light from two sources of unequal intensity, they orient and swim toward a point nearer the more intense source. It is, therefore, evident that the explanation of orientation in Volvox, suggested by HOLMES, is not consistent with the experimental results which I have presented.

I have demonstrated beyond a reasonable doubt that the difference in intensity on opposite sides of Volvox modifies its direction of motion regardless of the direction of the light rays, and since the direction of motion is changed by difference in the effective stroke of the flagella on opposite sides, it must be difference in intensity which influences the stroke of the flagella. But HOLMES, as stated above, concluded that the reaction of Volvox cannot be explained upon the assumption that difference in intensity on opposite sides of the body causes the flagella to beat with unequal vigor. Upon what does he base this conclusion and wherein lies the fallacy of his argument?

I can present his line of thought best by quoting verbatim ('03, p. 321–322): "Let us consider a *Volvox* in a region of sub-optimal stimulation and lying obliquely to the rays of light. If it orients itself to the light the backward stroke of the flagella, *i. e.* the stroke that is effective in propelling the body forward must be more effective on the shaded side than on the brighter side. This may conceivably occur in the following ways, which, however, amount practically to the same thing: the diminished intensity of light on the shaded side of the body may act as a stimulus to the backward phase of the stroke, or decrease the efficiency of the forward phase of the stroke of the flagella; or the light on the brighter side of the body may inhibit the backward phase or increase the forward phase of the stroke of the flagella; In any case, if the organism is passing into regions of ever-increasing intensity of light, we should expect its rate of speed would be lowered. If the orientation is affected by a shading of the side away from the light it would follow that in a region in which the shading were less the speed of the travelling body would be diminished. If the parts of the body which are most shaded are the parts where the effective beat of the flagella is the strongest, then, as the organism passes to a point where the illumination on both sides of its body is increased, its rate of transit would be diminished. If we suppose that the forward stroke is most stimulated, or the backward stroke most inhibited on the brightest side of the body we should expect that with more illumination the more inhibition there would be, or the more the backward phase of the stroke would be increased, and the rate of locomotion would likewise be reduced. If we imagine a machine in the form of a *Volvox* colony and provided on all sides with small movable paddles so adjusted that when they come into regions of diminished light as the machine rolled through the water their effective beat would be increased, it is clear that such a machine might orient itself to the direction of the rays and travel towards the source of illumination, but its rate of locomotion would be diminished the brighter the light into which it passed. We may conceive the light to increase or decrease the backward or forward stroke of the paddles in any way we please and we cannot explain how such a machine can orient itself and go towards the light and at the same time move through the water more rapidly as it comes into regions of greater illumination."

It is evident that the crux of this whole argument is the relation between rate of movement and light intensity. This relation was worked out in detail by HOLMES ('03, p. 323) with the following results: "It was found that, as the *Volvox* travelled towards the light, their movement was at first slow, their orientation not precise, and their course crooked. Gradually their path became straighter, the orientation to the light rays more exact and their speed more rapid. After travelling over a few spaces (centimeters), however, their speed became remarkably uniform until the end of the trough was reached." Unfortunately, HOLMES does not give the length of the trough, but he says the distance over which there is a marked increase of speed is considerably less than the space over which the speed is nearly uniform.

HOLMES concludes from these results that the increase in rate of speed is due to increase in light intensity and consequently that orientation cannot be due to difference in intensity on opposite sides of the organism, because if it were, the backward stroke of the flagella would have to be more effective on the side in the higher light intensity than on the side in the lower, and this would cause the organism to turn from the source of light instead of toward it. Are these conclusions correct?

If the increase in rate of speed is due primarily to increase in light intensity, one would certainly not expect the rate to become uniform after the colonies have traveled a few centimeters in the trough, nor would one expect it to increase if the colonies are exposed to light of a given intensity for some time. But HOLMES states that the rate does become uniform, and I frequently observed that if relatively quiet colonies in an aquarium containing water a few millimeters deep, are illuminated from above, they gradually become more active. Since, under these conditions, they cannot move toward the source of light, it is evident that this increase in activity is not due to increase in light intensity. It is very probable then, that the increase in rate of movement is more dependent upon the time of exposure to light than upon the increase in intensity. Moreover, HOLMES states that orientation is more exact after the colonies have traveled some little distance, *i. e.*, after the rate has become nearly uniform. It must, therefore, be least exact when the increase in rate of speed is greatest. If this be true, it follows that the factors which regulate rate of speed are quite different from those which regulate orientation. We have demonstrated that difference in light intensity on opposite sides of the colonies modifies the direction of movement. And since the factors which regulate the direction of motion and those which regulate the activity of the colonies are different, we may conclude, from this point of view, as well as from what has gone before, that the increase in the rate of speed is not primarily due to increase in light intensity. Such being the case, the argument of HOLMES cited above cannot be valid, for it is based upon the supposition that increase in speed in Volvox is due to increase in light intensity. We shall refer to this question again (p. 153).

If a colony which is not oriented turns toward the source of light, it is clear that the stroke of the flagella on the shaded side must be more effective in driving the organism forward than that on the illuminated side. This may be conceived to be caused directly by the difference in light intensity on opposite sides, or indirectly in that a Volvox colony may possibly act as a lens and thus cause the light on the side opposite that most highly illuminated to become most intense; or, since the zooids are intimately connected by protoplasmic strands, it is not impossible that impulses produced by excessive photic stimulation may be transmitted to the opposite side and result in action there. At any rate, it is undoubtedly true that these strands serve to transmit impulses from zooid to zooid, and thus bring about coördinate action.

It was found, as previously stated, that segments, *e. g.*, halves produced by cutting specimens parallel to the longitudinal axis, orient essentially like normal colonies. Such segments, however, cannot act as lenses, nor can impulses originating on one side be transmitted to the opposite side. The last two of the possible explanations suggested, therefore, must be abandoned, and it must be concluded that the unequal effect of the stroke of the flagella is due directly to difference in light intensity on opposite sides of the organism. But this unequal effect of the stroke on opposite sides may be caused, as HOLMES pointed out, by an increase in the backward phase of the stroke on the shaded side, or a decrease in the same phase on the illuminated side or a decrease in the forward phase on the shaded side, or an increase in this phase on the illuminated side. Can it be ascertained which of these is the cause of the difference between the effect of the stroke of the flagella on the shaded sides and that of those on the illuminated side of the colonies?

If the light intensity of the field is suddenly decreased while colonies of Volvox are swimming horizontally toward it, they stop forward motion, the longitudinal axis takes a vertical position due to the effect of gravity, and then the colonies swim slowly upward. It is not at all difficult to find specimens in which this upward swimming is just sufficient to overcome the effect of gravity, and under such conditions they appear to be hanging in the water motionless. They are, however, rotating on their longitudinal axis. If now the light intensity, to which these apparently motionless organisms are exposed, is increased they soon begin to turn toward its source; but in so doing they swim upward, as represented in the accompanying diagram.

In thus swimming upward and horizontally toward the source of light, it is clear that the effect of the backward stroke of the flagella increases both on the shaded side and on the illuminated side, for both sides move forward. But the shaded side moves farther than the illuminated side, consequently the increase in the effect of the backward stroke must be greater on the former than on the latter. The difference in the effect of the stroke of the flagella on opposite sides which results in orientation of positive Volvox colonies is, therefore, due to a greater increase in the backward stroke of the flagella on the shaded side than of those on the illuminated side.

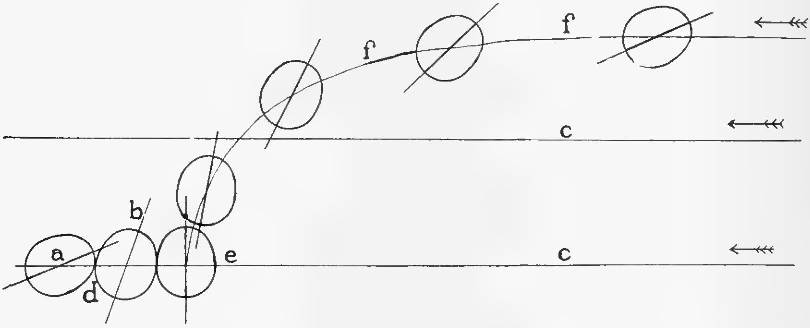


Fig. 13. Diagram representing the reaction of a Volvox colony when the light intensity is suddenly changed. *a*, outline of colony; *b*, longitudinal axis; *c*, light rays; *d*, point in the course where the light is suddenly decreased; *e*, point where it is suddenly increased; *f*, course taken by colony. In continuing from *e*, the side of the colony facing the source of light travels over a shorter distance than the shaded side. Consequently the backward stroke of the flagella on the latter side must be more effective than that of those on the former.

If the light thrown upon apparently motionless colonies is quite intense, they frequently may be seen to sink 4 or 5 mm. immediately after the light is turned on, but while they are sinking this short distance, they apparently become acclimated and soon turn toward the light, and at the same time swim upward, just as described above. During the time in which these colonies sink they continue to rotate in the same direction as before. The sinking must then be due to a decrease in the effect of the backward stroke of the flagella on all sides, and this decrease is due to an increase in light intensity. But when the colonies turn toward the source of light, and at the same time swim upward, it is evident that the increase in light intensity must cause an increase in the backward phase of the stroke of the flagella on all sides, for if this were not true there could be no upward motion. The side nearest the source of light, however, passes over a shorter distance than the opposite side, as will readily be seen by referring to the diagram, and therefore the increase in the effect of the backward phase must be greater on the latter than on the former. But the light intensity is greater on the former than on the latter (a paradox). When the light intensity in the field is increased the effect of the backward phase of the stroke of the flagella may be increased or decreased on all sides. If it is increased the effect is most marked on the side in lowest light intensity. Furthermore, if the light is strong the colonies turn toward its source more rapidly and do not swim upward so far and thus make a sharper curve than when it is weak; but the stronger the light the greater the difference between the intensity on the shaded and that on the illuminated side. It, therefore, follows that the greater the difference in intensity on these sides, the greater the difference in effect of the backward phase of the stroke of the flagella, the effect being greatest on the side least illuminated. These considerations support the conclusion arrived at above, *i. e.*, that the factors which regulate the activity of the colonies, as a whole, are different from those which regulate the direction of motion.

We have thus demonstrated that while orientation is due to difference in light intensity on opposite sides of the colonies, it is brought about in positive specimens by the flagella striking backward with greater effect on the side in lowest light intensity than elsewhere. I suggest the following explanation of this:

First, it must be remembered that the organism constantly rotates on its longitudinal axis. If then a colony is so situated that one side is more highly illuminated than the opposite, it is clear that the zooids will constantly be carried from a region of higher to a region of lower light intensity, and vice versa. They are thus subjected to constant changes in strength of illumination. As stated above, the flagella strike backward with greater vigor on the shaded side than on the opposite one and, therefore, it is evident that as the zooids reach the region of lower light intensity, in other words when the light intensity to which they are subjected decreases, they increase the effect of the backward stroke of the flagella, *i. e.*, they attempt to turn toward a structurally defined side (the side facing the anterior end of the colony). This is precisely what Euglena does when it passes from a region of higher to one of lower light intensity, *i. e.*, it turns toward a structurally defined side, the larger lip. The individuals in a colony then respond with a motor reaction induced by change in light intensity; they react on the same basis as do Euglena, Paramecium, Stentor and other unicellular forms, in their trial and error reactions, but owing to the way in which they are inter-related, and to the rotation of the colony on the longitudinal axis, this reaction of the zooids causes orientation in the colony as a whole, without error.

This explanation of orientation in entire colonies holds also for orientation in segments. As previously stated, only those segments orient which have such a form that they can rotate. As they rotate the cut surface constantly faces the center of the spiral, so that if the axis of the spiral is not directed toward the source of light, the outer surface where the zooids are situated is alternately turned toward the light and away from it. Thus the zooids are carried from regions of higher to regions of lower light intensity and vice versa, and the motor reaction is induced just as it is in entire colonies.

Orientation in negative colonies can be explained in precisely the same way as that in positive ones, assuming merely that in this condition the zooids respond with the motor reaction when they pass from lower to higher light intensity instead of when they pass from higher to lower (as is true when the organisms are positive). The backward stroke then becomes most effective on the side most highly illuminated.

### II. REACTION OF NEGATIVE COLONIES.

Volvox becomes negative when exposed to light of a certain intensity. The intensity, however, varies greatly in different colonies and in the same colony under different conditions. Radl ('03, p. 103) concludes his discussion on the difference between positive and negative phototropism with the following paragraph: "Ich glaube nun, dass der Unterschied zwischen positivem und negativem Phototropismus ähnlich wie beim Menschen nicht ein

Unterschied in der Orientierung, sondern nur in der Lokomotion ist; dass das Tier in beiden Fällen gegen die Lichtquelle orientiert ist, jedoch nicht gleiche Muskeln spannt."

This explanation will not hold for Volvox or Euglena, for both of them turn the anterior end from the source of light when they are negative.

When Volvox colonies are negative they orient in all essentials as they do when positive, except that they direct the anterior end from the source of light. In swimming horizontally from a source of light they seldom move parallel with the light rays. If the position of the light is changed after they have oriented, they change the direction of motion until the course again bears the same relation to the ray-direction it did before. If exposed to light from two sources, so arranged that the rays make a definite angle with each other, they move from a point between the two. If one source is more intense than the other, the point from which they move is nearer that source.

These facts and others are established by the following experimental results, which are presented in graphic form (Fig. 14).

By referring to path *A* it will be seen that the colony introduced at *n* was positive to light from the three glowers as well as to that from the arc, but that it became negative after swimming toward the arc for a short distance from *c*, turned about and moved across the aquarium to *c'*. That is, at the end of the experiment the colony was negative to a much lower light intensity than at the beginning. The arc was approximately 250 candle power. It was 15 cm. from the point where the organism became negative. The light intensity at this point was therefore 11,111 ± candle meters. But the colony was still negative after having crossed the aquarium, a distance of nearly 8 cm., or nearly 23 cm. from the arc, *i. e.*, in an intensity of 4726 ± candle meters, which is 6385 ± candle meters less than the intensity in which it first became negative. Similar results are represented in path *B* and the paradoxical nature of the results is even more striking than in the case of path *A*. Unfortunately, the distances between the sources of light and the aquarium, in this exposure, were not recorded.

The colony which produced path *B* was positive to the light from the arc when first put into the aquarium at *c*, but after moving toward the source of light a few centimeters, it became negative, turned about and moved in the opposite direction. When it reached *c′* the glowers were exposed and the colony promptly changed its direction of motion and proceeded on a course directed from a point between the two sources of light. This point, however, was much nearer the arc than the glowers, the light from the former being much more intense than that from the latter. When the light from the arc was cut off at *n*, the colony was found to be negative to the comparatively weak light from the glowers. It consequently changed its course and moved from this source; but

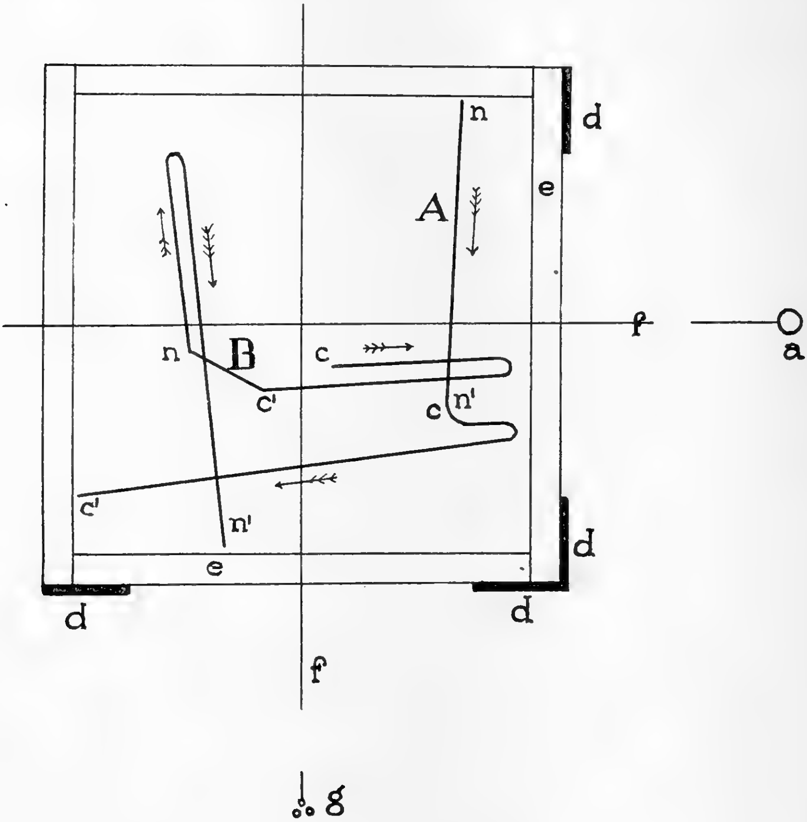


FIG. 14. The lines *A* and *B* represent the course taken by single colonies as seen in water 2 cm. deep in the plate glass aquarium, *e* (the paths are represented in approximately accurate proportions); *g*, a group of three 222 volt Nernst glowers in a vertical position; *a*, carbon arc; *f*, direction of light rays; *d*, opaque screens; *n n′*, path with glowers exposed and arc shaded; *c c′*, path with arc exposed and glower shaded; *c′ n*, path with both glowers and arc exposed.

after continuing about 3 cm. it became positive, turned about and moved toward the glowers to *n′*, and probably would have continued farther had it not been prevented from doing so by the wall of the aquarium. It will be noticed that the point *n′*, where the colony was still positive at the end of its course, was about 3 cm. nearer the glowers than *n*, where it proved to be negative, and nearly 7 cm. nearer than the point where it changed its course from negative to positive. That is, the organism was positive at *n′* in a much higher light intensity than that in which it was negative at *n* and at the point where it changed from negative to positive.

## 12. CAUSE OF CHANGE IN SENSE OF REACTION.

The results presented above demonstrate that Volvox may be either negative or positive in a given light intensity. This will be brought out more clearly later where it will be shown that Volvox, in certain conditions, is negative to light of all intensities to which it responds at all.

Since a Volvox colony may be either positive or negative in the same environment, it is clear that the transformation from positive to negative or vice versa must be due to some internal change. This change, whatever it may be, is induced by light. It is dependent upon the intensity and also upon the time of exposure, as is shown by the fact that when specimens are exposed to intense light they may be positive for a time and then negative to a much lower intensity than that in which they were positive when first exposed. Weak light tends to induce the change which causes the colonies to become positive, whereas strong light tends to induce the change which causes them to become negative.

Some photosynthetic process in chlorophyl bearing organisms, suggests itself as the probable condition upon which the sense of reaction depends. It might be assumed that the organisms are positive when a given amount of synthesized substance, such as carbohydrates, proteids, or fats, is present, and negative when this amount is decreased. This assumption fits the observed reaction in that such substances are formed in the presence of light, and in that they disappear in darkness, being either further synthesized to form protoplasm, or, perhaps, directly oxidized. But the short time and the slight change in light intensity necessary to produce a change in the sense of reaction is entirely inadequate to cause the formation and destruction of photosynthetic substances, such as those mentioned above. The inversion of the sense of reaction, therefore, cannot be due to a photosynthetic process. May it not be due to the effect of light on the chemical equilibrium of some other substance?

One of the more important results of recent investigation in physical chemistry is the establishment of the fact that substances in chemical equilibrium are dynamic and not static, as had formerly been supposed. If, for instance, alcohol be added to acetic acid, it is well known that water and ethyl acetate will be formed; but it is also true that if water be added to ethyl acetate, the formation of alcohol and acetic acid results, that is, the former reaction is reversed. When the reaction in both of these cases has reached a state of equilibrium, there is a certain amount of each of the following substances present: Alcohol, acetic acid, ethyl acetate, and water, and this amount remains constant; but the reaction continues; alcohol and acetic acid react to form ethyl acetate and water just as fast as ethyl acetate and water react to form alcohol and acetic acid. These reactions are expressed as follows:

$$C_2H_5OH + HOOC.CH_3 \rightleftarrows CH_3\ COO\ C_2H_5 + H_2O.$$

This indicates that two reactions are taking place simultaneously in opposite directions. The relative amount of substance indicated in the two members of an equation representing equilibrium in chemical reaction, depends upon the nature of the substances and the environment, *i. e.*, the temperature, pressure, etc. If, for instance, the temperature of compounds in equilibrium be raised, the equilibrium will be destroyed and the reaction in one direction will take place faster than that in the other. When equilibrium is again restored the relation of the amounts of the different substances will no longer be the same as it was at the lower temperature. If the temperature is lowered, the rate of motion will increase in the opposite direction. JONES ('02, p. 514) states this as follows: "The effect of a rise in temperature is to favor the formation of that system which absorbs heat when it is formed. . . Increase in pressure diminishes the volume and, therefore, favors the formation of that system which occupies the smaller volume."

Reversible chemical reactions were formerly supposed to be quite exceptional, but it is now known that they are not. JONES ('02, p. 481) writes: "We must regard chemical reactions in general as reversible."

No work, as far as I know, has been done directly on the effect of change in light intensity on equilibrium in chemical reaction; but we know that light does affect many chemical reactions, and since we must regard chemical reaction in general as reversible, it seems reasonable to assume that the relative amount of different substances present in a mixture is dependent upon the light intensity, provided the chemical reaction between the substance is at all affected by light. This means that substances in chemical equilibrium in one light intensity will not be in equilibrium in another, so that the direction in which the reaction takes place faster depends upon the light intensity.

To explain reversal in the sense of reaction on the basis of chemical reactions induced by light let us assume: (1) That Volvox contains substances $X$ and $Y$, the chemical reaction between which is regulated by the intensity of light; (2) that a sub-optimum intensity favors the formation of substances represented by $X$ and a supra-optimum those represented by $Y$; and (3) that the colonies are neutral in reaction when there are $Y$ substances in one member of the equation and $X$ in the other; positive when one member contains $(X+)$ substances and the other $(Y-)$, and negative when one contains $(X-)$ and the other $(Y+)$. Can the change in sense of reaction as represented in paths *A* and *B*, Fig. 14, p. 156, be explained on the basis of these assumptions?

The colony which produced path *A* was positive when put into the aquarium at *n*. In accordance with our assumption it, therefore, contained $(X+)$ and $(Y-)$ substances. The intensity at *n* was relatively low so that the chemical reaction favored the formation of compounds represented by $X$. This may be expressed thus $(X+) \leftrightarrows (Y-)$, indicating that the reaction toward $X$ takes place faster than that toward $Y$. The increase in the $X$ and decrease in the $Y$ substances continued until a state of equilibrium was attained or the organism reached *n′* and *c*, where the light from the glower was turned off and that from the arc turned on, and the colony was thus exposed to light of supra-optimum intensity. Why did it not then turn from the source of light at once? According to our assumption, because it contained $(X+)$ and $(Y-)$ substances. But since the colony was in a supra-optimum intensity, the chemical reaction favored the formation of $Y$ substances at the expense of $X$, represented thus $(X+) \rightleftarrows (Y-)$. As soon as this reaction had continued far enough so that $(X+)$

was decreased to $X$ and $(Y -)$ increased to $Y$, the colony became neutral. The point where this took place is represented in the path by the sharp curve. But why did the colony not remain neutral? Because it was in a supra-optimum light intensity and, therefore, in accordance with our assumption, $X$ continued to decrease and $Y$ to increase, $X \overset{\leftarrow}{\longrightarrow} Y$ resulting in $(X -)$ and $(Y +)$ compounds which caused the organism to become negative and it remained so to the end of its course. Had the aquarium been wider it would have reached a point at which it would have been neutral in an optimum light intensity. If the reactions are regulated as assumed, it would have reached this point as follows: $(X -) \overset{\leftarrow}{\longrightarrow} (Y +)$ expresses the condition of the colony as it proceeded from the source of light toward $c'$, but as the intensity decreases the rate of formation of $X$ increases and that of $Y$ decreases until the colony reaches the point of optimum intensity, when the rate in opposite directions is equal $(X -) \rightleftarrows (Y +)$. The organism, however, is still negative at this point, since it contains $(X -)$ and $(Y +)$ substances, and it therefore proceeds into a region of sub-optimum intensity, where $(X -)$ increases and $(Y +)$ decreases $(X -) \underset{\longleftarrow}{\rightarrow} (Y +)$. This results in $X$ and $Y$ substances and the colonies consequently become neutral. The chemical reaction, however, continues to favor the formation of $X$, since the light is sub-optimum, and this soon results in $(X +)$ and $(Y -)$ substances, which causes the organism to become positive. It therefore turns and proceeds toward the source of light again, but owing to the accumulation of $(X +)$ and $(Y -)$ substances, it passes the region of optimum intensity before it becomes neutral, and therefore becomes negative again. It may be conceived to thus pass back and forth several times, like a pendulum, before being neutral in the optimum region.

In accordance with our assumption, the conditions of the colony in producing the path $B$ could be represented as follows:

$(X +) \overset{\leftarrow}{\longrightarrow} (Y -)$ from $c$ to the beginning of the curve;
$(X) \overset{\leftarrow}{\longrightarrow} (Y)$ at the point in the curve nearest the arc;
$(X -) \overset{\leftarrow}{\longrightarrow} (Y +)$ from this point to $n$;
$(X -) \underset{\longleftarrow}{\rightarrow} (Y +)$ from $n$ to the beginning of the curve beyond;
$(X) \underset{\longleftarrow}{\rightarrow} (Y)$ at the point in the curve farthest from the glower;
and $(X +) \underset{\longleftarrow}{\rightarrow} (Y)$ from this point to $n'$, the end of the course.

We have thus presented a formal explanation of these paradoxical reactions, based upon possible chemical changes in the organism. But since the chemical changes are purely hypothetical, this explanation must be, of course, considered merely as a suggestion.

If our explanation proves to be correct, the process of acclimatization must be the process of such changes in the organism that the neutral condition will be produced when the relative amount of the substances represented by *X* and *Y* is changed.

Temperature changes, mechanical agitation, or any other agent which would in any way affect the chemical reaction between *X* and *Y* would, of course, influence the change in the sense of reaction, and thus we should have a possible explanation of the effect of such agents on the change from positive to negative reaction and vice versa, recorded in the literature on the subject.

## 13. EFFECT OF TEMPERATURE ON CHANGES IN SENSE OF REACTION.

On August 17, 1904, Volvox colonies which were strongly positive were put into a small aquarium containing water about 5 mm. deep and exposed to light from a group of three 222 volt glowers, 15 cm. from the aquarium. The light intensity in the aquarium was approximately 4000 candle meters. The colonies were therefore in an intensity which was nearly optimum. The water in the aquarium was then slowly heated to 45° C. As the temperature increased the organisms became slightly more active but showed no indication of becoming negative. When the temperature reached 45° nearly all were dead. This experiment was repeated and the temperature raised to 51°, a temperature which proved fatal to all the colonies. The results in the second experiment were similar to those in the first. It therefore seems evident that change in temperature does not induce reversal in the sense of reaction in Volvox. This, however, does not mean that change in temperature may not affect reaction to light; indeed, it is more than probable that it does, for at low temperature all light reactions cease.

These results agree with those obtained by Parker on Copepods ('02, p. 117) and by Yerkes ('03, p. 375) on Daphnia pulex, but they do not agree with those obtained by Loeb ('93, p. 91), who found that the sense of reaction in Polygordius larvæ was changed from positive to negative by a change in temperature from 24° C.

to 29° C.; Massart ('91, p. 164), who found Chromulina, a flagellate, to be positive at 20°, and negative at 5; and Strasburger ('78, p. 605), who states that swarm-spores, positive to a given light intensity at 16 to 18° C. are negative to the same intensity at 40. It seems strange that organisms so nearly alike as Chromulina, Volvox and swarm-spores should be affected so differently by change in temperature.

## 14. EFFECT OF MECHANICAL STIMULI ON THE CHANGE IN SENSE OF REACTION TO LIGHT.

In working on the light reactions of Temora longicornis, a copepod, Loeb ('93, p. 96) noticed that the animals, ordinarily negative, were frequently positive immediately after being caught. This change in the sense of reaction was due probably to mechanical agitation. Miss Towle ('00) found that the light reaction of Cypridopsis could be changed from positive to negative by taking the animals up in a pipette or by making them pass through a maze constructed with needles. Holmes ('01) thinks that the fact that Orchestia gracilis is positive in air and negative in water, may be due to the contact stimulus of the water. It was demonstrated by Parker ('02, p. 117) that certain forms of tactual stimulation cause the light reactions in the copepod, Labidocera, to change from positive to negative.

The effect of stimulation by light on Volvox can readily be overcome momentarily by mechanical stimulation, but it was found impossible to change the sense of reaction by such stimuli. In attempting to do this various methods were used, as, for example, shaking the organisms violently, lifting them in a pipette and squirting them into water, and making them swim toward the source of light among numerous large sand grains with which they came in contact.

Whatever the cause of reversal in the sense of light reaction in Volvox may be, it is clear that such reversal is of primary importance in the life of the organism. While continuous exposure to very intense light is fatal to Volvox colonies, they must have a certain amount of light, since they depend upon photosynthesis in the process of feeding. It is therefore evident that it is of great advantage to them to be able to move into regions of comparatively high intensity during dark, cloudy days, early in the morning, and late in the evening, and into shaded places when the light becomes very intense.

## 15. THRESHOLD.

In ascertaining the threshold of photic stimulation for Volvox, the colonies were put into a small glass aquarium constructed so as to reduce reflection from the exposed surfaces as much as possible and thus avoid excessive variation in intensity. A description of this aquarium was published in a preceding paper (MAST '06, p. 386). The aquarium containing the colonies was then moved from the source of light, a Nernst glower, until the light intensity became so low that the organisms no longer responded to it. The point at which reaction ceased could, however, be only approximately ascertained, owing to marked individual variation in the readiness with which they became acclimatized, to unavoidable variation in the intensity of the source of light, and to the difficulty of deciding, without the use of statistical methods, just where the response to light ceased. But since the reaction of Volvox depends quite as much upon its physiological condition as upon the intensity of the light, it is evident that it is of no particular importance to ascertain with great accuracy, either the threshold or the optimum, unless the variations thereof can be correlated with the physiological changes which cause them. We have no methods of measuring the physiological condition of this organism with any degree of accuracy, and therefore at present can hope to do no more than study the effect of various stimuli on the threshold and optimum. The following observations were made with the view of ascertaining the general effect of exposure to light on the variation in the threshold and optimum.

On July 30, 1904, at 5 p. m., it was found that Volvox which had been collected at 6 a. m. and kept in the dark all day responded definitely to light of 0.16 candle meters intensity, and rather definitely to light of 0.14 candle meters. This is the lowest intensity to which any response was obtained at any time. Specimens collected shortly after 12 m., July 14 and 15, respectively, and tested as soon as brought into the laboratory responded to light of 0.50 to 0.83 candle meters. The sky was clear on both of these days, but the organisms were found among the water plants in more or less shaded places.

It was found at different times that after being exposed to direct sunlight a few moments the colonies did not respond even to an intensity as high as 500 candle meters. We have thus observed the threshold to vary from 0.14 to 500 candle meters, and this variation seems to have been due largely to preceding exposure to light. The threshold is higher in colonies previously exposed to strong light than in those exposed to weak light.

### 16. OPTIMUM.

The optimum light intensity for practically all Volvox colonies is somewhat lower than that of direct sunlight, 5000 ± candle meters, but sometimes it is very much lower; it varies greatly. This variation is clearly shown in the following observation.

After a few very cloudy days the sun came out at 11 a. m., July 24, 1904, and the sky became exceptionally clear and remained so the remainder of the day. At 2 p. m. Volvox colonies were found in abundance freely exposed to the sunlight. Some of the colonies were collected and taken to the laboratory where it was accidentally discovered that they were negative in light intensities in which this organism had formerly always been found to be strongly positive. I then tested the colonies for the optimum and was greatly surprised to find that they were negative to all light intensities above 0.57 candle meters. In light from 0.57 to 0.29 candle meters, the lowest intensity to which they were exposed, their reactions were indefinite. There was no indication of any positive reaction whatever.

At different times a number of colonies were taken from a given jar and half of them put into each of two similar vessels containing equal amounts of water. One of the vessels was then exposed to direct sunlight and the other covered so as to exclude all light. After having been in this condition a short time the reactions of the colonies in the two vessels were compared by exposing both to the same light intensity. In such cases it was always found that the specimens which had been in direct sunlight were negative to light of lower intensity than those which had been in darkness. These results indicate that exposure to light of high intensity causes a lowering of the optimum. OLTMANNS did not find this to be true. He states ('92, p. 190) that he covered two lots of Volvox with the same kinds of prisms, July 31, in the evening. One of these lots with its prism was kept in darkness until 9 a. m., August 1, the other was exposed to light. During the following three days it was found that those which were in the darkness until 9 a. m. collected in regions of lower light intensity than the others. STRASBURGER found the same to be true with reference to the reactions of swarm-spores. It is difficult to criticise these experiments, since the light intensity and time of exposure are not definitely stated. However, it seems utterly impossible that the effect upon the optimum in colonies exposed for so short a time could, as OLTMANNS states, be observed after three days. For purely *a priori* reasons we should, nevertheless, expect exposure to light to cause the optimum intensity to be higher, provided it is exposed to light in which acclimatization takes place. It may be, then, that the reason why the exposure to light in my experiments caused a decrease in the intensity of the optimum, is because the organisms were exposed to very intense light for but a comparatively short time, in other words, because they did not become acclimatized. If our explanation of the cause of reversal in the sense of reaction is correct, we should expect exposure to intense light for a short time, to lower the optimum. This is expressed in Fig. 14, path $B$, $n\ n'$, which indicates that the colony was negative to a much lower light intensity immediately after it had been exposed to light of high intensity than later. In accordance with our assumption, in attempting to explain the reaction represented by this figure it would mean an accumulation of the hypothetical substances $(X -)$ and $(Y +)$ during the time of exposure to a supra-optimum intensity.

There are some indications that when Volvox is negative to light of low intensity, it becomes positive when exposed to a much higher intensity. This is shown by the following observations:

August 23, 1904, was a bright clear day. At 4 p. m. specimens were collected in a place which had been well exposed to the sun much of the afternoon. Soon after reaching the laboratory, these specimens were found to be positive in light intensities varying from 230 to 1400 candle meters. The colonies not used in these tests were put into a liter jar and placed in strong diffuse sunlight in a west window. Here many of the colonies soon aggregated on the side of the jar farthest from the source of light. At 5.45 p. m., after having been in the window about an hour, they were found to be negative to an intensity of 230 candle meters and at 6.45 p. m. to an intensity as low as 3 candle meters. They seemed to become more strongly negative the longer they were left in the window, although the light from 6.30 p. m. on was quite dim. At the close of the experiment, 7 p. m., certain colonies which had been strongly negative to an intensity of 230 candle meters were found to be positive to an intensity of 400 candle meters. The following day these organisms were exposed again to light of 1400 candle meters and to various lower intensities, but there were no indications of negative reactions.

I have no explanation to offer with reference to these reactions. The observations were not repeated.

### 17. REACTIONS ON REACHING THE OPTIMUM IN A FIELD OF LIGHT GRADED IN INTENSITY.

Oltmanns ('92) found that Volvox colonies collected and remained in a given light intensity, if put into an aquarium illuminated by light which first passed through a prism such that the light became gradually more intense from one end of the aquarium to the other. If, however, clouds passed over the sun or if the aquarium was in any way shaded, they hurried (streben) toward the more highly illuminated end of the aquarium, but when the clouds disappeared or the shading was removed, they returned to their former positions. If the prism was put between the source of light and a vessel containing Volvox which had a given direction of motion, the colonies changed their direction of motion almost instantly and moved toward the region of optimum intensity. Oltmanns writes ('82, p. 195): "So kann man leicht constatiren, dass die einzelnen Kugeln ihre ursprüngliche Bewegungsrichtung fast momentan verlassen und dann direct auf diejenige Region im Apparat zusteueren, in welcher sie später verweilen."

Was the course taken in the apparatus used by Oltmanns due, as he supposed, to difference in light intensity on opposite sides of the organism, resulting from rays perpendicular to the sides of the aquarium? It is impossible to calculate the difference in intensity produced by such rays, at any given point in the apparatus but it can be estimated with a sufficient degree of accuracy for our purpose. Let $x$ represent the intensity of the light before entering the prism. Oltmanns states that 80 to 90 per cent of this was absorbed at one end of the prism and 30 to 50 per cent at the other. We shall assume it to have been 90 and 40, respectively. The intensity in the aquarium then, due to rays perpendicular to the sides, was $\frac{1}{10}x$ candle meters at one end and $\frac{6}{10}x$ candle meters at the other, a difference of $\frac{1}{2}x$ candle meters. The length of the aquarium was 200 mm. The decrease in intensity was, therefore, $\frac{1}{400}x$ candle meters per millimeter. If the intensity of the light was 5000 candle meters, the general estimate of the intensity of the strongest direct sunlight, the decrease per millimeter in the aquarium was 12.5 candle meters. The difference in light intensity on opposite sides of the largest colonies due to direct light could, therefore, not have been greater than 12.5 candle meters. It probably was much less. As previously recorded (pp. 139-141), I found that if the decrease in light intensity is 6.4 candle meters per millimeter in a field of graded light, the deflection is only 1.5 + °. It is consequently evident that if the colonies in OLTMANNS' apparatus moved directly toward the region of optimum light intensity, the direction of such movement was not caused by the difference in light intensity due to rays perpendicular to the sides of the aquarium. It is clear, then, that there must have been sufficient diffusion in OLTMANNS' apparatus to affect tne direction of motion of the organisms.

If diffusion is practically eliminated, will Volvox still be able to reach the region of optimum intensity in graded light, and if so by means of what reactions? These questions are answered in the recorded observation and results of the following experiments. These experiments were performed in the light grader so arranged that the rays of light were horizontal and nearly perpendicular to the sides of the aquarium which contained water 1.5 cm. deep. The field of light gradually decreased in intensity from 238 ± candle meters at one end to total darkness at the other. It was not quite as long as the aquarium, and was a little narrower than the depth of the water, so that the surface of the water and the sides of the aquarium were not illuminated and thus reflection was prevented.

At 10 a. m., August 26, 1904, a large number of Volvox colonies were evenly scattered in the aquarium along the entire side farthest from the source of light. They started toward the opposite side almost as soon as they reached the water and all deflected to the left, moving across the aquarium in nearly parallel lines, reminding one of columns of soldiers. Those in the region of higher light intensity, however, swam noticeably faster than those in regions of lower. The deflection was toward the darker end of the aquarium, but it must be remembered from what has been stated in preceding pages, that this deflection was not in the main due to the difference in light intensity. It would have been in the same direction and only a little greater if the more highly illuminated end of the field had been to the left instead of to the right.

Owing to the deflection to the left there were but very few colonies within 2 cm. of the right end of the field immediately after they had crossed the aquarium; but a few minutes later it was clearly seen that a large majority were swimming toward the right along the glass wall. In this movement, some followed the wall closely but most of them made a zigzag course coming in contact with the wall at short intervals. This zigzag course seems to have been the result of the interaction between contact and light stimuli. In about 15 minutes most of the colonies collected within 5 cm. of the brightest end of the aquarium. At first they were closely packed together near the wall, but after a short time they began to spread out in the form of a right angled triangle, the perpendicular of which coincided with the end of the aquarium. Some entered the dark region near the end of the aquarium and thus no longer stimulated by light wandered back from the side of the aquarium facing the light, others left this side without entering the dark region. These evidently became acclimatized or negative after exposure for some little time. Thus they continued to move back and forth, gradually spreading out toward the darker end of the aquarium, until finally they began to become less numerous along the bright border of the field of light, the region of highest intensity. Then the whole aggregation appeared to work itself very slowly into the regions of lower light intensity, gradually spreading back from the side of the aquarium facing the source of light; thus at the close of the experiment, five hours after it was begun, most of the colonies were within 5 cm. of the darker end of the aquarium. Here they were scattered over a triangular area which extended from the side of the aquarium nearest the source of light almost to the opposite side. The light intensity within the limits of this area varied from zero at the left tc 47 ± candle meters at the right. The organisms were, however, most numerous in the portions most strongly illuminated. The limits of the area which contained most of the colonies were, in every instance, very indefinite. There was always quite a number scattered about in other parts of the aquarium.

This experiment was entirely, or in part, repeated seven times and the reactions and results in each repetition were in general like those described above. The optimum intensity, as was to be expected, varied greatly, as did also the time it required the colonies to reach the optimum. Thus on August 9 it required only about three hours for the organisms to collect in the region of optimum illumination. The light intensity of this region was 16 ± candle meters at the left side and 71 ± at the right. In repeating this experiment, the apparatus was several times so modified that the more highly illuminated end of the aquarium was to the left. Under these conditions the colonies reacted precisely as they did when this end was to the right. All of them aggregated in the right hand corner of the aquarium, now the region of lowest light intensity, and then gradually spread out until they reached the optimum.

The reactions of Volvox were also studied with the light grader in such a position that the rays were perpendicular to the bottom of the aquarium in place of parallel with it as they were in the preceding experiments, and with so little water in the aquarium that the organisms were forced to swim at right angles with the rays. In some instances under these conditions, there was no evidence of any aggregation whatever, but in others the colonies collected in regions of optimum light intensity. The limits of the regions in which they collected were, however, not well defined. In a few of the exposures some specimens of Euglena viridis were put into the aquarium with the Volvox colonies. These aggregated in a very definite narrow band, the center of which was in a light intensity of approximately 35 candle meters in every exposure. The Euglenæ reached the region of optimum intensity in the course of a few minutes, but it required one hour for any indication of aggregation of Volvox in any of these experiments.

There was absolutely no evidence of orientation and direct movement toward the region of optimum intensity, neither when the light rays were parallel with the bottom of the aquarium, nor when they were perpendicular to it. If there had been, we should certainly expect the colonies to have reached the optimum in much less time than was required in any of the above experiments. The fact that the colonies reach the optimum seems to be a matter of mere chance, the result of swimming about aimlessly. They are more active in sub- and supra-optimum light intensities than in the optimum and, therefore, tend to come to rest in the latter. It is evident that this would tend to cause them to aggregate in the region of optimum intensity.

OLTMANNS ('92, p. 186) states that he found the optimum light intensity for colonies bearing asexual cells to be higher than that for those containing fertilized eggs. I found, as stated above, that specimens which contain large daughter-colonies or spores deflect to the right more, in moving horizontally across the aquarium, than do those containing small daughter-colonies; and also that the former move to the right along the wall of the aquarium nearest the source of light, more definitely than the latter. OLTMANNS may have been misled in his conclusions by some such reactions. The effect of such reactions on the place of aggregation of Volvox colonies is strikingly brought out in the following observations:

After bringing specimens of Volvox to the laboratory, they were usually put into 4 liter battery jars, which were exposed to the light from a 16 candle power electric bulb placed at any desired distance from the jars. Under such conditions it was frequently noticed that the major portions of the colonies aggregated in a region some little distance to the right of the point in the jar directly opposite the bulb. At first this was thought to be due to reflection from the table or wall and other objects about, but after all such reflection was eliminated this reaction was still found to take place. It was also found that if the colonies were put into the plate glass aquarium and exposed to light from a Nernst glower situated so that the rays entered the aquarium at right angles to the side, many more collected along the side nearest the source of light, to the right of the middle than to the left, being most numerous but a short distance from the end of the aquarium.[3] The specimens to the right of the middle of the aquarium, in every instance, were nearly all large and contained well developed daughter-colonies or spores, while those to the left were nearly all small. The difference in size between those to the right and those to the left could be clearly seen with the naked eye, but they also showed a marked difference in reaction. Colonies taken from the right edge of an aggregation in a battery jar, July 26, 1905, deflected on an average 8° to the right in swimming horizontally toward a source of light, while the average deflection of others taken from the same jar near the left edge of the aggregation was 15° to the left. This accounts, in part at least, for the collection of the smaller colonies to the left and the larger ones to the right, but the chief reason why the larger ones are found to aggregate to the right is because they turn to the right, after coming in con-

---

[3] In all these experiments especial precautions were taken to eliminate reflection and refraction.

tact with the wall of the jar nearest the light, more definitely than do the smaller ones. The cause of this has been discussed elsewhere (pp. 128–131).

It was found by OLTMANNS ('92, p. 191) that the optimum light intensity for Volvox changes during the day. He discovered on August 4, that the colonies aggregated in a darker part of the aquarium at 4.30 a. m. than at 8.30 a. m., although it was not yet daylight at 4.30. On another day, however, the aggregation was found in a still darker region between 11 a. m. and 5.30 p. m., and this day it was found in a region slightly lower in light intensity at 5.30 p. m. than at 12 m. in spite of the fact that the sunlight was unquestionably stronger at 12 than at 5. OLTMANNS thought this variation in optimum intensity to be due to a periodicity analogous to that found in higher plants. I found no evidence of such periodicity. The change in position during the day noted by OLTMANNS corresponds to change in the sense of reaction, which can be induced at any time of the day by exposure to light of proper intensity. I did not, however, go into detail with reference to this point; it is therefore desirable to have more experimental results along this line before coming to definite conclusions.

## 18. WEBER'S LAW.

"On comparing objects and observing the distinction between them, we perceive, not the difference between the objects, but the ratio of the difference to the magnitude of the objects compared" (TITCHENER, '05, p. xvi).

This law was formulated by WEBER in 1834 with especial reference to the senses of touch and sight. DAVENPORT ('97, p. 43) has worded it as follows: "The smallest change in the magnitude of a stimulus which will call forth a response always bears the same proportion to the whole stimulus."

By means of his well known capillary tube method PFEFFER ('84) proved the law to hold approximately for the reactions of fern spermatozoids to malic acid, and later ('88, p. 634) also the reaction of Bacterium termo to meat extract. MASSART ('88) proved it to hold for the light reactions of Phycomyces, by placing the plants between two flames and thus obtaining the minimum difference in light intensity on opposite sides which induced a response. He found the minimum intensity difference to be 18 per cent of the total light intensity, and this held true for all degrees

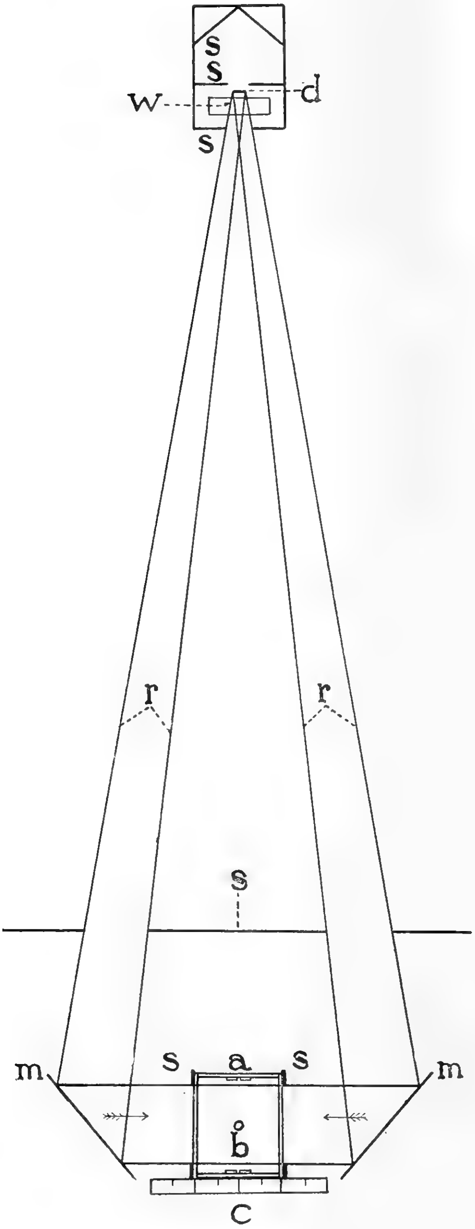


FIG. 15. Representation of apparatus and arrangement as used in ascertaining the minimum difference in light intensity on opposite sides which induces reaction in Volvox, in various intensities of illumination. *a*, glass aquarium 4 cm. long and 3 cm. wide; *b*, glass tube through which the colonies were introduced; *c*, metric gauge; *d*, Nernst glower, horizontal; *m m*, mirrors; *r*, light rays; *s*, dead black opaque screens; *w*, water screen.

of illumination which he used. SHIBATA ('05, p. 573) repeated PFEFFER'S experiments on the reactions of fern spermatozoids to malic acid, using the capillary tube method. He also ascertained the threshold for this organism when stimulated by potassium fumarate, succinate, or tartarate, in various degrees of concentration. He found the reactions to all of these chemical compounds to take place in accordance with the law of WEBER.

A number of other investigators have worked on this subject, but thus far no one has tested the validity of the law for the light reactions in motile organisms. In other words, no one has ascertained the minimum difference in light intensity on opposite sides which will cause a response of motile organisms in different degrees of total illumination. The following experiments were undertaken for the purpose of getting evidence concerning this matter.

The use and arrangement of apparatus used in these experiments will readily be understood by referring to the accompanying diagram.

The box, containing a small opening in front of which the Nernst glower was mounted, served as a non-reflecting background. The screens surrounding the glower were so constructed and arranged that no light escaped excepting that which passed through the opening represented in Fig. 15. This light was absorbed after being used to illuminate the aquarium, and since no other light entered the room in which the experiments were performed, it is clear that the reactions observed, and recorded in the following tables, were induced only by light directly from the glower.

The glass tube, represented in the center of the aquarium, Fig. 15, by a ring, extended about 2 cm. above the upper edges of the glass walls and was so fastened that it could be easily raised vertically. In each exposure enough filtered water was put into the aquarium to fill it to a point a few millimeters above the upper edge of the opening in the screen *s*, on either side of the aquarium. The glass tube was then put in place and a number of colonies introduced. The tube formed such close connections with the bottom of the aquarium that the colonies could not get out, but the water introduced with them could. As soon as a state of equilibrium was established, the colonies were set free by carefully raising the tube. After they had been exposed to the light from opposite directions for a few moments, the contents of the aquarium was divided into two equal parts by means of a piece of tin made to fit the groove represented at the middle of the ends of the aquarium, Fig. 15, *a*. The colonies in each half were then counted and the numbers recorded. The aquarium could be moved to the right or left along the metric gauge and in this way the intensity of the light entering opposite sides of the aquarium could be regulated. The candle power of the glower and the distances between it and each side of the aquarium being known, the difference in light intensity on opposite sides of any object in the middle of the aquarium could easily be calculated.

TABLE V.

Distance from glower to center of gauge 100 cm. Light intensity 27 candle meters.

| Position of aquarium. | | Number of colonies in left half of aquarium. | | | | | Number of colonies in right half of aquarium. | | | | | Ratio between totals. | Differential threshold. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| cm. | | In each trial. | | | | Total. | In each trial. | | | | Total. | | |
| | | *a* | *b* | *c* | *d* | | *a* | *b* | *c* | *d* | | | |
| To the right. | 1 | 18 | 11 | | | 29 | 30 | 26 | | | 56 | 1.931 | 1.080 candle meters = 4 per cent of light intensity at center of gauge. |
| | 0.5 | 29 | 19 | | | 48 | 31 | 22 | | | 53 | 1.104 | |
| At center of gauge. | | 27 | 18 | | | 45 | 29 | 21 | | | 50 | 1.111 | |
| To the left. | 0.5 | 37 | 25 | | | 62 | 34 | 22 | | | 56 | 1.107 | |
| | 1 | 32 | 24 | | | 56 | 21 | 12 | | | 33 | 1.696 | |

Distance from glower to center of gauge 200 cm. Light intensity 6.75 candle meters.

| Position of aquarium. | cm. | *a* | *b* | *c* | *d* | Total. | *a* | *b* | *c* | *d* | Total. | Ratio between totals. | Differential threshold. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| To the right. | 2 | 12 | 11 | 17 | | 40 | 20 | 20 | 17 | | 57 | 1.425 | 0.337 candle meters = 4.9 per cent of light intensity at center of gauge. |
| | 1.5 | 14 | 18 | 18 | | 50 | 20 | 23 | 22 | | 65 | 1.300 | |
| | 1 | 23 | 19 | 15 | | 57 | 21 | 37 | 20 | | 78 | 1.364 | |
| | 0.5 | 27 | 30 | 16 | | 73 | 25 | 38 | 13 | | 76 | 1.041 | |
| At center of gauge. | | 18 | 9 | 14 | 13 | 54 | 18 | 14 | 18 | 16 | 66 | 1.222 | |
| To the left. | 0.5 | 23 | 17 | 26 | | 66 | 24 | 13 | 21 | | 58 | 1.138 | |
| | 1 | 36 | 22 | 17 | | 75 | 30 | 14 | 21 | | 65 | 1.153 | |
| | 1.5 | 14 | 18 | 37 | | 69 | 8 | 16 | 24 | | 48 | 1.437 | |
| | 2 | 29 | 34 | 16 | | 79 | 17 | 21 | 11 | | 49 | 1.612 | |

Distance from glower to center of gauge 400 cm. Light intensity 1.6875 candle meters.

| Position of aquarium. | cm. | *a* | *b* | *c* | *d* | Total. | *a* | *b* | *c* | *d* | Total. | Ratio between totals. | Differential threshold. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| To the right. | 6 | 19 | 37 | | | 56 | 34 | 47 | | | 81 | 1.446 | 0.0842 candle meters—4.9 per cent of light intensity at center of gauge. |
| | 5 | 19 | 25 | 26 | | 70 | 27 | 29 | 38 | | 94 | 1.342 | |
| | 4 | 21 | 11 | 41 | | 73 | 22 | 14 | 42 | | 78 | 1.068 | |
| | 3 | 34 | | | | 34 | 34 | | | | 34 | 1.000 | |
| To the left. | 2 | 15 | | | | 15 | 16 | | | | 16 | 1.066 | |
| | 3 | 30 | | | | 30 | 31 | | | | 31 | 1.033 | |
| | 4 | 38 | | | | 38 | 34 | | | | 34 | 1.117 | |
| | 5 | 26 | | | | 26 | 20 | | | | 20 | 1.300 | |

TABLE VI.

Distance from glower to center of gauge 100 cm. Light intensity 27 candle meters.

| Position of aquarium. | | Number of colonies in left half of aquarium. | | | | | | | Number of colonies in right half of aquarium. | | | | | | | Ratio between totals. | Differential threshold. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | cm. | In each trial. | | | | | | Total | In each trial. | | | | | | Total. | | |
| | | *a* | *b* | *c* | *d* | *e* | *f* | | *a* | *b* | *c* | *d* | *e* | *f* | | | |
| To right of center of gauge. | 4.5 | 11 | | | | | | 11 | 26 | | | | | | 26 | 2.354 | 4.104 candle meters = 15.2 per cent of light intensity at center of gauge. |
| | 3.5 | 14 | 8 | 18 | 24 | 15 | 11 | 90 | 24 | 16 | 19 | 35 | 19 | 23 | 136 | 1.511 | |
| | 3 | 21 | 24 | 26 | 17 | 13 | 13 | 114 | 20 | 32 | 24 | 15 | 17 | 16 | 124 | 1.087 | |
| | 2.5 | 16 | 22 | 18 | 15 | 23 | 16 | 110 | 16 | 19 | 20 | 17 | 25 | 12 | 109 | 1.009 | |
| | 1.5 | 19 | 16 | | | | | 35 | 16 | 16 | | | | | 32 | 1.093 | |

Distance from glower to center of gauge 200 cm. Light intensity 6.75 candle meters.

| | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| To right of center of gauge. | 6.5 | 8 | 11 | | | | | 19 | 31 | 28 | | | | | 59 | 3.105 | 0.743 candle meters = 11 per cent of light intensity at center of gauge. |
| | 5.5 | 12 | 21 | 18 | 11 | | | 62 | 19 | 19 | 34 | 21 | | | 93 | 1.500 | |
| | 4.5 | 13 | 12 | 29 | 24 | | | 78 | 15 | 14 | 25 | 32 | | | 86 | 1.102 | |
| | 3.5 | 21 | 14 | 17 | 12 | | | 64 | 20 | 18 | 22 | 9 | | | 69 | 1.078 | |
| | 2.5 | 12 | 34 | 19 | 24 | 10 | | 99 | 22 | 37 | 15 | 19 | 10 | | 103 | 1.040 | |

Distance from glower to center of gauge 400 cm. Light intensity 1.6875 candle meters.

| | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| To right of center of gauge. | 11 | 13 | 29 | 18 | 26 | | | 86 | 26 | 39 | 23 | 28 | | | 116 | 1.348 | 0.1689 candle meters = 10 per cent of light intensity at center of gauge. |
| | 10 | 18 | 12 | 22 | 18 | | | 70 | 20 | 28 | 26 | 22 | | | 96 | 1.371 | |
| | 9 | 25 | 20 | 14 | 21 | | | 80 | 20 | 16 | 22 | 25 | | | 83 | 1.037 | |
| | 8 | 26 | 19 | 22 | 33 | | | 100 | 23 | 19 | 24 | 27 | | | 93 | 1.075 | |
| | 7 | 28 | 48 | | | | | 76 | 24 | 47 | | | | | 71 | 1.070 | |

The results recorded in Table V were obtained in experiments performed on August 22, 1904, and those recorded in Table VI in experiments performed on August 25. The experiments in both cases extended over a period of several hours. The specimens were collected at 6 a. m. on the day during which they were exposed. After being brought to the laboratory, they were kept in darkness or very dim light until used.

By referring to Table V, it will be seen that the minimum difference in light intensity on opposite sides of Volvox colonies which induced a reaction is approximately 4 per cent of the illumination on either side when the aquarium is 100 cm. from the glower, but 4.9 per cent when it is either two or four times as far away. Table VI shows that reaction is induced by a difference of 15.2 per cent when the distance between the aquarium and glower is 100 cm., 11 per cent when this distance is 200 cm., and 10 per cent when it is 400 cm. In accordance with WEBER'S law, the proportion between the difference and intensity on opposite sides and the intensity on either side should be the same in all degrees of illumination. The reactions of Volvox, as recorded in these tables, therefore, are not in perfect accord with this law. But in Table V the threshold is smallest in the highest light intensity, while in Table VI it is smallest in the lowest intensity. There was also a surprising difference in the threshold of the organisms used on the two different days, confirming the statement made elsewhere, that the reactions of these organisms at any given time depend largely upon previous environmental conditions. Considering these facts, it seems almost certain that the difference between the results recorded in the tables and those demanded by WEBER'S law are within the limits of error. If this be true the light reactions of Volvox may be considered to be in accord with this law.

## 19. SUMMARY.

1. The eye-spots in Volvox are located on the outer posterior surface of the individuals of which the colonies are composed, not on the outer anterior surface as represented by OVERTON.

2. They are much larger in the individuals at the anterior end than in those at the posterior end, and they probably function as light recipient organs.

3. In moving forward Volvox usually rotates on its longitudinal axis counter-clockwise, as seen from the posterior end. But under certain conditions the direction of rotation is frequently reversed. This is caused by continuous contact stimulation of the individuals located along the sides of the colonies.

4. In swimming horizontally Volvox colonies seldom move parallel with the light rays when exposed to light from a single source. They deflect upward or downward as well as to the right or left.

5. Specimens containing large daughter-colonies or spores deflect more strongly to the right than others. The degree of deflection depends upon the light intensity and the physiological condition of the organism as well as upon its contents. The more strongly positive they are, the more nearly parallel with the rays they appear to move as seen from above. When exposed to light of very low or very high intensity they deflect more than when exposed to light of moderate intensity.

6. The specific gravity of Volvox is greater than one. When not active or when dead the colonies slowly sink with the longitudinal axis vertical and the posterior end down. The vertical orientation under such conditions is much more precise in specimens containing large daughter-colonies than in others.

7. Volvox tends to swim in the direction of its longitudinal axis. Gravitation tends to cause this axis to take a vertical position. If the colonies are not strongly positive the anterior end is directed nearly straight up. If such colonies swim toward a source of light, the rays of which are horizontal, they deflect upward. But if the colonies are strongly positive the axis becomes nearly horizontal, and they tend to swim parallel with the rays. Under these conditions gravity causes them to sink gradually, so they deflect downward.

8. If the rays of light are parallel with the direction of gravitation, *i. e.*, vertical, and the source of light is above, the colonies swim upward in a narrow spiral course nearly parallel with the rays, but if the source of light is below and they swim downward, there is a tendency to turn over, owing to the difference in weight of the two ends, and this causes them to swerve to the side frequently.

9. Deflection to the right or left as well as deflection upward or downward, is caused by the effect of gravitation on the direction of the longitudinal axis in connection with rotation on this axis.

10. Deflection in negative colonies is in all essentials like that in positive.

11. If a colony is swimming at a given angle to the light rays and the direction of the rays is changed, the organism changes its direction of motion until it again takes a course which makes an angle with the rays equal to that it had before the ray direction was changed, *i. e.*, Volvox orients, but not necessarily so as to swim parallel with the rays.

12. If exposed to light of equal intensity from two sources, Volvox swims toward a point nearly half way between the two sources, provided it is strongly positive, but if the lights are unequal in intensity the colonies direct their course toward a point nearer the more intense light than the other.

13. If exposed to parallel rays such that one side of a colony, swimming toward the source of light, is more strongly illuminated than the other, it deflects toward the more strongly illuminated side.

14. Segments of a colony orient, in general, like normal colonies, but they usually take a spiral course, the width of which depends upon the form and size of the segment and the part of the colony from which it was taken.

15. The direction of motion in Volvox is regulated by the relative light intensity on opposite sides of the colony, regardless of the ray direction.

16. Orientation is not the result of "trial and error" reactions as in Stentor, Euglena and other forms. Volvox colonies make no errors in this process.

17. There is no evidence of motor reaction in a Volvox colony, taken as a whole. Orientation is, however, brought about by motor reactions in the individuals which constitute the colony. If opposite sides of a colony are unequally illuminated, the individuals in the colony continually pass from regions of higher to regions of lower light intensity and vice versa, as the organism rotates. This change in light intensity induces motor reactions in the individuals, which result in orientation of the colony. The motor reaction in positive specimens is induced only when the intensity to which the zooids are exposed is decreased, and in negative colonies only when it is increased.

18. In general, Volvox is positive in comparatively low and negative in comparatively high light intensities; that is, it has an optimum, but the optimum varies in the extreme. Colonies were found to be negative in intensities ranging from 57 to 5000 candle meters. The threshold also varies greatly, the lowest found being 0.14 candle meters.

19. Change in the sense of reaction can be induced by change in light intensity. It depends upon the physiological condition of the organism and the time of exposure as well as upon the intensity of the light. It cannot be induced by mechanical stimulation or change in temperature.

20. When compelled to move practically perpendicular to the rays, Volvox can still find its optimum in a field of light graded in intensity. Under such conditions it collects in the optimum intensity by merely wandering movements. There is no evidence of orientation or "trial and error" reactions of the kind that were found in Stentor under similar conditions (Mast '06, pp. 366-377).

21. If jars containing Volvox colonies are exposed to light from a single source, those specimens which contain large daughter-

colonies or spores, collect to the right of the region in the jars nearest the source of light; those without daughter-colonies or spores or with small ones collect nearest the source of light, but they spread out considerably both to the right and left. A majority of all the colonies are, therefore, usually found in that part of the jar to the right of the region of strongest illumination.

22. The cause of this collection to the right is found in the fact that when the specimens containing large daughter-colonies strike the wall of the jar, in swimming toward the source of light, they usually turn to the right. This is caused by the effect of gravitation, rotation, and contact stimulation.

23. Since the ratio between the difference in light intensity on opposite sides, which is sufficient to induce a reaction, and the intensity on either side is nearly the same for different degrees of illumination, WEBER's law holds approximately for the light reactions of Volvox.

## BIBLIOGRAPHY.

DAVENPORT, C. B.
1897. Experimental Morphology, *New York*, Vol. 1 and 2, 508 pp.
EHRENBERG, C. G.
1838. Die Infusions Thierchen als volkommene Organismen. *Berlin*, 532 pp.
ENGELMANN, T. W.
1882a. Ueber Licht und Farbenperception niederster Organismen. *Arch. f. d. ges. Physiol.*, Bd. 29, pp. 387–400.
FOCKE, G. W.
1847. Physiologische Studien. Erstes Heft. *Bremen*, p. 31.
HANSGIRG, A.
1888. Prodromus des Algenflora von Böhmen, Erster Theil, p. 101.
HOLMES, S. J.
1901. Phototaxis in the Amphipoda. *Amer. Jour. Physiol.*, Vol. 5, pp. 211–234.
1903. Phototaxis in Volvox. *Biol. Bulletin*, Vol. 4, pp. 319–326.
JENNINGS, H. S.
1904a. Contributions to the Study of the Behavior of Lower Organisms. *Carnegie Institution of Washington*, Publication No. 16, pp. 1–256, 81 Figs.
JONES, H. C.
1902. Elements of Physical Chemistry. *New York*, 549 pp.
KIRSCHNER, O.
1879, Zur Entwickelungsgeschichte, von Volvox minor. *Cohns Beitr. z. Biol. der Pflanzen*, Bd. 3, Heft 1, p. 95.
KLEIN, L.
1890. Vergleichende Untersuchung über morphologie und Biologie der Fortpflangung bei der Gattung Volvox. *Ber. d. Natur f. Ges. zu Freiburg, i. B.*, Bd. 5, Heft. 1, p. 92, Eaf. 5.
1889. Morphologische und biologische Studien über die Gattung Volvox. *Jahrb. f. wiss. Bot.*, Bd. 20, pp. 133–208.
LOEB, J.
1893. Ueber künstliche Umwandlung positiv heliotropischer Thiere in negativ heliotropische und umgekehrt. *Arch. f. d. ges. Physiol.*, Bd. 54, pp. 81–107.
1905. Studies in General Physiology. *Chicago.*

MASSART, J.
1888. Recherches sur les organismes inférieures. I. La Loi Weber vérifiée pour l'héliotropisme du champignon. *Bull. Belg. Acad.*, 16, pp. 590–597.
MAST, S. O.
1906. Light Reactions in Lower Organisms. I. Stentor cœruleus. *Journ. of Exp. Zoöl.*, Vol. 3, pp. 359–399.
MEYER, A.
1895. Ueber den Bau von Volvox aureus (Ehrenb.) und V. globator. *Bot. Centralb.*, Bd. 63, pp. 225–233.
OLTMANNS, F.
1892. Ueber die photometrischen Bewegungen der Pflanzen. *Flora*, Vol. 75, pp. 183–266.
OVERTON, E.
1889. Beiträge zur Kenntnis der Gattung Volvox. *Bot. Centralb.*, pp. 65–72.
PARKER, G. H.
1902. The Reactions of Copepods to Various Stimuli and the Bearing of this on Daily Depth Migration. *U. S. Fish Com. Bull. for 1901*, pp. 103–123.
PFEFFER, W.
1884. Locomotorische Richtungsbewegungen durch chemische Reize. *Unters. a. d. bot. Inst. Tübingen.* Bd. I, pp. 363–482.
1888. Ueber chemotaktische Bewegungen von Bacterien, Flagellaten und Volvocineen. *Untersch. bot. Inst. Tübingen*, Bd. 2, pp. 582–662.
RADL, EM.
1903. Untersuchungen über den Phototropismus der Tiere. *Leipzig*, 188 pp.
ROTHERT, W.
1901. Beobachtungen und Betrachtungen über tactische Reizerscheinungen. *Flora*, Bd. 88, pp. 371–421.
RYDER, J. A.
1889. The polar Differentiation of Volvox and the Specialization of possible anterior Sense-organs. *Amer. Natur.*, Vol. 23, pp. 218–221.
SACHS, J.
1887. Lectures on the Physiology of Plants. English Edition.
SHIBATA, K.
1905. Studien über die Chemotaxis der Isœtes-spermatozoiden. *Jahrb. f. wiss. Bot.*, Bd. 41, pp. 561–610.
STRASBURGER, E.
1878. Wirkung des Lichtes und der Warme auf Schwarmsporen. *Jenaische Zeitschr.*, N. F. Bd. 12, pp. 551–625.
TITCHENER, E. B.
1905. Experimental Psychology. *New York.* Vol. 2, Part 2, 424 pp.
TOWLE, ELIZABETH W.
1900. A study in the Heliotropism of Cypridopsis. *Amer. Jour. Physiol.*, Vol. 3, pp. 345–365.
WAGER, H.
1900. On the Eye-spot and Flagellum of Euglena viridis. *Jour. Linn. Soc., London*, Vol. 25, pp. 463–481.
WILLIAMS, W. C.
1853. Further Elucidation of the Structure of Volvox globator. *Transact. Quart. Journ. Micr. Soc.*, N. S., Vol. 1, pp. 45–56.
YERKES, R. M.
1903. Reactions of Daphnia pulex to Light and Heat. *Mark Anniv. Vol.*, Article 18, pp. 359–377.

# THE MID-WINTER MEETINGS AT NEW YORK.

The Convocation Week meetings held in New York City, December 27, 1906, to January 2, 1907, under the auspices of the *American Association for the Advancement of Science* were of unusual importance to all departments of science. The meeting is believed to have been the largest gathering of scientific investigators which has ever assembled in America, and undoubtedly was one of the most important in its influence on the course of research in this country. One of the most significant and encouraging features was the realization of a more cordial and effective coöperation among the various technical societies represented, in the interest of a broadening of scientific culture. Societies covering the same field as a rule combined their programs throughout; in other cases joint discussions of special topics were held under the auspices of the several societies concerned. The number of papers presented bearing on neurology and animal behavior was large, and we are able to print in this issue of the *Journal* abstracts of most of these contributions.

*The Association of American Anatomists* had a very full program, including a number of interesting neurological demonstrations. Among the papers read were the following.[1]

Experiments in Transplanting Limbs and their Bearing upon the Problem of the Development of Nerves. By Ross G. Harrison, *Anatomical Laboratory, Johns Hopkins University.*

Braus's[2] experiments were repeated in slightly different manner upon tadposel of Rana sylvatica and Bufo lentiginosus, but with results which show that his conclusions are not of general validity. The mode of procedure was as follows: The left hind limb bud, taken from a normal tapdole in a stage when the absorption of the yolk was about complete, was implanted into the left side of another individual of the same age and species; and similarly there was transplanted to the right side the right hind limb bud, taken from a larva of the same age, from which, however, the medullary cord had been removed shortly after closing over, and which in consequence had developed without nerves. In most cases, owing to a

---

[1] Taken from the Proceedings of the Association as prepared for the *American Journal of Anatomy.*

[2] H. Braus, Verhandlungen d. Anatom. Gesellschaft, 18 Versammlung in Jena, 1904; *Anatomischer Anzeiger*, Bd. 26, 1905.

probable injury at time of transplantation, a pair of limbs developed out of each transplanted bud, one by direct development and one by a process of budding or super-regeneration.[3] There were thus usually present in each specimen four distinct kinds of transplanted limbs, which may be termed primary and accessory normal, and primary and accessory nerveless.

The specimens were preserved from four to six weeks after the operation. Examination of serial sections shows that all four of the types of limb may, and in fact usually do acquire nerves of normal structure and arrangement, and that these nerves are always connected with the nerves of the host. In a typical specimen, in which all four transplanted legs contained nerves, the primary nerveless limb had a practically complete peripheral nervous system, derived from the sixth, seventh and eighth spinal nerves, *i.e.*, largely from nerves which normally do not enter the limb. In the accessory limbs of both sides the larger nerve trunks and some of the smaller branches were present, though a number of the branches, especially in the distal part of the limb, could not be found. All this is contrary to the observations of BRAUS, who found nerves only in the primary normal transplanted limbs. The difference in the results is due no doubt in a large measure to the fact that BRAUS did not keep his specimens alive sufficiently long after the operation.

The experiments cannot possibly be interpreted, as BRAUS interprets his, in accordance with HENSEN's theory of the development of the nerve paths. On the contrary, when we consider them in connection with my former experiments[4] we cannot but conclude that the nerves do actually grow from the host into the transplanted part, and further, that in so growing they are guided to the proper place by the peripheral organs themselves, for, it must be remembered, the nerves of the the transplanted limb except the n. cruralis are not derived from the same segmental trunks as the corresponding ones of the normal limb, and therefore the mode of branching cannot in any way have been predetermined in the nerves themselves.

## A Model of the Medullated Fiber Paths in the Thalamus of a New-born Brain.

By FLORENCE R. SABIN, *Anatomical Laboratory, Johns Hopkins University.*

The model is a reconstruction by the BORN method of the fiber tracts of the thalamus that are medullated at birth and shows their relation to the cortex and to the brain stem. In the pons, the medial lemniscus is shown as a band of fibers that separates the nuclei pontis from the tegmental part. On entering the mid-brain, the lemniscus begins to curve lateralward on account of the red nucleus. Just caudal to the red nucleus, the lemniscus gives off a small bundle of fibers to the substantia nigra. The main bundle of the lemniscus passes beyond the red nucleus on the way to higher centers, and divides into a ventral and a dorsal segment. The ventral segment is FOREL's *Feld H*, the dorsal his *Bath.* The ventral segment gives off a small bundle to the hypothalmic nucleus of LUY, similar to the bundle given off to the substantia nigra; a second larger mass of fibers curves into the hypothalmic region and enters the globus pallidus of the lenticular nucleus. The rest of the ventral segment passes to the ventro-lateral nucleus of the thalamus

---

[3] D. BARFURTH, *Arch. f. Entwickelungsmech.*, Bd. 1, 1894; TORNIER, *Arch. f. Entwickelungsmech.* Bd. 20, 1905; BRAUS, *op. cit.*

[4] HARRISON, *Am. Journ. Anat.*, vol. 5, 1906.

and its external medullated lamina. The bundles running to this nucleus represent the main tract to the cortex, for from the lateral surface of the ventro-lateral nucleus a large bundle of well-medullated fibers passes to the cortex of the lower part of the posterior central gyrus. The sensory path is almost entirely broken in the lateral nucleus. The dorsal segment of the medial lemniscus, FOREL'S *Bath*, passes to the *centre médian* of LUY and to the cup-shaped nucleus.

The motor path is medullated only down to the cerebral peduncle. It makes connections with the lenticular nucleus, the hypothalmic nucleus and the substantia nigra. The model shows that the motor and sensory paths are parallel throughout the brain stem. The sensory path is always dorsal to the motor. In the medulla, the paths are adjacent, in the pons, they are separated somewhat by the cells of the nuclei pontis; in the midbrain and hypothalmic region, the substantia nigra and hypothalmic nucleus come in between the two paths, while in the thalamus and subcortical regions, they are adjacent.

In the thalamus, the nuclei that contain medullated fibers from the medial lemniscus are the lateral nucleus, the *centre médian* of LUY, and the cup-shaped nucleus. The lateral geniculate body and the pulvinar have medullated optic fibers, while the medial and anterior nuclei contain no medullated fibers whatever. The fasciculus retroflexus stands out very clearly, however, passing through the lower border of the medial nucleus.

Development of the Inter-forebrain Commissures in the Human Embryo. By GEORGE L. STREETER, *Wistar Institute of Anatomy, Philadelphia.*

A morphological study of the corpus callosum, anterior commissure and the commissure of the hippocampus, based on a series of wax-plate reconstructions of human embryos varying from 80 to 150 mm. in length. All three structures cross the median line in that portion of the brain wall developed from the lamina terminalis. In 80 mm. embryos, the corpus callosum consists of a round bundle of fibers lying directly on the commissure of the hippocampus, representing the condition found in non-placental animals. The succeeding growth consists in the lengthening of the fornix and caudal migration of the hippocampal commissure, the latter remaining in close relation to the caudal end of the corpus callosum, which, in the meantime, by increase in number of fibers has extended anterior to the anterior commissure and posterior so as to deck over the region of the third ventricle. The formation of a cavity in the septum lucidum occurs in embryos of about 95 mm. The anterior or olfactory division of the anterior commissure does not enter the olfactory bulb but is traced to the cortex dorsal to the bulb.

The Relations of the Frontal Lobe in the Monkey. By E. LINDON MELLUS, *Anatomical Laboratory, Johns Hopkins University.*

The Terminal Distribution of the Eighth Cranial Nerve in Man. By JOSEPH H. HATHAWAY, *Cornell University Medical College, Ithaca, N. Y.*

Statistical Studies of the Brachial Plexus in Man (A Preliminary Note). By ABRAM T. KERR, *Cornell University Medical College, Ithaca.*

These studies are based on the record of 175 plexuses dissected and drawn by students, mostly in the Johns Hopkins Medical School, some in Cornell. The records were verified in order of time by Drs. ELTING, BARDEEN, and KERR. This note deals with the type of plexus according to the origin and combination of branches. Seven types are recognized: A. With outer cord formed from the 4th to the 7th nerves inclusive, the inner from the 7th to the 9th, the posterior from the 4th to the 8th, occurred in .57 per cent of cases; B, like A except posterior cord which was formed from the 4th to the 9th in 1.71 per cent of cases; C, with outer cord from 4th to the 7th, inner from 8th to the 9th and posterior from 4th to 9th, in 58.28 per cent of cases; D, like C except outer cord from 4th to 8th in 2.28 per cent of cases; F, with outer from 5th to 7th, inner from 8th to 9th, posterior from 5th to 9th, in 29.77 per cent of cases; G, like F, except the 5th sends a branch to the 4th, in 6.85 per cent of cases; H, like G, except the outer cord from the 5th to the 9th, in .57 per cent of cases. No record was made of the relation of the 10th spinal nerve to the plexus. Attention was also called to the outer head of the ulnar nerve which when searched for will be found in over 50 per cent of the cases.

A Racial Peculiarity in the Temporal Lobe of the Negro Brain. By ROBERT BENNETT BEAN, *University of Michigan.*

Measurements were made of 236 temporal lobes, 54 from white brains and 182 from negro brains. Six measurements were made from fixed points on each temporal lobe, at three levels, two at the base (antero-posterior and transverse), 2 at 1 cm. toward the pole, and 2 at 5 mm. from the tip of the temporal lobe. At each level, the lobe is smaller in the negro, more nearly approaching the white in size at the base, and diverging from the white in size as the pole is approached. The widest divergence is found in the transverse measurement about the middle of the temporal lobe. There is a variable difference with a mean of about 5 mm. in each measurement. The temporal lobe of the negro is more slender than that of the white, narrower transversely, and more pointed at the extremity, the length being about the same in each race. The differences in general conform to the other characteristics previously described in the negro brain.

Supplementary Report regarding the Innervation of the Leg of Rana virescens. By ELIZABETH H. DUNN, *Department of Anatomy, University of Chicago.*

A partial report upon this material was made at the 1905 meeting of the Association. The histological examination of the muscle on the operated side in which all the efferent neurones were degenerated, shows but a slight change from the normal. The cross striations were not obliterated and the nuclear staining was unaltered. The staining with acid dyes was slightly less deep in the muscles of the operated side. The bulk of muscle seemed unchanged.

As the counting was done upon osmic acid material, only medullated nerve fibers entered into the enumerations. On the intact side, both afferent and efferent fibers were present. On the operated side, the efferent fibers had been eliminated, and the count was of afferent fibers destined for the skin and for the muscles. Among both the afferent and the efferent fibers, splitting occurred. This splitting was in the main trunks of the various segments of the leg. In both classes, the proportion of splitting fibers increases progressively from the thigh to the foot.

A greater amount of splitting occurred among the purely afferent fibers of the operated side than among the mixed nerves of the intact side. Hence the proportion of splitting afferent fibers is greater than that of splitting efferent fibers. This splitting seems to occur in both the cutaneous and muscular afferent fibers. This result carries with it some important physiological corollaries, as for instance that some afferent neurones must have two "local signs" according to the point at which they are stimulated. In considering the distribution to the various segments, correction must be made for the splitting fibers.

When this is done, it is found that the unit area of skin received the same number of afferent fibers in either the thigh, shank or foot. In a similar way, a study of the muscular afferent fibers shows that the muscles are uniformly innervated by muscular afferent fibers according to the unit weight of muscle.

### The Electric Organ of Astroscopus as Compared with that of Other Fishes. By CHARLES F. SILVESTER, *Princeton University.*

### Concerning a New Ganglionic Mass of the Hind-brain, the Corpus Ponto-bulbare. By CHARLES R. ESSICK, *Student of Medicine, Johns Hopkins University.*

A ganglionic mass accompanied by a layer of myelinated fibers is found overlapping the restiform body just caudal to the dorsal cochlear nucleus. It forms a direct lateral process or extension of the ganglion mass of the pons. It is constantly present in all human brains, though in some brains it reaches a greater size than in others. Its relations and general characteristics are constant. It makes its appearance on the ventro-lateral surface of the pons near the emerging root bundles of the trigeminal nerve and extends backward, passing between the roots of the facial and acoustic nerves. It continues caudalward passing dorsal to the glossopharyngeal nerve and ends on the dorsal surface of the restiform body, forming part of the lateral boundary of the fourth ventricle. It may end as a prominent tongue-shaped mass or may spread out as a thin coating of the restiform body that is only discernible microscopically.

### The Migration of Medullary Cells into the Ventral Nerve-roots of Pig Embryos. By F. W. CARPENTER and R. C. MAIN, *University of Illinois.*

In sections of pig embryos 11 mm. long, medullary cells were observed apparently migrating from the neural tube in company with the fibers of the ventral nerve roots. These cells have been found just inside the external limiting membrane in an intermediate position half in and half out of the neural tube and in the base of the nerve root just outside the limiting membrane. A few sections show continuous lines of medullary cells, touching end to end and reaching from the nidulus across the boundary of the tube into the proximal part of the nerve root. These migrant cells do not appear to be directly connected with the embryonic nerve fibers. A few were observed undergoing mitotic division. Evidence of a similar migration of medullary cells has been seen in sections of a cat embryo.

In these medullary elements escaping from the neural tube, we recognize the "indifferent cells" of SCHAPER. Such cells remaining in the medullary wall become either supporting elements (neuroglia cells) or nervous elements (neurones). Those which escape, in part at least, probably contribute to the formation of the sheaths of SCHWANN, which are supporting in function. Whether any migrant indifferent cells become the nerve cells of sympathetic ganglia we are at present unable to say.

### Glycogen in the Nerve Cells of the Brain and Spinal Cord of Larval Lampreys and in the Central Nervous System of the Amphioxus from Naples. By SIMON H. GAGE, *Cornell University.*

At the ninth annual meeting of the *American Physiological Society*, the following papers of special interest to neurologists were presented:

Functions and Structures in Amœba proteus. By C. F. Hodge and O. P. Dellinger.

The material of this study consisted of Amœba which had been killed in various ways and stained *in toto*, and of series of sections stained by different methods. The function of contraction is effected by a meshwork of fibrillæ, these being woven into heavy trabeculæ with wide intertrabecular spaces in the interior (endosarc), and united to form a fine web over the exterior (ectosarc). This mechanism is all that can be demonstrated to account for movements: locomotion, ingestion, egestion, contraction of vacuole, division of nucleus and of entire body, and internal circulation. This tissue forms, without essential differentiation, the outer membrane (ectosarc), trabeculæ, wall of contractile vacuole and of all food vacuoles, nuclear membrane and nuclear reticulum. Movements are coördinated, but no differentiation of conducting fibrillæ has been clearly demonstrated. This tissue, when supplied with necessary nutrient substances, must possess the function of growth. The function of digestion is mediated in all animals by gland cells, characterized by zymogen granules. The only structure in Amœba which is definitely granular is the nucleus. Sections show nuclear granules apparently passing out of the nucleus into the food vacuoles. These two mechanisms, together with a circulating fluid, account for all the functions of the animal, reproduction being undifferentiated from growth, and respiration, excretion and circulation being effected by movements of the whole body and supplemented by a similar action of the contractile vacuole. Except as noted above, sections reveal no difference between ectosarc and endosarc.

Physiological Reactions of Physa. By J. Dawson.

Vasomotor Reflexes. By W. T. Porter.

The Cause of Treppe. By F. S. Lee.

Methods of Studying Fatigue. By F. S. Lee.

The Functions of the Ear of the Dancing Mouse. By R. M. Yerkes.

Both the static and the acoustic functions of the ear of the dancer differ markedly from those of the common mouse. Orientation and equilibration are fairly good. There is no evidence of turning dizziness. The whirling movement which is characteristic of the race appears as soon as the young mouse is strong enough to stand. It is somewhat more pronounced in the female than in the male, and it occurs chiefly toward evening. With respect to this movement there are three well defined groups of dancers: those which almost always whirl toward the right, those which whirl toward the left, and those which whirl now one way now the other. At present, I have no satisfactory evidence of the inheritance of the tendency to whirl in a certain way.

Direct and indirect methods of testing acoustic sensitiveness have given negative results in the case of the adult, but the young dancer responds to certain sounds for from two to five days during the third week of life. This brief period of sensitiveness to sound is preceded by a marked change in behavior.

The Effect of Section of One Vagus upon the Secondary Peristalsis of the Œsophagus. By S. J. Meltzer and J. Auer.

### On the Alleged Adaptation of the Salivary Glands to Diet. By F. P. UNDERHILL and L. B. MENDEL.

The experiments reported corroborate the current statement that the saliva of dogs and cats is devoid of amylolytic properties. NEILSON and TERRY (*American Journal of Physiology*, vol. 15, 1906, p. 406) have announced that dog's saliva frequently will digest starch; and they claim to have increased the amylolytic power by appropriate (carbohydrate) feeding. An inspection of their data, however, indicates that the amylolytic activity is not very pronounced when compared with that ordinarily observed in human saliva. We have failed to note similar results in ordinary dogs and to obtain adaptation in animals maintained on a special diet rich in starchy foods. Special attention was devoted to the conditions under which the digestion trials were conducted.

After the presentation of this paper Dr. NEILSON stated that he had additional evidence obtained since the publication of his paper with Dr. TERRY, of adaptation of the salivary glands in man as well as in dog.

### Some Observations on the Œsophagus after Bilateral Vagotomy. By W. B. CANNON.

### On the Mechanism of the Refractory Period in the Heart. By A. J. CARLSON, *University of Chicago*.

One series of the experiments was directed toward determining whether the refractory state of the heart is a property of the heart muscles or the nervous tissue or both. The other series aimed to determine the degree of refractory state exhibited by the different parts of the vertebrate heart. If there is a causal connection between automatism and a refractory state in the sense of an absolute inexcitability, we ought to find this condition in the *primum movens* of the heart, the sinus, or in mammals, the mouth of the great veins; and we would expect a less degree of refractory state or even none at all in parts of the heart not automatic, for example, the tortoise ventricle or the apex of the frog ventricle.

I. *The Tissues of the Heart Concerned in the Property of the Refractory State.* 1. The automatic heart ganglion of Limulus exhibits the typical refractory period of the heart or a state of reduced excitability during systole.

2. As long as the heart ganglion is in physiological connection with the heart muscle, the heart muscle and nerve plexus exhibit a condition of reduced excitability at the beginning of systole. This result is obtained from all regions of the heart. A stimulus strong enough to produce an extra beat by acting on the heart muscle and nerve plexus fails to produce any visible effect when sent through the same tissues, at the beginning of the normal systole.

3. Do the Limulus heart muscle and motor nerve plexus exhibit a systolic refractory state after being severed from the ganglion? The results of the experiments were not conclusive, mainly because of the difficulty of getting a series of contractions of absolutely uniform amplitude from the Limulus heart after the nerve cord is removed.

4. Is the refractory state in the vertebrate heart a property of the heart muscle apart from the intrinsic heart ganglia and nerve plexus? (1) It is needless to say that this question has not so far, and perhaps never can be, attacked by direct experiments. ROHDE and SCHULTZ have attempted to settle this question by studying the action of chloral hydrate on the heart. But in chloral hydrate nar-

cosis a systolic refractory period in the sense of diminished excitability is in evidence as long as the heart retains excitability and contractility. (2) Nerve tissue probably dies sooner than muscular tissue when circulation and nutrition are stopped. If the refractory state depends on the nervous tissue in the heart, the excised or dying heart ought to exhibit a condition of diminished or abolished refractory state in the later stages while it still retains some excitability and contractility. But even in the last stages of dying the ventricular tissue or tissues retain the property of systolic refractory state in the sense of diminished excitability. (3) The sodium chloride rhythm of the ventricular apex is probably idio-muscular. In case the refractory period is a property of the nervous tissue alone we might expect a diminution or abolition of the systolic refractory state in this rhythm. But fresh ventricular strips exhibit practically as marked refractory state in the sodium chloride rhythm as in the normal rhythm.

It is therefore evident that *the question whether heart muscle when isolated from the intrinsic nervous tissues exhibits the property of refractory state to greater degree than skeletal and smooth muscle is still an open one, since the facts bearing on the question can be interpreted either way.* In Limulus the heart ganglion exhibits the typical refractory period of heart tissue, and as this is a characteristic of at least many ganglion cells in the central nervous system of vertebrates, it is probable that the ganglion cells in the vertebrate heart possess a systolic refractory state similar to that of the Limulus heart ganglion.

II. *The Degree of Refractory State in the Heart of Different Animals, and in the Different Parts of the Heart of the Same Animal.* 1. The ventricles of higher vertebrates do not exhibit the same degree of refractory state. A strong induction shock sent through the ventricle at the beginning of systole produces a supermaximal beat in the frog, toad and salamander, but not in the tortoise. In the case of the latter the strong induction shock diminishes the amplitude of the beat. But inasmuch as the inhibition of a phenomenon is just as much evidence of irritability as the augmentation of it, it is obvious that even the tortoise ventricle is excitable at the beginning of systole. The refractory state in the heart is therefore a condition of diminished excitability and not a state of absolute inexcitability.

2. The degree of refractory state is not necessarily the same in the different parts of the heart of the same animal. In one tortoise (Cistudo) supermaximal beats are readily produced in the sinus venosus by stimulation at the beginning of systole, while the ventricle responds to the same stimulation with a diminution of the beat.

3. There is probably no causal connection between the property of automatism and the property of refractory state, for the following reasons: (1) The property of refractory state is exhibited by tissues that do not have the property of automatism under normal conditions—the apex of the frog and tortoise ventricle, nerve centers or ganglion cells in the central nervous system, the mammalian intestines (Magnus), the nerve plexus and heart muscle of Limulus. (2) Some tissues that are normally automatic do not exhibit an absolutely refractory state, but only a condition of greatly diminished excitability—the hearts of invertebrates, the hearts of many vertebrates. (3) In the same heart the parts possessing the greatest degree of automatism may exhibit a less degree of refractory state than the part of the heart not automatic.

At the fifteenth annual meeting of the *American Psychological Association*, the following papers in the fields of comparative psychology and sense physiology were read:

The Photography of Ocular Movements. By G. M. STRATTON.

The Rotation of the Eye during Fixation and in Movement. By C. N. McALLISTER.

Studies in Binocular Depth Perception. By J. C. BELL.

Some Results of Experiments on Cerebral Circulation during Sleep. By J. F. SHEPARD.

This was a preliminary report on volume reactions during sleep while the subject was lying down. Two subjects were used. For part of the records the influence of movements was eliminated by placing the subject's head in a swing.

With the first subject, the volume of the brain and of peripheral parts increases as he goes to sleep, and decreases as he awakes. There is often a temporary fall of the brain volume preceding the more marked rise which shows itself as sleep becomes deeper. There is a prominent breathing wave in the records from both brain and periphery. In this wave, the fall in the circulation record very nearly corresponds to an inspiration, the rise to an expiration. Stimuli that disturb but do not awake the subject cause a temporary increase in breathing in both chest and abdomen, a fall of volume of the brain and peripheral parts with comparative elimination of the breathing wave therein. While the subject is sleeping soundly and there are apparently no distinct stimuli acting, one often finds a more or less rhythmic repetition of such changes, analogous to the TRAUBE-HERING wave. There is always some evidence of this wave, and the changes in brain and periphery are always parallel. If discussed in detail, these statements would require some modification.

With the second subject the results have not been so definite. There is usually a distinct increase of volume of the brain when he goes to sleep, and in several cases there is a marked fall with awakening. The TRAUBE-HERING wave in the volume and in the breathing is not so prominent, but is still present; and its relations are the same. The breathing wave in the brain curve, on the other hand, often seems to follow the depth of breathing, and to be larger while the subject is awake. The variations may be due in part to the fact that the subject was more nervous, and never slept very soundly nor very long during the experiments.

The Difference between a Habit and an Idea. By S. H. ROWE.

The Relation of Imitation to the Theory of Animal Perception. By G. H. MEAD.

Kinæsthetic and Organic Sensations: Their Rôle in the Reactions of the White Rat to the Maze. By JOHN B. WATSON.

The work here reported grew directly out of the experiments carried out some years ago by SMALL at Clark University. In our experiments a maze very similar to the one used by SMALL was adopted. The floors and sides of the galleries, however, were made of four inch boards instead of wire netting. Very gentle male rats were used in all crucial experiments. An accurate record was kept of the formation of the maze association, consisting of the variations in time, number of errors, and so on. The normal behavior in learning the maze was first observed. Nineteen normal rats were used for this purpose.

Tests were then made to determine the principal sense organs used in learning the maze. Normal rats which had previously learned the maze in the light, were tested with the maze in the darkness. All the rats with one exception, ran the maze perfectly in the dark. Normal animals were then allowed to learn the maze in the dark from the beginning. Their records were quite normal. It was found that animals trained to the maze in the light can run the maze almost perfectly after both eyeballs have been extirpated. Likewise untrained rats, with both eyeballs removed, can learn the maze in normal time.

Animals without olfactory bulbs learn the maze in normal time, two of our animals making phenomenal records. These anosmic animals after being trained to the maze in the light are not at a loss if forced to run the maze in the dark.

From further experiments, which we shall not report in detail, it becomes evident that neither auditory sensations nor cutaneous sensations set up in the drum membrane by the changes in the pressure of the various air columns in the maze play a part in the formation of this association. Likewise it is improbable that the discrimination of the correct turns in the maze is effected by means of differences in the contact values of the various parts of the floor of the maze. The vibrissæ, which are probably used in the beginning of the association, are not used after the association has been thoroughly established; for if after their removal a short period of adaptation is allowed the rats in their living cages, no disturbance in their reactions is noticeable when they are forced to run the maze. The correct turns are likewise not made upon the basis of any possible difference in the temperature in the various places in the maze. Differences in the pressure of the air columns do not form the basis of the discrimination for changing the air pressure does not disturb the rats.

It is of interest to note that the simple turning of the maze through the angles of 45°, 90°, etc., badly disturbed both the normal and the defective animals for the first three or four trips after the change was made. The method adopted in this case was as follows: The animals, *e.g.*, were allowed to learn the maze with the entrance south; after they had become thoroughly familiar with it in this position the entrance was placed east. Now, although the relations of the turns within the maze are exactly the same as with the entrance south, the animals are confused. No explanation of this is offered at present.

Summarizing the results obtained from this series of experiments, we may say that neither visual, auditory nor tactual sensations furnish the animal with the cue for making the correct turns in the maze. The final conclusion is that kinæsthetic and organic sensations are the principal sensory factors in this association. A suggestion as to how the kinæsthetic sensations are "controlled" is offered.

This paper is to appear soon as a monograph supplement to the *Psychological Review.*

Habit Formation in the Starfish. By H. S. Jennings.

An account of experiments showing that by a course of training the starfish may be induced to use habitually a certain pair of rays on which to turn in the righting reaction. The habit lasted in certain cases three or four days.

Modifiability of Behavior in the Dancing Mouse. By R. M. Yerkes.

Visual discrimination tests show that the dancer avoids a disagreeable stimulus after about one hundred experiences. This modification of behavior occurs more quickly in the male than in the female. It persists several weeks.

Labyrinth tests are serviceable in the study of the dancing mouse only when the avoidance of an unfavorable condition is demanded. Neither escape from confinement nor the obtaining of food furnishes satisfactory motives for the following of a labyrinth path. The animal can find its way readily in a simple labyrinth without the guidance of sight, smell and touch. Thus far my experiments indicate the superiority of the female in the acquirement of labyrinth habits.

Further Study of Variability in Spiders. By J. P. PORTER.

Results indicative of the variability of the instinctive behavior of spiders were reported.

The Effect of Distraction upon the Intensity of Sensation. By I. M. BENTLEY.

Some Contributions to Applied Tone-psychology. By C. E. SEASHORE.

Total Reactions. By E. H. CAMERON

Non-sensory Components in Sense Perception. By R. S. WOODWORTH.

The familiar "staircase figure" presents a problem which may be stated in the following terms: What is the difference in conscious content between seeing the figure as the upper side and as the lower side of a flight of stairs? Previous work has shown that the difference cannot be ascribed to the stimulus; and inquiry by the author showed that there was no detectable sensory imagery present in consciousness that could serve to differentiate the two appearances. The two appearances have, not different sensory qualities, but what may be called different "percept qualities." Other non-sensory percept qualities are found in the subjective grouping of dots, in a subjective rhythm, in perception of size and distance, and in perception of things. A percept is not properly described as a synthesis of sensation and image, for the image is often not present when the percept is perfectly clear and definite. It is better to call the percept simply a mental reaction to sensory stimulus, and to recognize that a reaction, as a new event, probably has a quality of its own. This point of view is borne out by brain physiology, especially by cases of word-deafness, etc., in which there is a loss of mental content, without a corresponding loss of sensory consciousness.

Visual Pressure Images: Their Nature and their Relations to the Visions due to Mescal and other Drugs. By E. B. DELABARRE.

Indications of Incipient Fatigue. By W. S. MONROE.

BENJAMIN RUSH, M. D., On Mental Diseases. By I. W. RILEY.

Section F. (Zoölogy) of the *American Association for the Advancement of Science* and the *American Society of Zoölogists* held joint sessions for the reading of papers, during which the following papers, among others, were read:

The Artificial Production of a Single Median Eye in the Fish Embryo by Means of Sea-water Solutions of Magnesium Chlorid. By CHARLES R. STOCKARD, *Columbia University.*

Fundulus embryos when developed in certain strength solutions of $MgCl_2$ in sea-water form a large single median eye. This condition is comparable to the one eyed human monsters known as Cyclops, Cyclopia or Synophthalmia.

The single eye results from an antero-medio-ventral fusion of the elements of the two optic vesicles at an early developmental stage. This fusion is more or less complete in the different embryos.

The large compound optic cup induces the formation of a single lens. This lens is formed from ectoderm different in position from that of the normal lens forming region. The lens is abnormally large in size as is also the optic cup, and the size of the former varies directly with that of the latter. It is probable that there is no localization of lens forming substance in the ectoderm of the fish embryo. This inter-relationship in the development of the optic cup and lens is interestingly compared with the processes of development in the amphibian eye as shown by recent experiments.

Mixed sea-water solutions of $MgCl_2$ and NaCl also cause the one eyed condition. Since such a defect is characteristic of the $MgCl_2$ action when used in sea-water solutions one must infer that the Mg constituent in the mixture is responsible for the result.

### On the Place of Origin and Method of Distribution of Taste Buds in Ameiurus melas. By F. L. Landacre, *Ohio State University.*

This paper appeared in full in the last issue of this *Journal.*

### The Central Reflex Connections of Cutaneous Taste Buds in the Codfish and the Catfish: An Illustration of Functional Adaptation in the Nervous System. By C. Judson Herrick, *Denison University.*

The substance of this paper appeared in the article by the same author in the last issue of this *Journal.*

### Some Little-known Shark Brains, with Suggestions as to Methods. By Burt G. Wilder, *Cornell University.*

This paper continues that of which an abstract was printed in *Science* for May 26, 1905. Now first, so far as I know, are shown the brains of Heterodontus (Cestracion) and Pristiophorus. With the former the cerebrum and cerebellum resemble those of the "acanth" (Squalus acanthias), indicating an antiquity little if any greater. Notwithstanding certain ectal resemblances of the two dentirostral genera, Pristis, the "saw-ray" and Pristiophorus, the "saw-shark," their brains differ markedly, the latter being the more primitive. Their inclusion within the same family or even the same division would seem to me an error only less in degree than would be their combination with Xiphias, Polyodon and Psephurus as "Rostrata," or than was Günther's association of Ganoids and Selachians as "Palæichthyes," aptly characterized by Gill as a "piece of scientific gaucherie." Upon encephalic grounds I think Pristiophorus and Scymnorhinus should be excluded from the Squalidæ, and Sphyrna from the Carchariidæ. The brain of each selachian genus is, I think, recognizable, but I am less certain as to family forms. The Notidanoid or Diplospondylous type is well marked, and includes Scymnorhinus. At present the rays cannot be distinguished from the sharks in any such simple way as, *e. g.*, the Anura may be from the Urodela by the secondary fusion of the olfactory bulbs. Perhaps, in no shark is the prosocele so nearly obliterated as it seems to be in all rays. In no ray do the cerebral protrusions remain unconjoined as in some sharks; but, paradoxically, in no ray is there, as in several sharks, so nearly a complete obliteration of the evidence of their primary independence. Under "Methods" may be enumerated: (1) The need of well-preserved brains of all species; (2) maintaining the natural contours, especially of thinner parts, by injecting the preservative into the cavities; (3) making solid injections of the cavities; (4) exposing brains with a "shoe-knife," obliquely shortened; (5) exploring with the "syringotome" or canaliculus knife; (6) the use of sheets of uniform size, say 35 x 45 cm., upon which, in a manner permitting change, are drawn outlines of the animal and of its characteristic parts, especially the brain; such sheets may be arranged and rearranged upon the wall so as to facilitate research and exposition to small classes.

### An Experimental Study of the Image-Forming Powers of Various Types of Eyes.

By LEON J. COLE, *Rhode Island Agricultural Experiment Station, Kingston, R. I.*

The responses of certain phototropic animals to two areas of light of different size, but of equal intensity, were used as criteria in drawing inferences as to the image-forming powers of their eyes. To one side was a ground-glass, lighted from behind, which gave an evenly illuminated area 41 cm. square. To the other side was practically a point of light; but at the position midway between them, where the experiments were performed, the intensities of the two lights were equal. Eyeless forms (the earthworm was used) turned practically an equal number of times toward each light, showing no power of discriminating between them. Animals with "direction eyes" were but little better in this respect (*e. g.*, Bipalium, Oniscus, larva of Tenebrio). On the other hand, animals with well-developed "compound eyes" (Vanessa, Ranatra) and "camera eyes" (frogs) discriminated readily, positive animals turning much more often to the large light, and negative animals more often to the small. This discrimination was taken as evidence of image-formation by the eyes. Frogs (Acris gryllus) with the skin covered but eyes exposed reacted like normal frogs; without the use of the eyes their responses corresponded to those of the earthworm.

We have thus a physiological test of the image-forming powers of the eyes, and in these experiments it corroborated in the main inferences which would be drawn from a study of the structure of the eyes in question.

### The Influence of Direction vs. Intensity of Light in Determining the Phototropic Responses of Organisms.

By LEON J. COLE, *Kingston, R. I.*

The large land planarian, Bipalium kewense, was the principal animal experimented with. Its responses were first tried to shadows from a light directly overhead, *i. e.*, non-directive. It was then tested in a *partial* shadow, a strip of less intense light in an area of more intense illumination. In this case all the light came from one direction, namely, horizontally from one side. Although strongly negative, the worms would crawl directly *toward* the light in the partial shadow rather than turn out into the greater intensity. A similar result was obtained with the earthworm (Allolobophora fœtida). In these experiments Bipalium and Allolobophora appeared to respond to *intensity* alone, regardless of the direction of the impinging light.

The Sense of Vision in the Dancing Mouse. By ROBERT M. YERKES. *Harvard University.*

That brightness vision is fairly well developed in the dancer is shown by its ability to discriminate blacks, greys and whites. Color vision is extremely poor. There is some indication of the discrimination of red and green and of red and blue, but none whatever of blue and green. All my experimental tests as well as my observations of the habits of the mouse support the conclusion that such visual guidance as is received results from stimulation by brightness differences. There are many reasons for believing that the red end of the spectrum is much lower in brightness value for the mouse than for man. The general behavior of the dancer and the results of form, brightness and color tests show that vision is not very important in the life of the animal.

The Breeding Habits of the Florida Alligator. By ALBERT M. REESE, *Syracuse University.*

The habits of the alligator were studied during parts of three summers in the Everglades, in the swamps of central Florida, and in the Okefenokee Swamp. The time of laying is the month of June, usually during the second and third weeks. The nests, which are built on the bank near the caves of the alligators, vary considerably in size, and consist of a very compact mass of damp, decaying vegetation. They probably serve more as a means of keeping the eggs moist and at a constant temperature than as a means of heating them. The average number of eggs in a single nest is about thirty, forty-eight being the greatest number found in one nest. The eggs are so closely packed in the nest that it seems hardly possible that the young alligators, on hatching, should be able to dig their way out; it is possible that the female who laid the eggs may hear the noise made by the young before hatching and may dig them out of the nest before they suffocate. The period of incubation is probably about eight weeks, and sometimes is found to have begun before the eggs are laid, so that eggs taken directly from the oviducts may contain well advanced embryos. There is considerable variation in the size of the eggs, the variation in long diameter being greater than that in short diameter. The average long diameter of the four hundred eggs measured was 73.742 mm. The average short diameter was 42.588 mm.

Analysis of the Cyclical Instincts of Birds. By FRANCIS H. HERRICK, *Western Reserve University.*

The behavior of wild birds is primarily determined by a number of commanding instincts of ancient origin. These cardinal instincts are of two kinds, namely: (1) *continuous instincts*, which are needed for the preservation of the individual, such as preying, fear, concealment and flight, and (2) *cyclical instincts*, which are necessary for the maintenance of the race. By cyclical instincts we mean those discontinuous, recurrent impulses which attend the reproductive cycle, and which may be described as parental instincts.

The cyclical or parental instincts as a rule recur with almost clock-like precision, in spring or summer, with repetitions within the breeding season in certain species. They are modified by the continuous instincts, such as fear, and the instinctive behavior as a whole is liable to modification at every point by intelligence. Neglecting such changes for the present, we will briefly analyze the cyclical instincts, reserving details and tabular statements for a fuller presentation.

The reproductive cycle is made up of a series of terms, representing discrete acts or chains of actions in a definite succession. Eight or more terms may be recognized, many of which, such as brooding and feeding the young, are recurrent within the series. The cycle may be graphically represented by a series of tangent circles, each one of which stands for a distinct sphere of influence, or subordinate series of related impulses, named and numbered as follows: (1) Spring migration; (2) courtship and mating (often attended by song); (3) selection of nesting site and building nest (often accompanied by the fighting instinct); (4) egg-laying; (5) incubation—including care of eggs, such as shielding, rolling, cleaning and covering (fear often completely blocked by brooding instinct); (6) care of young in nest, subject to the following analysis: (*a*) feeding young, including capture and treatment of prey, return to nest (pause), call-stimulus, testing reflex response of throat, watching for reflex response (pause); (*b*) inspection of young and nest; (*c*) cleaning young and nest; removal and disposition of excreta; (*d*) incidental care of young and incidental behavior in this and other terms of cycle—brooding, shielding or spreading over young whether sitting or erect, bristling and puffing, preening, gaping, stretching and yawning, guarding and fighting; (7) care and incidental education of young when out of nest; guarding, feeding, play, and other instinctive acts; (8) fall migration. Beginning at 2, 3 or 4, according to circumstances, the cycle may be repeated once or oftener within the season.

The coördinated instinctive responses of the young begin in the sixth term, and are mainly as follows: (6) Initial responses at moment of hatching or shortly after, including grasping movements of limbs, elevation of head, opening of mouth, and the swallowing reflex in response to contact of bill of old bird or of food in deep part of throat; characteristic actions in muting following feeding, in response to the attitude of inspection in adult; call-notes, pecking, and gaping, stretching, and spreading in response to heat, flapping, fear and flight; (7) calling (teasing), following, crouching and hiding, play, imitation, preying and flight; (8) fall migration.

The formula of the reproductive cycle given above is a composite, which with slight changes will apply to most of our common wild birds. In the most aberrant cases of behavior, where the parental instincts have been reduced to a minimum as in the cow buntings and the megapodes, the cycle ends abruptly at term 5, and in the cowbird there is no attempt to either build a nest or to conceal the eggs.

The Blending and Overlap of Instincts. By Francis H. Herrick, *Western Reserve University.*

There are many anomalous actions or peculiarities of behavior in wild birds which have not been satisfactorily explained, although certain of them have been long known. Some of the eccentricities of conduct referred to are the following: (1) Repair of the old nest or the building of a new one at the close of the breeding season; (2) omission of nest building, and dropping of eggs on the ground; (3) leaving young to perish in nest, and starting on migration; (4) offering strings or other objects to young in the place of food; (5) building more than one nest including the "cock nests" of marsh wrens; (6) rebuilding on the same site, producing superimposed nests or nests of from two to four "stories" "to conceal" foreign bodies, such as the cowbirds' eggs in the nests of vireos and warblers.

All of these curious actions receive much light, and in most cases are satisfactorily explained by what we shall call the blending or overlapping of instincts. As shown in the previous paper, the wild bird commonly passes through a cycle of instincts which mark the breeding season. This cycle is made up of eight or more terms, which follow in serial order, and some of which are recurrent. Normally the bird passes from center of influence 1 to center 2, 3, and so on, to the end of the cycle. There is little overlap or blending, the bird remaining under the influence of a given instinct or series of instincts, such as nest building, incubation, or feeding the young until its instinct in any given direction has been satisfied, before entering a new sphere or being swayed by new impulses. When the correlation or attunement is perfect the instincts of mother and child fit like lock and key. Like clocks beating synchronously the instincts of mother and child are generally in harmony, but one of the clocks occasionally gains or loses, stops or runs down; one term is liable to be weak or to drop out altogether, so that there is an overlap or a gap in the series which may be serious. On the other hand, one term may be unduly strengthened, like nest building or incubation, and a preceding or following term correspondingly weak. In all such cases there are eccentricities of conduct, which, if not fatal to the young, are very puzzling to the naturalist.

Most wild birds normally pass one reproductive cycle in the season; a certain number, however, begin, but do no complete a second cycle; further, many like the robin and bluebird not only begin but complete a second and even a third cycle within the breeding period.

The repair of the old nest in autumn by fish hawks or eagles is not done "in anticipation of spring," and implies no more intelligence than the building of the original nest. It is simply the recrudescence of the building instinct, due to the beginning of a new reproductive cycle which is never finished.

Leaving the young to perish in the nest in autumn is brought about by the scamping of the cycle at the other end. The migratory impulse overlaps and replaces the parental instinct.

An adult robin has been seen to offer a string to its fully grown young, and try to cram it down the throat of the fledgling. Later, the old bird flew with the string into a tree. This was the result of the overlapping of two reproductive cycles, or of the last term of one cycle, and the first term of a succeeding cycle. The bird was alternately swayed by opposing impulses, now being impelled to gather nesting material, when she picked up the string, now by parental instinct to feed her young, when she tried to serve it, and again possibly by the instinct of building when she flew with the string into a tree.

Building more than one nest can be accounted for by excessive development of the building instinct, or by the influence of fear repeatedly interrupting the cycle, together with attachment to nesting site, but the discussion is too long for this abstract.

The rebuilding of nest on nest, giving rise to the wonderful storied structures sometimes produced by the summer yellow bird, or vireo, when plagued by the cowbird, so that the foreign egg is buried out of sight, is not an illustration of reason, as commonly suggested, but the curious result of a pure instinct. The reproductive cycle is broken by fear, and a new one is begun, and in these rare cases the old nest is retained as a site to be build upon. Instead of having two supernumerary nests, both of which may contain eggs, as in reported cases of the phoebe, we have a series of superimposed nests. The new nest is not built to conceal the cowbird's egg, although it does so perfectly, any more than the addition of new materials to the osprey's nest in the fall is in the nature of repairs, although it answers this purpose admirably. The nest is built because the bird is at the opening of a new cycle, and is impelled by the building instinct.

Many confirmatory facts could be given. The herring gull will not only bury an egg, in rebuilding on its old site the nest, when its cycle has been interrupted by fear, but will bury its dead young which it treats as so much nesting material.

The Interrelation of Sensory Stimulations in Amphioxus. By G. H. Parker, *Harvard University.*

To weak acid solutions and other like mixtures the anterior end of Amphioxus was found to be most sensitive, the posterior end less so, and the middle trunk region least sensitive. To the pressure of a camel's hair brush, the middle region was less sensitive than the two ends which, however, were not distinguishable one from the other by this method of stimulation. To a current of warm water (40° C.) the anterior end was most sensitive, the middle less, and the posterior end least. There were no reactions to a current of cold water (2° C.) To a fine pencil of strong sunlight, previously passed through water to eliminate heat, the anterior end including the "eye spot" was not sensitive, the region immediately behind the "eye spot" was most sensitive, the posterior region slightly less so, and the middle region least so.

The distribution of sensitiveness to light corresponds to the distribution of the pigment cups in the central nervous organ and these cups are without doubt the mechanisms concerned with the reception of light. The distributions of the other classes of sensitiveness are in mutual agreement, and, from the nature of their stimuli, these classes are doubtless represented by integumentary nerve terminals. To what extent these classes are independent may be inferred through the effects of exhaustion. After the tail of Amphioxus has been repeatedly stimulated with weak acid, the animal ceases to respond to this stimulus but is still normally sensitive in that part of its body to heat or to mechanical stimulation. In a similar way after exhaustion to mechanical stimulation or to heat stimulation, the particular part of the body experimented upon is still sensitive to the other classes of stimuli. Exhaustion to light stimulation has no effect upon the sensitiveness to the other classes of stimuli. These observations lead to the conclusion that light, heat, mechanical and chemical stimuli are received by physiologically separate mechanisms and that these mechanisms are located in the skin except in the case of light, whose receptive organs are the pigment cups in the central nervous organ.

The Habits and Life History of Cryptobranchus allegheniensis. By Bertram G. Smith. (Introduced by Dr. O. C. Glaser.)

The adult Cryptobranchus has its dwelling place in a cavity or cavern under a large rock, in swift and shallow water. The animal seldom comes out during the daytime, except during the breeding season. The eggs are laid and fertilized during the first two weeks of September. They are deposited in the usual dwelling-place of the animal. About 450 eggs are laid by a single female. Fertilization is external as in fishes; no spermatophores are formed. After the eggs are deposited they are usually guarded for a time by the male, who fights and drives away other hellbenders which attempt to eat the eggs. The male himself eats some of the eggs, but on account of the slowness of his digestion is unable to eat more than a small proportion, hence his presence is in the main protective. In defending the eggs the male is merely guarding his own food-supply: the origin of the brooding habit in this case seems to be the feeding habit. The eggs hatch about six weeks after fertilization. The newly hatced larva is about 25 mm. long, and has a large yolk sac. Larvæ kept in the laboratory for two months after hatching retain a remnant of the yolk sac, and refuse food. Year-old larvæ are 6–7 cm. long, and retain the external gills. Larvæ two years old are about 12 cm. long and the external gills are greatly reduced. Sexual maturity is attained with a length of about 34 cm. and probably requires three or four years.

### Movement and Problem Solving in Ophiura brevispina. By O. C. Glaser, *University of Michigan.*

1. Ophiura brevispina moves in practically all of the ways possible to a pentaradiate animal.

2. Its behavior in removing obstructions from its arms is not perfected by practice under ordinary conditions.

3. Preyer's conclusion that Ophiurans are intelligent is not substantiated by this study; for not only is it impossible to demonstrate "resolution" or improvement, by the method that he employed, but the assertion that an animal is intelligent because when stimulated it performs varied movements until some one of these brings about cessation of the stimulus, leads into difficulties, for these animals often perform in instantaneous succession movements that fail for the same reason. Ophiura, moreover, hardly ever executes a single movement, but usually a considerable number. Each of these on Preyer's view results in learning, but it is impossible without striking evidence to the contrary, to believe that Ophiurans can learn half a dozen things at the same time. If some of all the movements performed at a certain instant are "correct," the case is farther complicated in that some of all the things which the animal learned fall into the category of successes, some into the category of failures.

4. The reason why Ophiura brevispina does not improve under ordinary circumstances is probably due to its versatility. This animal can perform a surprising number of movements. Of all these some are better fitted to meet a certain difficulty than others, but a considerable number will serve the purpose. Where the number of solutions to a problem is large, it is not surprising that no particular method of solution shall be perfected, viz., that resolution should not occur.

### Notes on the Behavior of Sea-Anemones. By Chas. W. Hargitt, *Syracuse University.*

The paper discussed the aspects of behavior of several species of sea-anemones studied both under natural conditions and those of the laboratory. The points chiefly under observation had reference to the behavior of these creatures under the influence of light. So far as known few details along this line have been recorded.

At least three species of anemones were found which showed very evident reactions to photic stimuli: namely, Eloactis (Halcampa) producta, Sagartia modesta, and S. leucolena. Of these two are tube-dwelling, burrowing in the sand near tide lines, and forming rude tubes or burrows through the adhesive secretions of the ectoderm. S. leucolena is occasionally found in similar habitat, though chiefly adhering to rocks or among colonies of ascidians, or sponges, on piles of docks, etc. Experiments showed that the first two species are most sharply responsive to light, and this sensory sense is located chiefly in the tentacles and oral regions of the body. S. leucolena, while less sensitive, is yet evidently so in strong light. Exposed to direct sunlight it quickly closes up into a hemispherical mass, or creeps over the edge of the rock or shell into shaded portions of the aquarium. In its native haunts it may be found protruding its crown of tentacles from a crevice while the body is hidden.

Sagartia luciæ is a free living species found abundantly almost everywhere, on rocks in open pools, or on floating fucus, and freely exposed to direct sunlight, action of waves, etc. Of similar habit is Metridium marginatum. Neither of these species seems in the least degree responsive to photic stimuli. Under a strong beam of sunlight reflected directly upon them for ten minutes they showed no response whatever.

These facts, together with others as to food habits, etc., render it quite certain that their behavior is due to several factors, and that in response to light there is an evidence of adaptation involving varying physiological conditions, of which the burrowing habit is one of several expressions.

Further Observations on the Behavior of Tubicolous Annelids. By Chas. W. Hargitt, *Syracuse University.*

Following up the work done on these animals and reported elsewhere, the writer has extended the observations to aspects of behavior other than those already recorded. Three points are concerned in the following observations:

First, a study of behavior under natural conditions of environment. This has been possible in quiet pools near low tide lines. Experiments on Hydroides dianthus with shadow stimuli, or light intensity of varying degree, under these conditions have confirmed in all essentials those made last year.

Experiments as to tactile responses showed considerable variations as compared with the former series. This may be attributed to the fact that specimens living under these conditions become more or less inured to similar stimuli from the actions of waves which naturally buffet them almost constantly.

Second, experiments on the relative sensory acuteness of specimens from deep water, about twenty fathoms compared with those from shallow waters, one to three or four fathoms. In cases tested there were shown a definite preponderance of positive reactions among the latter, and a corresponding preponderance of negative responses in the former.

Third, a comparative study of the aspects of behavior shown in the growth of colonies taken from shore waters, subject to the action of waves, and those from quiet waters of bays, etc., shows an unmistakable variability in the aspects of the tubes, which clearly indicates environmental adaptation. Furthermore, specimens growing in an environment, such as marly bottom, or silt, or other similar condition, show the same evident response of adaptation. On the other hand, specimens growing along shore lines, or on rocky bottoms, show likewise the unmistakable response natural to such condition. Not a single colony among hundreds along the shore lines showed any free and vertical tubes. Likewise specimens dredged from muddy bottoms showed the erect and vertically directed tubes which would bring the animals above the obstructing mud.

Any careful consideration of the facts would hardly fail to convince one that no single factor, such as heliotropism, or geotropism, or any other tropism alone, was adequate for their explanation.

Rhythmical Pulsation in Animals. By Alfred G. Mayer.

Experiments made at the Tortugas Marine Laboratory of the Carnegie Institution upon Cassiopea, Salpa, Lepas, and the loggerhead turtle give results as follows:

Rhythmical pulsation can be sustained only when a strong stimulus is counteracted by an inhibitor, so that the pulsating organism is maintained at or near the threshold of stimulation, in a state analogous to that of unstable equilibrium, thus allowing weak internal stimuli to produce recurrent movement.

In the lower marine animals the NaCl, calcium, and potassium of the sea-water combine to form a powerful stimulant, which if unchecked would produce only sustained tetanus, but the magnesium overcomes this effect by its anesthetic (diastolic) influence.

The pulsating organs of terrestrial animals are also stimulated by optimum combinations of NaCl, with potassium and calcium, and this is held in check by a definite proportion of magnesium.

A Ringer's solution resembles this optimum combination of NaCl, calcium and potassium, and is only a stimulant, not an inorganic food. It must be counterbalanced by magnesium in order to enable it to sustain pulsation indefinitely.

In Cassiopea any paralyzed strip of sub-umbrella tissue, cut in the shape of a closed circuit, will remain indefinitely in rhythmical pulsation, if once a contraction wave be started in the circuit. Every time this wave returns through the circuit of tissue to the place whence it started, it is re-stimulated and sent forth anew, and being thus reinforced at each return it is sustained indefinitely.

In the scyphomedusa, Cassiopea, the diffuse nervous or epithelial elements of the sub umbrella transmit the pulsation stimulus to which the muscles respond by contraction.

The peripheral muscular layer of the wall of the loggerhead turtle's heart is the only part actively concerned in the rhythmical movement, and the internal cavernated mass of the heart's tissue may be removed without checking the pulsation. This peripheral part of the muscular wall of the heart tends to maintain itself in pulsation very much as will circuits made of the sub-umbrella tissue of Cassiopea.

The pulsation-stimulus acts solely upon the peripheral muscular layer of the heart's wall, the inner cavernated tissue remaining passive.

The above is a brief review of Publication No. 47, of the Carnegie Institution of Washington, "Rhythmical Pulsation in Scyphomedusæ," 1906.

# LITERARY NOTICES.

**Sherrington, Charles S.** The Integrative Action of the Nervous System. *New York, Charles Scribner's Sons.* 1906. Pp. xvi–411. 85 Figs. $3.50.

The material of this book was presented as the second series of the Yale University Mrs. Hepsa Ely Silliman memorial lectures.

Professor SHERRINGTON, who by his brilliant researches on the structure and functions of the nervous system has proved himself a master investigator, has gathered together in the ten lectures which constitute this volume a large number of the most important facts of nerve physiology. But, further than this, he has presented the results of his investigations, for the book is essentially the product of his own and his students' researches, in an interesting manner and has skillfully pointed out their meaning. Physiologists, students of animal behavior and psychologists alike recognize the value of the author's investigations, and of his interpretations of his results. As the title suggests, the lectures deal primarily with certain of the relations of the nervous system to the activities of the organism; they are preëminently important contributions to the comparative study of behavior. Indeed, "The integrative action of the nervous system" might well be read as a sequel to JENNINGS'[1] masterly discussion of the behavior of organisms which either totally lack a nervous system or possess a very simple one, for SHERRINGTON deals with the nature and relations of the reflex in higher animals, and with the regulation of behavior by the nervous system.

Because of the striking individuality of the author's style and his relatively new terminology the reader is likely to get an over-emphasized impression of the originality of the book. Even old, familiar facts as expressed in it at first appeal to the reader as new discoveries. Nevertheless the work is original, unusually so, not alone in its materials but even to a greater degree in method of presentation and point of view of interpretation. For most readers the careful study of SHERRINGTON's book will mean a new and research inspiring conception of the rôle of the nervous system, of the place of the study of activity, and of the relations of the physiology of the nervous system to psychology.

My first plan was to make this review an abstract of the volume, but I soon found that anything like an adequate summary of the lectures would demand an unreasonable amount of space. I shall therefore attempt, instead, after describing by title several lectures, to give a vivid impression of the nature and value of the book by selecting for presentation certain of the most important points made by the author; and while thus describing the materials of the work, I shall attempt to exhibit the interesting style and terminology of the author by the use of his own words in illustrative quotations. Anent the terminology of the book, it may be observed that it is the best example of the application of something like the objective terminology of BEER, BETHE and VON UEXKÜLL that has ever appeared in physio-

---

[1] The Behavior of the Lower Organisms. 1906.

logical literature. It is reasonably self-explanatory, simple and direct and as employed by the author it serves the excellent end of enabling him to speak of objective and subjective facts without confusion.

Lectures I, II and III, coördination in the simple reflex, discuss the nature of the structural and the functional units of the nervous system (the neurone and the nerve-arc) and of the interconnection of the various parts of the body through the integrative action of the nervous system. The phenomena of refractory phase and inhibition are dealt with at length and in a most illuminative manner. Lecture IV, interaction between reflexes, points out the artificiality of the conception of the simple reflex, the features of reflex-arc functions which result in the harmonious compounding of reflexes and the existence of two important classes of reflexes, the allied and the antagonistic, the mutual relations of which provide us with the manifold phenomena of facilitation and inhibition.

Lectures V and VI, compound reflexes, are devoted, the first to simultaneous combination of reflexes, the second to successive combination. In connection with simultaneous combination it is made clear that PFLÜGER's laws of spinal irradiation are contradicted by many of the facts of the author's investigations. Under the subjects, irradiation and "reflex pattern" the main features of the simultaneous compound reflex are thoroughly discussed. In the lecture on successive combination chain-reflexes receive attention. The current theories of inhibition are examined. Noci-ceptive (pain) nerves are shown to bring about reflexes which are prepotent. Lecture VII, reflexes as adapted reactions, is an excellent discussion of the purposes of reflexes and of the conditions which reveal and conceal the same. Lecture VIII, some aspects of the reactions of the motor cortex, in addition to giving with delightful clearness the topography of the motor cortex of the chimpanzee, the orang-outang and the gorilla, suggests the relation of the motor cortex to receptors (sense ? organs), more especially to distance receptors. Lecture IX, the physiological position and dominance of the brain, adds to a splendid résumé of the results discussed in the previous lectures, a convincing array of facts in support of the contention that the cerebrum is preëminently the ganglion of the distance-receptors, the cerebellum the ganglion of the proprio-ceptive (that is, the internal as contrasted with the surface-receptor) system. Lecture X, sensual fusion, consists of a comparison of the nervous integration of movement and of sensation by reference to results of the study of certain visual phenomena.

Of the three prominent points of interest from which the functions of the nervous system may be studied, metabolism, conduction and integrative action, this series of lectures deals almost exclusively with the last. This integrative or interconnecting activity of the nervous system which serves to make of the complex multicellular organism a functional unit of a high degree of efficiency is in large part the coördination of parts of the body by reflex action. Structurally the unit of the nervous system is the neurone, functionally it is the nerve-arc, which consists in its simplest form of a receptor and an effector which are linked by a conductor. The series of functional stages in the action of the nerve-arc may be termed initiation, conduction and end-effect. So far as integrating activity is concerned the reflex-arc is the unit of mechanism, the reflex-act the unit of reaction. And a reflex-act, according to the author, is a reaction "in which there follows on an initiating reaction an end-effect through the mediation of a conductor, itself incapable either of the end-effect or, under natural conditions, of the inception of the reaction" (p. 6).

The simple reflex is an abstraction for in reality no reflex exists independently; there is always coördination. This coördination is of two sorts; simultaneous and successive; the former gives origin to the reflex-patterns, the latter to the chain-reflexes or shifting patterns by which the parts of the body are constantly brought into adaptive relation to one another and to the changing environment.

Briefly and pointedly the author discusses the rôle of each of the elements of the reflex-arc. The chief function of the receptor is selective excitability; "it lowers the threshold of excitability of the arc for one kind of stimulus, and heightens it for all others" (p. 12). Point by point the characters of nerve-arc conduction are exhibited in the light of the reflexes of the spinal dog. Nerve-arc conduction differs from nerve-trunk conduction in eleven important respects: latent period, after-discharge, relation of rhythm of end-effect to rhythm of stimulus, relation of intensity of stimulus to end-effect, summation, irreversibility of direction of impulse, fatigability, variability of the threshold, refractory period, dependence on blood-circulation, susceptibility to drugs (p. 14). The first three lectures present the results of intensive research concerning each of these eleven features of nerve-arc conduction, together with interpretations of the results in terms of adaptive reactions.

Many of the differences between the conduction of the reflex-arc and the nerve trunk SHERRINGTON thinks are to be referred to the inter-neurone region, the synapse. Irreversibility of the direction of conduction is due, possibly, to the fact that the synaptic membrane is more permeable in one direction than in the other (p. 42).

In the discussion of refractory phase, we have an excellent illustration of the way in which the author gives life to his book by pointing out the significance of his facts. "The scratching-reflex, in order to secure its aim, must evidently consist of a succession of movements repeated in the same direction, and intervening between the several numbers of that series there must be a complemental series of movements in the opposite direction. Whether these two series involve reflex contractions of two antagonistic muscle-groups, respectively, in alternate time, I would leave for the present. The muscle groups or their reflex-arcs must show phases of refractory state during which stimuli can not excite, alternating with phases in which such stimuli easily excite. Evidently this is fundamental for securing return to the initial position whence the next stroke shall start. The refractory phase secures this. By its extension through the whole series of arcs it prevents that confusion which would result were refractory phase in some of the arcs allowed to concur with excitatory phase in others" (p. 63). And further, in the same connection, to show the value of inhibition and the reasons for the existence of central as well as peripheral inhibition, he states that the scratch-reflex "is but one of several reflexes that share in a condominium over the effector organ—the limb. It must, therefore, be possible for the scratch-reflex taken as a whole, to be, as occasion demands, replaced in exercise of its use of the limb by other reflexes, and many of these do not require clonic action from the limb—indeed, would be defeated by clonic action. It would not do, then, for the peripheral organ itself to be a clonic mechanism. The clonic mechanism must lie at some place where other kinds of reflex can preclude the clonic actuator from affecting the peripheral organ. Now such a place is obviously the central organ itself; for that organ is, as its name implies, a nodal point of meeting to which converge all the nervous arcs of the body, and among others all those which for their several ends have to employ the same mechanical organ as does the scratch-reflex itself. It is, therefore, only in accord with expectation that the seat of the refractory phase of the scratch-reflex lies where we trace it, in the central nervous organ itself, and somewhere between the motor neurone to the muscle and the receptive neurone from the skin" (p. 65).

In the principle of the *final common path*, Sherrington has found an explanation of many of the complex relational aspects of reflexes. Each receptor has its *private path;* these come together in the so-called *internuncial paths*, which in turn unite in the *final common path*. Results of the necessity for the use of the same final common path by a number of receptors are: (1) That receptors which have different or opposite end-effects are forced to use the path successively, not simultaneously. "The result is *this* or *that* reflex but not both together" (p. 117). Thus the final common path prevents the harmful interference of antagonistic reflexes. (2) That receptors which have similar or harmonious end-effects reinforce one another in the use of their final common path. "If, while the scratch-reflex is being elicited from a skin point at the shoulder, a second point distant, *e. g.*, 10 cent. from the other point but also in the receptive field of skin, be stimulated, the stimulation at this second point favors the reaction from the first" (p. 120).

Between the two classes of receptors, the extero-receptors, which supply the surface of the body and the proprio-receptors, which lie in the depths of the organism, important relations of reinforcement and inhibition are shown to exist. Thus, in the case of the flexion-reflex, "the receptive field includes not only reflex-arcs arising in the surface field, but reflex-arcs arising in the depths of the limb. Combined, therefore, with an extero-ceptive area, this reflex has, included in its receptive field, a proprio-ceptive field. The reflex-arcs belonging to its extero-ceptive and proprio-ceptive components coöperate harmoniously together, and mutually reinforce each other's action. In this class of cases the reflex from the muscle-joint apparatus seems to reinforce the reflex initiated from the skin" (p. 131). According as a reflex initiated by a given receptor exalts or depresses another simultaneously or successively occurring reflex it may be spoken of as excitatory or inhibitory. In this mutual relation of interference we have, according to Sherrington, an expression of the fundamental importance of the principle of the common path. For every convergence of afferent neurones furnishes a condition for the interference of their reflexes or, in other words, it constitutes a mechanism of coördination.

The author, far from making hasty or ill-supported general statements concerning these matters, builds his structure of facts with skill, system and rare insight to the point at which his conclusions, and in many cases his interpretations as well, are forced upon the reader. I do not wish to give the impression that the book is a highly speculative discussion of the integrative action of the nervous system. It is first of all an account of experimental study of the subject, and secondly an exceedingly valuable discussion of the meaning of the facts which are available.

In connection with his investigation of the phenomena of irradiation it is noteworthy that Sherrington has discovered a number of important inconsistencies between observed facts and the laws of spinal action as formulated by Pflüger (p. 161). And it is also significant that in calling attention to important evidences of the inadequacy of the so-called laws of reflex action he does not attempt to formulate laws after his own observations but with the wisdom of an investigator who realizes that we are working in the infancy of nervous physiology describes the appearances which he has observed, and, so far as his observations go, states the rules which certain classes of reflexes follow. These descriptions are given in terms of the reflex figure, a most convenient scheme for the presentation of the total visible effect of a given stimulus or stimulus complex. "Thus at any single phase of the creature's reaction, a simultaneous combination of reflexes is in existence. In this combination the positive element, namely, the final common paths (motor neurone groups) in active discharge, exhibits a harmonious discharge directed by the dominant reflex-arc, and reinforced by a number of arcs in alliance with it. * * * But there is also a negative element in this simultaneous combination of reflexes. The reflex not only takes possession of certain final common paths and discharges nervous impulses down them, but it takes possession of the final common path whose muscles would oppose those into which it is discharging impulses, and checks their nervous discharge responsive to other reflexes. * * * In this way the motor paths at any moment accord in a united pattern for harmonious synergy, coöperating for one effect" (p. 178). A number of reflex figures, with their respective nervous patterns, are described in detail.

A good illustration of the author's aptitude for indicating the utility and developmental conditions of activities is furnished by the following fragment from the discussion of immediate induction. "If a parasite in its travel produces excitation which is but close below the threshold, its progress is likely to so develop the excitability of the surface whither it passes that the scalptor-reflex will be evoked. In the skin and the parasite respectively we have, no doubt, two competing adaptations at work. It is perhaps to avoid the consequences of the spatial spread of the "bahnung" that the hop of the flea has been developed" (p. 184).

In the competition of reflexes for the use of a common path dominance is determined in large measure by four factors: spinal induction, relative intensity of the stimulus, relative fatigue, and the functional species of the reflex. Each of these factors has been investigated by the author and receives adequate consideration in the lecture on the successive combination of reflexes. Concerning fatigability and its excuse for existing, he writes in his characteristic style: "The waning of a reflex under long maintained excitation is one of the many phenomena that pass in physiology under the name of 'fatigue.' It may be that in this case the so-called fatigue is really nothing but a negative induction. Its place of incidence may lie at the synapse. It seems a process elaborated and preserved in the selective evolution of the neural machinery. One obvious use attaching to it is the prevention of the too prolonged continuous use of "a common path" by any one receptor. It precludes one receptor from occupying for long periods an effector organ to the exclusion of all other receptors. It prevents long continuous possession of a common path by any one reflex of considerable intensity. It favors the receptors taking turn about. It helps to insure serial variety of reaction. The organism, to be successful in a million-sided environment, must in its reactions be many-sided. Were it not for such so-called "fatigue," an organism might, in regard to its receptivity, develop an eye, or an ear, or a mouth, or a hand or leg, but it would hardly develop the marvelous congeries of all those various sense organs which it is actually found to possess" (p. 222).

Under the subject, species of reflex, it is convincingly argued, in the light of a wealth of experimental evidence, that reflexes initiated by noci-receptors (such as are especially adapted to the reception of nocuous or harmful stimuli) are prepotent. Such stimuli do not demand specialized sense organs adapted to a particular form of energy and possessing for the adequate stimulus a low threshold, but instead it is to the advantage of the organism to have in certain naked nerve endings themselves, which are called by SHERRINGTON the noci-ceptive nerves, a form of receptor which is capable of responding to a wide range of different kinds of stimuli. The noci-ceptive function would be cramped, as the author puts it, by the specialization of an end-organ.

The lecture on adapted reactions is of special interest to students of behavior and of psychology since in it the author considers the purposes of reflexes, the nature of spinal shock and its relation to the brain, the local sign of reflexes, and the relations of reflexes to emotion and its expressions. We may not do more than note a few of the main results of this lecture. With reference to the purposive aspect of reflex action the author writes: "In the flexion-reflex of the hind limb excited by noxuous stimuli, *e. g.*, a prick of a faradic current, the limb itself is drawn up—if weakly, chiefly by flexion at the knee; if strongly, by flexion at hip as strongly as at knee. At the same time the crossed hind limb is thrown into action, primarily in extension, but this is soon followed by flexion, and alternating extension and flexion is the characteristic result. The rate of this alternation is about twice a second. That is to say, the foot which has stamped on the thorn is drawn up out of way of further wounding, and the fellow hind limb runs away; and so do the forelegs when, —which is more difficult to arrange, owing to the height of the necessary spinal transection—they also are included, fairly free from shock, within the 'spinal' animal" (p. 240).

Although it is well known, it may not be amiss to mention the fact that the JAMES, LANGE and SERGI notion that emotion is the result of certain organic processes, vaso-motor, visceral, cutaneous, has been tested experimentally by SHERRINGTON and found to lack satisfactory support. There can be no doubt that SHERRINGTON effectually did away with the possibility of influence of the organic process to which the above writers had ascribed an all important rôle in the production of an emotional state, but in the opinion of the reviewer, it may fairly be objected that he has not conclusively proved that the emotion-expressing reflex figures, which he observes after spinal transection, are not the result of changes induced in the central nervous system by these same organic processes previously to the spinal transection. In an attempt to meet this possible objection the author writes: "But it is noteworthy that one of the dogs under observation had been deprived of its sensation when only nine weeks old. Disgust for dog's flesh could hardly arise from the experience of nine weeks of puppyhood in the kennel" (p. 265). Surely, however, during that time the puppy may have acquired the experience of the disagreeable, perhaps it need not be that of the taste of dog's flesh.

Investigation of the effects of stimulation of the cortex of the anthropoid apes and of the influence of strychnine and tetanus toxin upon the reflexes induced by stimulation of the motor cortex has brought into clear light the fact that excitation and inhibition constantly accompany one another. Under certain conditions inhibition is converted into excitation and serious confusion results. The disorders brought about by tetanus and by strychnine poisoning "work havoc with the coördinating mechanisms of the central nervous system because in regard to certain great groups of musculature they change the reciprocal inhibitions, normally assured by the central nervous system, into excitations. The sufferer is subjected to a disorder of coördination which, though not necessarily of itself accompanied by physical pain, inflicts on the mind, which still remains clear, a disability inexpressibly distressing. Each attempt to execute certain muscular acts of vital importance, such as the taking of food, is defeated because from the attempt results an act exactly the opposite to that intended. The endeavor to open the jaw to take food or drink induces closure of the jaw, because the normal inhibition of the stronger set of muscles—the closing muscles—is by the agent converted into excitation of them" (p. 298).

SHERRINGTON's work has discovered the existence of two systems of innervation controlling two sets of musculature. These systems are named by him the phasic and the tonic reflex systems. "The phasic system exhibits those transient phases of heightened reaction which constitute reflex movements; the tonic system maintains that steady tonic response which supplies the muscular tension necessary to *attitude*" (p. 302).

If receptors be classified as those which receive impressions which are referred beyond the organism (SHERRINGTON's distance-receptors) and those whose impressions are referred to the organism (proprio-receptors), it is to be noted that the cerebellum is the main ganglion of the proprio-ceptive system, while the cerebrum stands in a like relation to the distance-receptors. "It is the long serial reactions of the "distance-receptors" that allow most scope for the selection of those brute organisms that are fittest for survival in respect to elements of mind. The "distance-receptors" hence contribute most to the uprearing of the cerebrum. One of the most important of the groups of proprio-ceptive organs is that of the labyrinth, and these together with those other receptors whose chief function is the control of *attitude* have as their center of reference the cerebellum. The distance-receptors, and therefore the cerebrum, are the chief inaugurators of reaction; the proprio-ceptors, and therefore the cerebellum, control the habitual taxis of the skeletal musculature.

In the lecture on sensual fusion it is shown that the fusion of sensation does not follow the rules which have been established for the fusion of reflexes. "The cerebral seats of right-eye and left-eye visual images are thus shown to be separate (referring to an experiment previously described.) Conductive paths no doubt interconnect them, but are shown to be unnecessary for visual unification of the two images. The unification of a sensation of composite source is evidently associated with a neurone arrangement different from that which obtains in the synthesis of a reflex movement by the convergence of the reflexes of allied arcs upon its final common path" (p. 383).

Finally, it should be mentioned that SHERRINGTON firmly believes in the right of psychology to existence and in the mutual helpfulness of physiology and psychology. Their workers should, in his opinion, give close attention to one another's results. Of comparative psychology he says: "Despite a protest ably voiced by v. UEXKÜLL, comparative psychology seems not only a possible experimental science but an existent one" (p. 307).

A few months ago in reviewing JENNINGS' "Behavior of the Lower Organisms"[1] I saw good reason to characterize it as the most important book on animal behavior that had ever been written. To that statement of my opinion I may now add that

---

[1] *Jour. of Phil., Psy. and Scientific Methods.* Vol. 3, p. 658. 1906.

SHERRINGTON's book is an equally important analysis of behavior from the side of nerve physiology. JENNINGS has indicated the essential features in the behavior of the lower organisms and the problems which are presented to the student of the evolution of organic activity; SHERRINGTON has shown a way to the scientific study of the behavior of the vertebrates and has made an important contribution to our knowledge of certain forms of activity in the higher animals.

ROBERT M. YERKES.

**Bean, Robert Bennett.** Some Racial Peculiarities of the Negro Brain. *American Journal of Anatomy*, vol. 5, No. 4, pp. 353-432, with 16 figures, 12 charts and 7 tables. September, 1906.

To quote the author's own summary of his work, this is "an effort to show by measurement of outline drawings of brains in different positions, by composites of these outlines, and by actual drawings from individual brains that there is a difference in the size and shape of caucasian and negro brains, there being a depression of the anterior association center and a relative bulging of the posterior association center in the latter; that the genu of the corpus callosum is smaller in the negro, both actually and in relation to the size of the splenium; and that the cross section area of the corpus callosum is greater in relation to brain weight in the caucasian, while the brain weight of negro brains is actually less. The amount of brain matter anterior and posterior to the fissure of Rolando is roughly estimated, but other points of possible difference, as in the gyri, the insula, the opercula, the Affenspalte, the proportions of white and gray matter, and the cerebro-cerebellar ratio are necessarily omitted in this study."

Only those who have attempted to institute exact comparisons between the brains of representatives of different human races can fully realize how great a debt of gratitude we owe to Dr. BEAN (and to Professor MALL and Dr. HRDLICKA, who suggested the investigation) for this simple and graphic method of exhibiting the contrasts in form and in the proportions of various parts of the brain in negroes and people of European extraction. Many writers have called attention to individual points of racial difference in the brain and some investigators have attempted to indicate these differences in figures; but hitherto no one has given us so comprehensive a means of expressing in exact measurements the distinctive features of the brain as a whole and the relative size of those parts which exhibit distinctively racial and sexual variations in form and magnitude.

The method adopted is very simple and perhaps even crude—as, in fact, every attempt at expressing in figures the distinctive characters of such a complicated organ as the brain in a large series of examples is bound to be—yet it admirably serves the purpose for which it was invented, *i. e.*, to present in a numerical form the broad contrasts in the form and proportions of the brain in different races and sexes.

The memoir is based chiefly upon the results obtained by the measurement of 152 brains, of which 103 were "American negroes" and the rest "American caucasians." All the measurements were made from an arbitrary axis proposed by Dr. MALL—a line passing in the mesial plane "just above the anterior commissure and just below the splenium." By measuring the distance to the surface of each hemisphere along radii drawn from the center of this line at angles of 60° and 120°, respectively, to the anterior half of the axis in three planes—vertical sagittal, horizontal and midway between these two, *i. e.*, a plane making an angle of 45° with the horizontal—it is possible to obtain three pairs of measurements in each hemisphere, by which the relative development of the frontal and parietal association areas can be compared the one with the other, as well as with those of the other hemisphere and of other brains, and can be expressed in an arbitrary numerical form which lends itself to statistical treatment.

As an example of the results obtained by the use of this method I might quote some figures taken from Table IIa (p. 366). In a series of 34 brains of white men and 43 black men, in which the average length of MALL's axis is the same (168 mm.), the average distance of the center of the left frontal area (the place where the 60° radius cuts the surface in the plane 45° above the horizontal) from the center of the axis is 70 mm. in the whites and only 66 mm. in the blacks, whereas the center of the left parietal area (measured along the 120° radius) is 71 mm. in the whites and 73 mm. in the blacks.

The time will soon come when we must attempt to estimate the exact area and volume of gray matter in each different histological area of the cerebral cortex in a series of brains of different races. This possibility has become opened up by the discovery that in perfectly fresh human brains the difference in the color and texture of the different cortical areas is quite recognizable by the naked eye, so that each area can be cut out and by snipping away the white matter (with a scissors under water) the cortex may be spread out in one plane and its exact extent estimated. This method, however, is so exceedingly difficult and exacting that it will be a long time before a large series of records can be obtained. Until this is done the results obtained by the much simpler method devised by Dr. MALL will provide us with information of the utmost value.

In the absence of any absolute measurements of the extent of the cortical areas, the exact size of the surface of the corpus callosum and its various parts as exposed in mesial sagittal section is the surest guide to the relative development of the cerebral cortex and its parts that we possess at present. It is, therefore, particularly instructive to note that the separation of the races exhibited in Dr. BEAN's table of the relative proportions of the anterior and posterior halves of the corpus callosum, and of its genu and splenium, is much sharper than that shown in the cruder measurements of the radial distances of the frontal and parietal areas from an arbitrary point.

The results obtained by Dr. BEAN in his comparison of the left and right hemispheres (pp. 37–373) are particularly interesting, seeing that they agree with the evidence yielded by other modes of investigation and give numerical expression to the differences.

The fact that a "smaller posterior association center" is found "on the left side of the caucasian" (p. 371) is a very instructive observation when it is recalled that as a general rule the left occipital region is much more pithecoid than the right because the visual cortex has been pushed backward toward the mesial surface by the parietal expansion to a much less extent than in the other hemisphere.

The fact that there is "a more marked racial difference on the right side than on the left" (p. 372) is borne out by my own observations that in all human brains the left parieto-occipital region shows a tendency toward a simpler and more ape-like conformation than the right and that in negro brains there is much less asymmetry in this area than there is in non-negro races. This implies a much greater dissimilarity between the right than the left sides of the brain in blacks and whites.

For Dr. BEAN's interpretation of the psychological significance of his results, the reader is referred to the original.

G. ELLIOT SMITH.

**Guyer, Michael F.** Animal Micrology. Practical Exercises in Microscopical Methods. *University of Chicago Press.* 1906. 240 pp. $1.75 net.

This work is intended as a laboratory manual in microscopic anatomy and embryology for college classes. While the work is much more complete than the pamphlets of laboratory outlines usually furnished to the histology classes of the medical schools, it is by no means designed to replace the larger standard works of reference on the microscope and microscopical methods. It does present in very clear form a judicious selection of methods, including an excellent untechnical account of the microscope and its optical principles, adequate for the undergraduate course in histology. The author has also succeeded very well in his attempt to include the minor cautions (usually omitted from the manuals on methods) necessary to enable the beginner to avoid failure or correct it. In an appendix is given an extensive table of the more important tissues and an approved method of preparation for each. The nervous tissues have not been emphasized in this book, for they are adequately treated in HARDESTY's "Neurological Technique," though the neurological methods necessary in a course in general histology are briefly given.

C. J. H.

## BOOKS AND PAMPHLETS RECEIVED.

**Edinger, L.** Ueber das Gehirn von Myxine glutinosa. Aus dem Anghang zu den Abhandlungen der König. Preuss. Akademie der Wissenschaften vom Jahre 1906. *Berlin.* 1906.

**Terry, Robert J.** The nasal skeleton of Amblystoma punctatum (Linn.). Reprinted from *Transac. Acad. Sci. of St. Louis*, Vol. 16, No. 5. 1906.

**Wright, Ramsay.** An early anadidymus of the chick. Reprinted from *Trans. Roy. Soc., Canada*, Second Series, Vol. 12, Section 4. 1906.

**Dieulafe, Leon.** Morphology and embryology of the nasal fossæ of vertebrates. Translated by HANAU W. LOEB, St. Louis. Reprinted from *Annals of Otology, Rhinology and Laryngology.* 1906.

**Peters, Amos W.** Chemical studies on the cell and its medium. Part I. Methods for the study of liquid culture media. Reprinted from *Am. Jour. of Physiology*, Vol. 17, No. 5. 1907.

**Tower, W. L.** An investigation of evolution in chrysomelid beetles of the genus Leptinotarsa. *Publications of the Carnegie Institution of Washington*, No. 48. 1906.

**Linton, Edwin.** Note on the habits of Fierasfer affinis. *Am. Nat.*, Vol. 41, No. 481. 1907.

**Wilder, B. G.** Anatomic nomenclature: an open letter to Professor LEWELLYS F. BARKER. Reprinted from *Science*, N. S., Vol. 24, pp. 559-560, Nov. 2, 1906; also the same reprinted from *American Medicine*, N. S., Vol. I, Nov., 1906, p. 459.

Neuropathological Papers from the Harvard University Medical School. 1905.

CORRECTION.—In the last number, in the List of Books and Pamphlets Received, B. G. WILDER's paper, "Some Linguistic Principles," etc., should have been credited to the *American Philological Association.*

The Journal of
Comparative Neurology and Psychology

VOLUME XVII MAY, 1907 NUMBER 3

# CONCERNING THE INTELLIGENCE OF RACCOONS.

BY

L. W. COLE.

(*Professor of Psychology, University of Oklahoma.*)

WITH TWO FIGURES.

CONTENTS.

## INTRODUCTION.

This paper is a report of experiments which were made with the raccoon, Procyon lotor, to determine what type of associations it is able to form, the complexity and permanency of its associations, and to ascertain whether mental images and a tendency to imitate are present in this animal. The paper as originally planned contained also observations on the senses, instincts and habits of raccoons, together with comparisons of their behavior with that of other mammals under similar experimental conditions. These observations, as well as most of the tables on "Learning to release fastenings," have necessarily been omitted from this article. I am greatly indebted to Dr. R. M. YERKES for valuable criticisms of the experimental results and for many suggestions for the preparation of this paper.

In all I have had six young raccoons under observation, four males and two females. The descriptions refer in the main to the four individuals which were received July 3, 1905. With these individuals experiments were made twice each day during the remainder of the summer and almost daily from September to the following May. Subsequently, series of new experiments and repetitions of old ones were given at irregular intervals. During each series of experiments, however, the successive tests were made on consecutive days, so that the conditions of hunger and fatigue might be as nearly uniform as possible. The four raccoons must have been, at the time I secured them, about eight weeks old. Comparisons with the other two, Nos. 5 and 6, whose age I definitely knew, make the above estimate fairly accurate.

The four raccoons are designated by the numbers 1, 2, 3, and 4 respectively. The reader should remember that No. 4 alone is a female. When no ambiguity results, I shall use the word "animals" as a synonym for the word raccoons, or, in other connections, for the expression "dogs and cats." This usage, however, does not imply the opinion that different mammals are alike psychologically.

It was my purpose to use tests so similar to those already used in the case of other animals that I might learn by comparisons the place of the raccoon in the scale of mammalian intelligence. This purpose was rather strictly adhered to except in the experiments to test visual discrimination and the presence of visual images. I am not aware that the card-showing device and my method of using it have been employed by other investigators.

## LEARNING TO RELEASE FASTENINGS.

The method employed in the experiments with fastenings was that used in the laboratory by THORNDIKE[1] in his study of cats and dogs. The peculiar facility of the raccoon in the use of his forepaws and his tendency to investigate objects by touch suggested at once that he might learn readily to operate simple fastenings.

Before proceeding to a description of the fastenings used, and the tabulated records, I may say that I do not believe that my raccoons can fairly be called "victims" of experimental conditions. As long as they continued to suckle, or until August 30, 1905, they were fed from a bottle twice each day until fully satisfied. During August, bits of apple, lumps of sugar and water were added to their

[1] THORNDIKE, E. L. Animal Intelligence. *Psychological Review Monogr. Suppl.*, vol. 2, no. 4. 1898.

bill of fare. From August 30 to the present time the animals have been fully fed and given fresh water once each day. They had to work hard for their food and it is possible that their growth may have been retarded slightly, but I think that this was not the case, for a table of their weights during the period shows a fair increase with age. The year-old raccoons apparently are not quite full grown. The animals have been kept in a room 14 by 10 feet, in which they could climb about on several rolls of poultry wire which were hung on the walls. They had there a nest of hay. Two windows, in which they frequently sat, were open in summer. They could climb about, and they were frequently let out to follow me over an open field, climb nearby trees, or play about the house. *Since their eighth week they had never experienced any other environment.* No one of the four ever showed a tendency to pace up and down in the windows barred (?) with poultry wire. Raccoon No. 6, however, did this by the hour, and if chained by the neck he would continue to pace to and fro at the end of his tether. This is often observed in captive raccoons. That no restlessness ever appeared in the four would seem to be evidence of their general contentment and of nearly normal conditions in their unusual environment.

The animals worked well and, although they possibly might have formed certain associations more rapidly under the stimulus of what THORNDIKE calls "utter hunger," I believe that my results indicate approximately their normal rate of learning. The cases of slow work, due to approaching satiety, were noted and valued accordingly. Readers of the tables will note that the loss of time due to fatigue or satiety is small in many cases, for the animals often work merely for the sake of working, or, more probably, playing. Too great hunger results in much eagerness to secure food and this seems invariably to prolong the time of escape from the experiment box. This is to be observed in the case of the first trial each day for each animal.

*Description of Fastenings.*—In the following descriptions the dimensions of the boxes are given in inches; length, breadth and height being stated in order. The doors varied much in size and in their position in the front of the box. Some were high in the front, others low; some were in the middle from right to left, others at one side. Since none of these variations delayed the animal's attack on the fastenings, I soon ceased attempting to construct uniform doors. Some doors were hinged at the bottom, others at the right or left side. This variation also seemed to have little effect on the animal's work, for, after experience in one or two boxes, he seems to attack fastenings rather than doors, unless as happened once, shaking the door would release it. In that case, the door was attacked in about one-half the total number of trials.

My difficulty with single or double fastenings was not in making one sufficiently easy for the raccoon to operate, but rather in making one difficult enough.

Box 1. 20″ x 10″ x 13″. This box had a door in front, hinged at the right (looking outward), and fastened by a button at the left. The door opened outward the instant the button was turned to a vertical position. This box had solid sides and back but the front was made of upright slats 1¼ inches apart. This fastening is very similar to KINNAMAN's[2] A 1, and it corresponds to THORNDIKE's Box C, save that the door did not drop inward. Had the raccoon's forepaw been bruised or even rapped sharply by the falling door he would have hesitated to open it again.

Box 2. 14″ x 13″ x 26″. This box had a door in the front six inches from the bottom. It swung outward, was hinged at the right and fastened by a vertical bolt at the top. To this bolt was fastened a cord which passed over a pulley, then down through the top of the box and ended in a loop which hung near the side of the door. Pulling down on the loop raised the bolt and allowed the door to swing open. This box, which we may call "Loop at front," is comparable with THORNDIKE's Box A, "O at front."

Box 3. 26″ x 14″ x 14″, had entirely closed sides with the exception of the front, which was made of vertical slats about one inch apart. On a level with the floor of the box and in the middle from right to left was a front door. This door was hinged at the left and fastened at the right by a horizontal bolt, to which was attached a string which ran in a horizontal position parallel with the front of the box but outside it. The door could be opened by reaching through between the upright slats and clawing the cord which was attached to the bolt. A loose piece on top of the box enabled the experimenter to put the raccoon through the top and then to close the opening by replacing the piece. This is designated in the tables as "1st put-through box," because of the kind of learning it was designed to test. I have compared it with THORNDIKE's Box E, "String outside."

Box 4. 14″ x 13″ x 26″, "Loop at back." This was similar to Box 2, "Loop at front," with the addition of a second pulley at the back of the top of the box. The cord passed over both pulleys so that the terminal loop hung in the back of the box. The door was six inches above the floor of the cage. This box is comparable with THORNDIKE's Box B, "O at back," save that the string could not be clawed where it passed along the top of the box. The only way to open the door, therefore, was to pull downward on the loop.

Box 5. 14″ x 13″ x 26″, "2d put-through box," two fastenings. This was Box 2 with a button added. To open the door it was necessary both to pull the loop and turn the button. Either might be done first. A door was also added at the side of the box through which the experimenter could push the animal into the cage or through which the raccoon could walk into the box. This side-door extended down to the floor. Two raccoons, No. 4 and No. 3, were put through the acts necessary to open the door, the other two were not put through. I have compared this with THORNDIKE's Box J, "double."

Box 6. 14″ x 13″ x 26″, two fastenings, was Box 5 except that the loop was now hung in the center. This change was made to test whether the raccoons "would claw at the place where the loop had been," whether this arrangement would change the order in which acts were performed, and whether they would associate this loop with the loop in the other position.

Box 7. 32″ x 20″ x 20″, two fastenings. Both the sides and the top of this box were made of slats so as to admit light. The door in the middle of the front, hinged at the bottom, swung, or rather fell, outward when the fastenings were released. The latter consisted of a button at the right of the door and a bolt at the top operated by a loop in the back part of the box. The raccoons went into the box through a door opposite the front door. This box was much larger than the preceding ones so that the

---

[2] KINNAMAN, A. J. Mental Life of Two Macacus rhesus Monkeys in Captivity. *American Journal Psychology*, vol. 13, pp. 98-148, 173-218. 1902.

relative positions of loop and button were changed. The object was to see whether these changed positions would delay escape or whether the fastenings would be at once attacked as if recognized in the new positions. This box also has been compared with THORNDIKE's Box J, "double."

Box 8. 32" x 20" x 20", three fastenings. This was Box 7 with an added loop. Thus we had loop 1 at the left side of the back part of the box, loop 2 at the right side of the back, and button 1 at the right side of the door. I have compared this with THORNDIKE's Box L, which consisted of "A (O at front), D (string), I (lever)." It is also comparable with KINNAMAN's F 31.

Box 9. Four fastenings. This was Box 8 with an added button at the left side of the door, "button 2."

Box 10. 26" x 13" x 14". The ends and back of this box were entirely closed. The top and front were closed with slats only. In the middle of the front was a door hinged at the left. The door was fastened with a thumb-latch which could be released with slight pressure. The bar of the thumb latch would fall back in place unless the door was pushed out a little. This is comparable with THORNDIKE's Box G, "Thumb-latch."

Box 11. Five fastenings. This was Box 9 plus the thumb-latch which had been learned singly. There were, therefore, 2 buttons, 2 pulleys, and 1 latch. The latter had to be operated last lest its bar fall back into the catch.

Box 12. Six fastenings. A third bolt was added to Box 11 but the cord from it extended to a treadle or platform which extended across the right end of the box. Depressing the raised end of this treadle released the bolt.

Box 13. Seven fastenings. This was Box 12 with the addition of a horizontal hook at the left side of the door. For convenience I used the following notation in recording: 1 = button 1, 2 = button 2, 1' = loop 1, 2' = loop 2, 5 = thumb-latch, 6 = treadle, 7 = hook.

Box 14. Hook. 26" x 13" x 14". A door hinged at the right and fastened with a horizontal hook was placed in the middle of the front. The animals were put into the box through a door in the back. I have compared this with KINNAMAN's Box 12, "Horizontal hook."

Box 15. 50" x 20" x 20", one fastening. Imitation. This box was divided into two equal compartments. A door at the back admitted an animal to either compartment and a door in the partiton allowed me to change a raccoon from one compartment to another. The right compartment only had a door in front, which was fastened by means of an old-fashioned barn-door latch. This consisted of a wooden bolt which might be pushed to and fro from either side of the door by means of a pin which passed through the bolt and through the door. Pushing the bolt to the right unfastened the door and it could then be pushed open. The plan was to place a raccoon in the closed compartment and let him see another open the door and get out. After this had been done many times the observer was to be let into the other compartment in order that I might observe whether he had learned by seeing the other open the door. All sides and the partition were made of poultry wire so that I might count only those times the imitator apparently saw the act performed and so that he could readily see the performance.

Box 16. Imitation. This was Box 15 plus a second latch placed below the first one. This was a difficult box to open because pushing either latch to the left fastened the door. In the early trials of course the animals pushed the latches first to one side, then to the other.

Box 17. 10" x 10" x 4". Imitation. This box had solidly closed sides. A three inch square was sawed out of the top and replaced to close the opening. Round holes at the corners of this square enabled the raccoon to claw it out and he could then reach into the box and get food. The animals secured food by getting *into* this box, instead of getting out of it.

Box 18. 36" x 24" x 14". Varying means to an end. An opening was made in the center of the top large enough for the raccoon to go in and get food. This opening could be closed and fastened. The box, which had no bottom, rested on a foundation of a single row of bricks. Removing a brick enabled the animal to crawl through the foundation. The object was to see whether the animal would change *promptly* from one opening to the other when the opening through which he had been going was closed. If so, perhaps there was some notion of apple-in-box instead of the imageless coupling of a fixed set of muscular movements with a fixed sense impression of the box.

Box 19. 21" x 18¾" x 20", two fastenings. A door in the middle of the front, hinged at the bottom, was fastened by a bolt at the top, operated by a loop inside the cage. It was also fastened by a stick leaning against it from the outside. In addition it had to be pushed open. This is the same as THORNDIKE's Box J.

Box 20. 21" x 18¾" x 20", one fastening. Same as Box 19 except that the bolt was removed. Thus the door was fastened only by a stick leaning against it from the outside.

Box 21. 20½" x 11" x 11½", three fastenings. This box had a door in the middle of the front, hinged at the bottom and fastened by a lever at each side and also by a wooden plug which was thrust obliquely into a hole in the door frame. The box had entirely closed sides. The raccoons were taught to go into this box to get food. At first both levers had to be pushed up but later they were arranged so that considerable force would push them downward. The plug was very difficult to draw. I have compared this with THORNDIKE's Box K.

*Observations on Reactions to Fastenings.*—The raccoons learned very readily to perform a certain act in a particular situation. This learning is doubtless of the trial and error type, yet when a latch has been operated a few times there is probably present in the animal's mind a distinct memory image of the act, including a memory of its difficulty. Experiments with colored cards, to be described later, gave evidence in support of this opinion. At first I supposed that, as was true in THORNDIKE's work with cats, the raccoons would be found to learn chiefly from the stimulus of hunger. As already stated, however, they soon showed a tendency to unfasten latches and set themselves free from the mere pleasure of performing the act. This motive was not strong enough to overcome the discouraging difficulties of a box of six or seven fastenings, but the tables show so-called "play trials" for all boxes of fewer fastenings. The term "play trials" means, then, that though the animal unfastened the latches and escaped from the box, he refused to eat or drink milk on coming out or at best merely tasted the milk and turned away from it. Generally this work was deliberately done, but often rapidly. It seemed, therefore, that this tendency to be occupied was the motive for some of the raccoon's normal learning and careful records were kept of all play trials. In Table I, I have indicated the cases that were certainly play trials with italics, but the cases which were certain to the observer were fewer than the actual number, for as the raccoon's hunger was gradually allayed he worked partly for the mere pleasure of doing the work and partly from hunger. This is shown in the longer times taken to escape toward the close of each day's work. When the animal showed any eagerness for food, the reaction was recorded as a hunger trial even though play trials had preceded it. The tables show that this was unusual, the rule being that play trials began only when hunger began to be satisfied. Even when using the most complicated fastenings I did not employ "utter hunger." I usually gave the raccoons considerable food after I had finished the day's experiments. In several trials with the raccoons, when they were young, I was able to get one to work, which otherwise would not do so, by bringing another near the door of the cage. As they grew older this was of no use.

Under ordinary experimental conditions the motives from which a raccoon learns are, therefore, hunger, an apparent desire to be occupied, called by several writers curiosity, and in the young, loneliness.[3]

One may ask, were not the play trials actuated by a desire to escape from the narrow confines of the box? I cannot say so with certainty, for all four raccoons would go into a box willingly enough unless it took prolonged work to escape. In that case it was difficult even to put them in, and they developed a tendency to snap at the experimenter's hand before he could withdraw it from the box. Evidently the memory of previous hard work to escape was the cause of this resistance, for with easy fastenings the animal would re-enter the box time after time and then deliberately work the latches as a part of an aimless activity which included toying with loose objects, reaching out with the forepaws through the slats or trying to pull dust or straws into the cage. A change of food from meat to sugar at this moment would often stimulate the animal to escape instantly. Without some such stimulus as this the animal might not come out of the box when the door swung open or it might come out very slowly. Reluctance to re-enter a box being in direct proportion to the difficulty of its fastenings, I can but believe that the raccoons felt no sense of confinement in a box which they knew how to open very quickly. At any rate their behavior toward re-entering easy boxes was the *exact reverse of that toward re-entering difficult ones.*

The conditions which prevented quick working of the mechanisms and consequently delayed the forming of an association were too great eagerness due to hunger, approaching satiety and distraction of attention.

(1) *Eagerness.*—In most cases the first attempt each day, or each half-day, required more time than succeeding attempts even though the animal had operated the mechanism quickly many times before. The eagerness seemed in most cases to amount to great excitement. In the first trial the animal seemed to fall back on primitive impulses. It made many ineffective movements. In the second trial each day it seemed to depend on memory, and often made but one movement for each latch.

---

[3] I do not mention the motives of pain, danger, etc., as they were not employed in this study.

(2) *Approaching satiety* usually, but not always, inhibited quick work. The animals seemed to form associations more rapidly when their work was deliberate.

(3) *Distraction of attention* inhibited all work. The animals never seemed to work a latch as a *purely* reflex performance. Consequently, I never could get them to claw where a loop had been or when the door was open, as THORNDIKE's cats did. The nearest approach to this occurred with Box 3. This box had its fastening at the right of the door (looking outward), while Box 1 had a button at the left and the loop of Box 2 hung at the left side of the door. The doors of Boxes 1 and 2 swung to the right, the door of Box 3 swung to the left. No. 4 clawed four times (first, second, third and tenth trials) at the left side of the door (125 experiences in preceding two boxes). No. 3 *went to* the left side of the door the first four trials in the morning and the first, second and fourth trials in the afternoon of his first day's experience in this box (200 trials in preceding boxes). A third raccoon, No. 2, clawed twice at the left side of the door after 132 experiences in the preceding boxes. Therefore, after six days of work with latches at the left side of the door, seven is the maximum number of times an animal *went to* that side of the door in the new box, and four the maximum number of times an animal clawed at that side. In all future new boxes the animals seemed to pick out the new latch and work directly at that, as if experience led them to attack movable objects within the box, or else objects which gave a click or other sound when operated. Only the buttons were noiseless. These facts, with others to be mentioned, indicate, I think, that the raccoon's learning to operate a latch includes something more than the mere mechanical coupling up of a certain instinctive act with a given situation.

In each day's or half-day's work, there was usually a slow success due to eagerness, several rapid ones due to hunger without too great eagerness, and finally several reactions, which gradually became slower, in which the stimulus was but little more than a native desire to be occupied. Most of the latter are recorded as "play trials."

I give in Table I the time in seconds for the first forty trials in each of seven boxes. As these results are typical those with other fastenings are omitted. Where the results obtained with other boxes are mentioned in the text the records are quoted with sufficient fullness, I think, to verify the deductions made from them.

A light vertical line following a figure indicates the termination of one-half day's experiments, a heavy line indicates the termination of a day's experiments. Unoccupied spaces *preceding figures indicate the number of times a raccoon was put through the act of operating a fastening*, for example, No. 4 was put through Box 5 four times the first half day. The records show that putting through is not a great obstacle to the raccoon's learning as it seems to be in the case of cats. The times were originally taken in seconds and fifths, but in this table the nearest whole number of seconds is given. For example, No. 2's first two records in Box 1 were 45.6 and 41.8 instead of 46 and 42 seconds.

It we take the average of the times required for all first and second trials with single fastenings for the raccoons not put through the act, we find that they stand approximately in the ratio of 3 to 2 (Boxes 1, 2, 3, 4). KINNAMAN'S results show that the male monkey's first and second trials in the "Button," "Vert. Hook," "Bolt," and "String and Nail" boxes (I omit the T-Latch Box, as its first time is unusually long), when averaged are approximately in the ratio 2 to 1 (strictly 156 : 74). After having been trained in seventeen boxes the monkey reduced the average time of second trials to one-fourth that of first trials.

Among THORNDIKE'S records for cats there are many failures on second trials, and he insists on the *extreme gradualness* of the formation of associations in the animals. In rapidity of forming associations with single fastenings the raccoons, therefore, stand next to the monkeys. Had we records for four monkeys instead of one, the ratios would probably be still more nearly the same.

The table shows that often a raccoon may operate a fastening quickly two or three times, after which there follow immediately longer times. The case seems to be like that of a man who may find a house in the city once by fortunate accident, but only after he has had to search for it does he *know* where it is in relation to its surroundings.

The time records for the raccoons show greater and more numerous variations than those for cats, or even those for monkeys. Perhaps this is due to the fact that the cats were utterly hungry and the rhesus monkeys did not exhibit play trials.

## TABLE I

Time in seconds for trials **1** to **40**.

| Box Fastening. | Raccoon. | 1 | | | | 5 | | | | | 10 | | | | | 15 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Box 1, Button | No. 1 | 27 | 56 | 4 | 24 | 8 | 11 | *45* \| | 360 | 10 | 10 | 29 | 41 | 40 | 14 | 18 | 24 |
| Box 1, Button | No. 2 | 46 | 42 | 309 | F \| | 5 | 39 | 13 | 25 | 45 | 41 | 129 | 23 | 15 | 19 | 11 | 10 |
| Box 1, Button | No. 3 | 12 | 12 | 12 | 75 | 10 | 60 | 130 | F | 60 \| | 80 | 57 | 51 | 20 | 27 \| | 10 | 3 |
| Box 1, Button | No. 4 | 300 | 10 | 65 | 345 | 135 | 12 | 10 | 4 | 80 | 12 | 5 | 10 | 10 | 20 | 55 | 15 \| |
| Box 4, Loop at back | No. 1 | 62 | 24 | 13 | 12 | 4 | 8 | 3 | 2 | 6 | 4 | 3 | 3 | 10 | 5 | 4 | *214* |
| Box 4, Loop at back | No. 2 | 150 | 20 | 12 | 50 | 6 | 3 | 4 | 5 | 3 | 9 | 2 | 9 | 2 | 7 | 3 | 2 |
| Box 4, Loop at back | No. 3 | | | | | | | | | | 7 | 7 | 17 | *47* | *133* | *233* | 11 |
| Box 4, Loop at back | No. 4 | | | | | | | | | | | | | | | | |
| Box 5, 2d Put-through Box | No. 1 | 46 | 25 | 15 | 4 | 3 | 3 | 9 | 4 | 5 | 6 | 5 | 5 | 4 | 21 | 3 | 14 \| |
| Box 5, 2d Put-through Box | No. 2 | 51 | 10 | 26 | 24 | 9 | 2 | 3 | 3 | 4 | 6 | 3 | 2 | 2 | 2 | 3 | 3 |
| Box 5, 2d Put-through Box | No. 3 | | | | | 20 | 8 | 4 | 5 | 17 | 8 | 4 | *909* \| | 11 | 7 | 4 | 4 |
| Box 5, 2d Put-through Box | No. 4 | | | | | 4 | 4 | 3 | 2 | 7 | 3 | 3 | 13 | 6 | 5 | *3* | *3* \| |
| Box 9, Four Fastenings | No. 1 | 45 | 24 | 16 | 10 | 7 | 6 | 18 | 8 | 9 | 8 | 7 | 18 | 25 | 63 \| | 11 | 24 |
| Box 9, Four Fastenings | No. 2 | 29 | 15 | 19 | 15 | 7 | 8 \| | 23 | 28 | 12 | 15 | 6 | 6 | 6 | 16 | 16 | 11 |
| Box 9, Four Fastenings | No. 3 | | | | | | | 20 | 16 | 12 | 25 | 12 | 16 \| | 496 | 40 | 44 | 28 |
| Box 9, Four Fastenings | No. 4 | | | | | | | 16 | 18 | 11 | 12 | 10 | 10 | 119 \| | 25 | 20 | 50 |
| Box 10, Thumb-latch | No. 1 | F | F | F | 6 | F \| | 6 | 59 | 173 | 158 | 7 | 6 | 2 | 1 | 1 | 1 | 1 |
| Box 10, Thumb-latch | No. 2 | 30 | 153 | 7 | 21 | 4 \| | 7 | 2 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 3 | 1 |
| Box 10, Thumb-latch | No. 4 | 18 | 7 | 7 | 31 | 14 | 9 \| | 6 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 1 |
| Box 14, Hook | No. 1 | F | | | | | | 3 | 7 | 19 | 10 | 87 | 10 | 5 | 6 | 2 | 1 |
| Box 14, Hook | No. 2 | 75 | 39 | 12 | 19 | 4 | 7 | 1 | 7 | 14 | 4 | 7 | 3 | 5 | 8 | 5 | 9 |
| Box 14, Hook | No. 3 | 545 | 23 | 16 | 2 | 6 | 6 | 2 | 1 | 2 | 1 | 1 | 1 \| | 1 | 1 | 1 | 1 |
| Box 14, Hook | No. 4 | | | | | | | | | | | 231 | 62 | 23 | 5 | 4 | 5 |
| Box 13, Second Attempt* | No. 1 | 11 | 165 | 86 | 106 | 43 | 72 | 85 | 45 | 24 | 29 | 26 | 22 | 89 | 48 | 28 \| | 22 |
| Box 13, Second Attempt | No. 2 | 35 | 20 | 13 | 14 | 661 | 186 | 38 | 37 | 24 | 24 | 35 | 44 | 15 | 45 | 64 | 29 |
| Box 13, Second Attempt | No. 3 | 31 | 746 | 296 | 482 | 601 | 223 | 56 | 39 | 37 | 22 | 27 | 49 | 32 \| | 19 | 20 | 57 |
| Box 13, Second Attempt | No. 4 | 71 | 12 | 27 | 38 | 24 | 17 | 33 | 19 | 15 | 139 | 34 | 35 | 14 | 21 | 29 \| | 31 |

*In the first attempt with Box 13 all the raccoons failed on the "hook." They were therefore tried with the hook alone in Box 14.

TABLE I—Continued.

|  |  |  | 20 |  |  |  |  | 25 |  |  |  |  | 30 |  |  |  |  | 35 |  |  |  |  | 40 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 20 | 32 | 6 | 30 | 10 | 8 | 5 | 6 | 8 | *12* | *14* | *13* | *21* | *25* \| | 6 | 28 | 4 | 4 | 1 | *15* | *34* | *36* | *9* | *13* |
| 43 | 14 | 21 | 9 | 10 | 13 | 19 | 15 | 9 | 8 | 7 | 19 | 6 | 8 | 6 | 75 | 14 | 18 | 22 | 4 \| |  |  |  |  |
| 3 | 5 | 6 | 4 | *3* | 9 | *24* | *7* | *14* | *3* | *9* | *20* | 7 | *143* | 71 \| | 21 | 1 | 1 | 1 | 3 | 16 | 9 | 12 | 4 \| |
| 75 | 39 | 4 | 57 \| | 57 | 17 | 3 | 2 | 13 | 4 | 4 | 8 | *50* | *7* | *6* | *5* | *6* | *5* | *95* | *1* \| | 35 | 3 | 2 | 2 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *19* \| | 5 | 7 | 8 | 5 | 4 | 3 | 27 | 15 | *336* | 6 | 10 \| | 5 | 3 | 3 | 3 | 4 | 3 | 5 | 4 | 3 | 4 | 3 | *434* \| |
| 3 | 5 | 5 | 9 | 6 \| | 8 | 2 | 3 | 3 | 1 | 2 | 3 | 5 | 4 | 3 | 91 \| | 4 | 20 | 5 | 8 | 2 | 2 | 3 | 6 |
| 10 | 12 | 13 | 2 | 8 | 591 \| | 7 | 5 | 2 | 1 | 2 | 2 | 2 | 6 | 6 | 4 | 31 | 4 \| | 12 | 14 | 2 | 15 | 3 | *22* \| |
|  |  |  |  |  |  | 48 | 21 | *75* | *149* | *23* | *263* \| |  |  | 23 | 16 | 44 | 5 | 485 \| | 15 | 14 | 22 | 11 | 18 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 7 | 4 | 4 | 4 | 5 | 4 | 3 | 10 | *149* \| | 5 | 4 | 5 | 4 | 3 | 7 | 10 | 3 | 4 | 5 | 13 | 4 | 5 \| | 10 | 9 |
| 3 | 7 | 3 | 3 | 4 \| | 8 | 3 | 4 | 8 | 2 | 2 | 5 | 6 | 3 | 2 | 3 | 1 | 1 | 2 | *12* \| | 11 | 3 | 2 | 9 |
| 3 | 3 | 4 | 3 | 3 | 11 | 15 | *12* \| | 3 | 2 | 2 | 3 | 4 | 15 | 17 | *153* \| | 4 | 3 | 4 | 4 | 4 | 3 | 4 | 3 |
| 23 | 4 | 11 | 8 | 11 | 5 | 4 | 7 | 3 | 3 | 12 | 5 | 2 | 4 | 3 | 173 \| | 3 | 5 | 4 | 5 | 5 | 9 | 5 | 4 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 13 | 15 | 15 | 8 | 9 \| | 7 | 7 | 9 | 6 | 16 | 9 | 7 | 9 | 13 \| | 7 | 11 | 7 | 7 | 7 | 8 | 7 | 5 | 7 | 6 |
| 13 | 11 | 13 \| | 6 | 13 | 5 | 13 | 7 | 14 | 17 | 6 | 5 \| | 9 | 7 | 22 | 6 | 8 | 8 | 12 | 13 \| |  |  |  |  |
| 11 | 87 | 7 | 9 | 7 \| | 12 | 8 | 12 | 5 | 6 | 8 | 5 | 15 | 6 | 10 | 7 | 11 | 12 | 5 | 478 \| |  |  |  |  |
| 18 | 865 \| | 26 | 27 | 9 | 8 | 10 | 12 | 15 | 10 | 985 \| | 17 | 15 | 17 | 6 | 6 | 6 | 6 | 5 | 7 | 8 | 11 | 28 |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 2 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 1 \| | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 2 | 1 |  |  |
| 1 | 1 | 1 | 1 | 1 | 1 | 2 \| | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 2 | 3 | 1 | 4 |  |  |
| 1 | 1 | 2 | 1 | 1 | 3 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 1 |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 \| | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 1 |
| 13 | 17 \| | 10 | 2 | 4 | 3 | 3 | 2 | 2 | 4 | 2 | 3 | 2 | 2 | 2 | 6 | 2 | 1 | 1 | 1 | 1 | 3 | 1 | 1 |
| 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 60 |  |  |
| 1 | 1 | 2 | 1 | 1 | 1 | 17 | 1 | 1 | 1 | 1 | 1 | 2 | 3 \| | 3 | 21 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 1 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 30 | 38 | 15 | 23 | 16 | 20 | 18 \| | 226 | 154 | 19 | 49 | 21 | 25 \| | 386 | 35 | 97 | 26 | 50 |  |  |  |  |  |  |
| 18 | 25 | 15 | 25 \| | 26 | 17 | 11 | 18 | 11 | 42 | 23 | 24 | 15 | 16 | 14 | 17 | 14 | 27 | 10 | 22 | 19 | 16 | 13 | 30 |
| 19 | 44 | 40 | 22 | 19 | 40 | 18 | 19 | 45 | 61 | 27 \| | 8 | 18 | 31 | 181 | 55 | 22 | 93 | 39 | 55 | 133 \| | 19 | 34 | 17 |
| 30 | 48 | 82 | 14 | 14 | 25 | 30 | 17 | 15 | 48 | 17 | 8 | 23 | 11 | 12 | 45 | 16 | 14 | 27 | 56 | 13 | 16 | 15 | 12 |

*Complexity of Associations.*—It was my purpose to compare the complexity of the associations a raccoon is able to form with those formed by monkeys. I therefore combined new fastenings with those already learned until in Box 13 I came very near the limit of their abilities. In Box 21, I also tested the animals' ability to operate three hitherto untried fastenings and I changed the plan from coming out to be fed to going into the box for that purpose. The animals all succeeded in learning to work seven fastenings: namely, two buttons, two bolts lifted by a pull on each of two loops hung in different parts of a large box, one thumb-latch, one bolt raised by the animal's mounting a platform and a horizontal hook placed at the left side of the door. The thumb-latch had to be worked last. The raccoons thus learned a combination of seven latches. The rhesus monkey did the same, but no doubt the raccoons were given more trials. The average time required for the first trial in boxes of two to seven fastenings, inclusive, is 65 seconds, for the second trial, 44 seconds. KINNAMAN[4] gives 25.5 as the average of first trials in similar combinations and 16.5 as the average of second trials. Thus, for both raccoons and monkeys working with groups of fastenings, the time required for the second success is but two-thirds the time for the first. The anomalous case of raccoon No. 3 in Box 13 in which he required only thirty-one seconds for the first trial, and seven hundred forty-six for the second, has not been included in the average, for to include it would have been to let one peculiar case be equal to eighteen ordinary cases. His third trial is two hundred ninety-six seconds. This case of No. 3 in Box 13 is an example of the fact already mentioned that a raccoon may operate a mechanism quickly once or twice before his actual learning begins.

In boxes of two to seven fastenings there is almost no tendency to follow a routine order in undoing them. Occasionally a definite order may appear one day and another the next in the same box, but neither is followed very closely. Several hundred experiences in Boxes 12 and 13 failed to establish a definite order. The raccoon often seems to begin with the first fastening which attracts his attention. With more than four fastenings each animal showed a tendency to forget a certain one of them, for example, one button or one loop throughout the day's training, or perhaps for two successive days. The case seems not unlike that

---

[4] *Amer. Jour. of Psychol.*, vol. 13, p. 118.

of a man who makes the same mistake each time in adding a long column of figures. Not only was no routine order followed, but often the raccoons worked one or more fastenings more than once, never, however, was a latch operated after the door was open. The temptation is strong to say that the raccoon has no memory of having already released a latch, since he operates it a second time. I think this interpretation of the animal's conduct incorrect, however, for in Boxes 11 to 13 inclusive, in which a thumb-latch had to be released last, it was operated almost twice as many times as any other fastening. The animals would work one or two latches, then try the thumb-latch, and so on. This indicates that the animal had a distinct association of the opening of the door *immediately after the depression of that latch*, that is, *the perceptual factor of the opening door was a part of the association.* No such perception was possible after the release of any other of the latches so they were worked at random because *in the past* each of them had resulted in the opening of the door. If the door did not open they were worked again. Surely it is asking too much of the animals to expect them to know that each latch when released partly unfastens the door although the door does not move until the last latch is worked. Such a view would demand of the animals either reasoning or a human being's knowledge of bolts and pulleys. His association, his idea, if he has one, is that the last act opens the door. It is noticeable, too, that the two buttons and the hooks which could be seen to be out of the way when unfastened were not operated a second time nearly so often as the loops and platform which presented no perceptible change of place after having been depressed. Consequently it seems quite as fair to argue that the raccoon pulls a loop a second time because no desired result perceptible *to him* followed the first pull, as to urge that he pulls it a second time because he has no memory of having pulled it the first time.

Since, therefore, so far as the animal can see, only the final act opens the door and gains the reward of food, the conditions of the experiments were probably quite unfavorable to the acquisition of a fixed order in performing the acts. Combinationlocks, the second element of which could not be unfastened until the first had been operated did not entirely obviate this difficulty in experiments with monkeys (see KINNAMAN, p. 124), so it remains to add to this device some means of making the effect of releasing each fastening perceptible to the animal. It might at least be arranged that each act should bring the animal nearer to the food. Until this has been done we cannot confidently assert that an animal cannot learn to perform a series of acts in a fixed order.

In Box 21, which had three hitherto untried fastenings and in which the plug was extremely difficult to draw, all the raccoons failed in their first and second attempts. The average time required for their first success was 132 seconds, for the second, 85 and for the third, 37. Some failures followed the third trial in the records of all except No. 3. The records in this box serve to show the rate of learning of raccoons compared with the more slowly formed associations of cats.

All the raccoons showed a tendency to abbreviate their acts. They would merely turn toward a loop without clawing it or make a slight motion toward it without touching it.

Only rarely did one of the raccoons press down two buttons simultaneously. In Box 12, however, raccoon No. 3 was observed to try to pull a loop while standing on the platform whose depression raised another bolt. The next day he succeeded several times and finally settled down to doing both these acts at the same moment. A few days later No. 4 had also combined these two acts, and thereafter she did both simultaneously in about one-half the trials. The other two raccoons never combined these acts. Often the thumb-latch and one button would be worked simultaneously; but this, we believe, was a mere physical convenience, since the animal could press on the latch with one forepaw and depress the button with the other without changing the position of its body.

*Variability.*—I have shown that in a series of acts no routine order was established. Was there variation in the method of performing the act? Box 14 was fastened with a horizontal hook which could not be raised with the paw and was therefore very difficult for the animals to learn. All except No. 2 lifted it with the nose; he did the act with his teeth for thirty trials and only twice the first half-day with his nose, and six times the second half-day, up to the twentieth trial. That time he raised the hook with his nose and continued to do so thereafter. He was escaping by means of the mouth reaction in the average time of two and one-half seconds, so he had fully mastered the mechanism before changing thus abruptly to the muzzle reaction. All of the raccoons turned a button once or twice with the nose in early trials then settled down to working it with the paw. In acts so difficult to learn that the animal *had to be* put through them, there was no change from the act put through to one accidentally hit upon.

The raccoons were observed to operate fastenings with either the right or left paw or with both at once. We may say in general that the first successful act was not always stamped in because it was not always the most convenient. Sooner or later the more convenient was substituted for the more awkward performance, and the change was sometimes abrupt. We cannot say, of these animals, therefore, that a given situation has power fatally to evoke the formerly successful act. No. 2's behavior at least was entirely unpredictable. Wherever else in psychology we find the employment of two different means to the same end we account for it by means of an image or notion. But we may speak of this later.

### MEMORY FOR FASTENINGS.

As I built up combinations of fastenings from those which the raccoons had already learned, it was not possible to give memory trials for single fastenings with a time interval sufficiently long to find the limit of their power to remember such acts. Intervals of three or four days or of two weeks showed no appreciable forgetting. After completing work with Box 13, however, I allowed an interval of one hundred and forty-seven days to elapse. This box had seven fastenings and was very difficult for the raccoons to master. At the end of this period No. 3, No. 2 and No. 1 were again tried in this box. Only the first succeeded in working all the fastenings and releasing himself. He undid the seven fastenings and came out of the box in 34, 28, 131, and 182 seconds, successively. The other two worked nearly but not quite all the fastenings, the horizontal hook being most frequently missed. This period, therefore, may be regarded as very near the limit of the raccoon's memory for the most complex motor associations he is able to form. It seems likely that No. 3's superior memory for this box was due to the extreme difficulty he encountered in mastering it. No. 2 had had more trials in Box 13 than No. 3 and he is fully as intelligent an animal, yet No. 3, whose difficulties were very great at first, reached the extremely low minimum time of seven and two-tenths seconds and remembered the combination better. Were raccoon No. 3 a human being, we should have no hesitation in saying that he had to give closer attention to the mechanism in order to learn it. If the learning were nothing more than the formation of a habit, No. 2, who had had more experiences with the combination, should have been superior in operating it after a long time interval. Additional memory tests will be described in connection with the tests of discrimination.

## DISCRIMINATION.

*Visual Discrimination.*—In the tests of visual discrimination no attempt was made to determine whether the raccoons distinguished colored objects by differences in color or by differences in brightness. In fact, the greater number of trials required to distinguish two colored objects as compared with the number required to distinguish white from black is, in so far, evidence that the animals were reacting to brightness alone and that the diminished difference in brightness rendered discrimination more difficult. The tests for discrimination of colored objects presented in succession led naturally to a test for the presence of visual images and this question was investigated rather than that of color-vision. I hope in the future to test color-vision. Meanwhile, where colors are named in this and succeeding sections it will be understood that colors exclusive of brightness differences are not implied.

In the first tests a modification of the apparatus used by KINNAMAN in his study of the color perception of monkeys was employed. Two ordinary drinking glasses were covered on the convex surface with papers of different colors. Of one pair, one glass was covered with white paper, the other with black; of another pair, one was covered with red, the other with green. The black and white papers were of Milton Bradley manufacture and were of the same intensity respectively as his black and white Maxwell disks. The red and green also were the Bradley standard colors.

In the experiments a bit of food was placed in one glass and the glasses were then brought into the view of the animal and placed side by side on the floor, from six to thirty inches apart in different trials. An assistant set the raccoon free facing the two glasses. The animal came to the glasses and secured the food. He was returned to the assistant, food was put in the same glass as before and their positions from right to left were reversed. This reversal was made in each successive trial at first, then the feeding glass was left in the same place twice in succession, then three times, so that neither position nor illumination should influence the choice. The usual distance between the two glasses was six or eight inches, for beyond this distance the animal seemed to get his eyes fixed on one of the glasses and to go straight to that one. His reaction was influenced by the direction of his gaze at the moment he was set free. This seems unusual, yet it appeared regularly whenever the glasses were placed from twelve to thirty inches apart. The distance from the point at which the raccoon was set free to the glasses was eight feet.

No. 4 and No. 1 were tried with black and white. Food was always placed in the black glass. No. 4 was given 25 trials the first day, 68 the second and 50 the third; No. 1 was given 25 trials first day and 100 the second. Thus both were practically perfect toward the close of the second day's test.

TABLE II.

| | *No. 1.* | | *No. 4.* | |
|---|---|---|---|---|
| No. of trials. | Black. | White. | Black. | White. |
| 1–10 | 4 | 6 | 5 | 5 |
| 11–20 | 5 | 5 | 4 | 6 |
| 21–30 | 6 | 4 | 5 | 5 |
| 31–40 | 4 | 6 | 5 | 5 |
| 41–50 | 5 | 5 | 6 | 4 |
| 51–60 | 3 | 7 | 8 | 2 |
| 61–70 | 6 | 4 | 9 | 1 |
| 71–80 | 7 | 3 | 9 | 1 |
| 81–90 | 10 | 0 | 9 | 1 |
| 91–100 | 9 | 1 | 10 | 0 |
| 101–110 | 10 | 0 | 10 | 0 |
| 111–120 | 10 | 0 | | |
| 121–130 | 10 | 0 | | |
| 131–140 | 10 | 0 | | |

After five days without practice No. 4 in fifty trials went directly to the black forty-five times. On the third, seventh, tenth, fourteenth, twentieth and twenty-second trials she went to the white.

Two days later No. 1 was perfect in fifty trials, and after an interval of five days in 46 out of 50. The animals, therefore, learn to discriminate black from white in from seventy to ninety trials.

No. 2 and No. 3 were tried with red and green glasses. Food was placed in the latter. No 2 was given approximately 120 trials per day for five days; No. 3 approximately 140 trials each day for 5 days. The number of trials per day varied slightly with the degree of the animal's hunger.

TABLE III.

| | *No. 2.* | | | *No. 3.* | |
|---|---|---|---|---|---|
| No. of trials. | Green (right). | Red (wrong). | No. of Trials. | Green (right). | Red (wrong). |
| 1–100 | 52 | 48 | 1–100 | 54 | 46 |
| 101–200 | 50 | 50 | 101–200 | 54 | 46 |
| 201–300 | 51 | 49 | 201–300 | 53 | 47 |
| 301–400 | 68 | 32 | 301–400 | 64 | 36 |
| 401–500 | 84 | 16 | 401–500 | 52 | 48 |
| 501–595 | 87 or $91\frac{11}{19}\%$ | 8 | 501–600 | 55 | 45 |
| | | | 601–690 | 75 or $83\frac{1}{3}\%$ | 15 |

It is evident from these tests that many more trials are required to learn to distinguish red from green, than to discriminate black from white. As already stated, this may be evidence of a response to difference in brightness alone.

At this point I devised a "card displayer" by which the two colors could be shown in succession instead of simultaneously; it was also necessary to arrange the experiment so that it could be carried on by one person (Fig. 1).

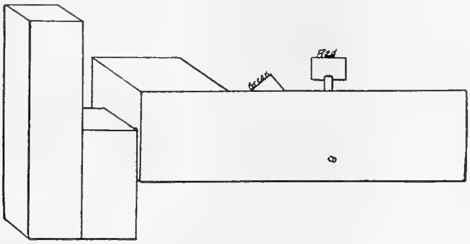


Fig. 1.

The front of the card-displayer consisted of a board twelve inches high. A round pin or pivot on which two levers could be turned was inserted in a hole near the lower edge of the board. In the upper ends of these levers colored cards were fastened so that raising one of the levers to a vertical position displayed red, for example, raising the other displayed green. During one test red would be on the forward lever one inch in front of the other, during the next test on the rear lever. The animal could not, therefore, react to the position of the cards. On account of the difficulty of one person alone having to display the colors, feed the raccoon and keep the record, my notes are not perfectly reliable in respect to the exact number of times required for the mastery of each pair of colors. Consequently when a pair of colors seemed to have been mastered, each animal was given a final test of either twenty-five or fifty trials, an experienced assistant keeping the record. If out of twenty-five trials there were at least twenty-three correct reactions, or out of fifty trials at least forty-five, I assumed that the colors were discriminated. In most of these final tests the raccoon never failed to react to the right (food) card and never attempted to react to the wrong one. The response demanded of the animal was that he mount a box $2\frac{1}{2}$ feet high by means of another 15 inches high which served as a step to the first, when the food-card was displayed, and that he refuse to go up when the other card appeared. If he started up but returned at once after a second look at the no-food card, the reaction was recorded as correct. If he did not come back immediately from the lower box, the reaction was recorded as incorrect. On the other hand, he was required to go to the top of the two steps when the food card was displayed.

According to the above standard the animals learned to discriminate the following pairs of cards of different colors and intensities.

No. 4. Black-white, Black-yellow, Black-red.

No. 3. Black-white, Black-red, Black-blue, Black-yellow, Black-green, Blue-yellow.

No. 2. Black-white, Black-red, Black-blue, Black-yellow, Black-green, Blue-yellow.

No. 1. Black-white, Black-red, Black-blue, Black-yellow, Black-green, Red-green.

By this method also it always required many more trials for the discrimination of red from green, or blue from yellow than for the discrimination of black from white, or of black from the colors. The female, No. 4, though given many trials, did not succeed in discriminating red from green, nor blue from yellow, hence in this case the brightness difference seemed too slight to serve as a means of distinguishing the colors. Further evidence that No. 1 distinguished cards of different colors and intensities is given on p. 256. The fact of his discrimination of the series white, orange, blue, from the series blue, blue, blue, whether each series was shown alternately or twice in succession is mentioned on p. 257, and the reactions of all three males to similar series are recorded on p. 259. These tests of visual discrimination may be regarded merely as experiments preliminary to the test for visual images.

One peculiarity in the behavior of the raccoons should be emphasized. When they were discriminating well their eyes were never more than 18 inches from the colored cards, more often within a foot of the cards and still more often within three inches, *i. e.*, the animal took a position with his forepaws on the front board of the card displayer and looked intently for the card to appear. I have never seen the animal look at the card from a distance of several feet and respond to it. This shows the difficulty of such discrimination, and it may indicate that the distance for perceiving color or brightness is extremely short. If this be so, the apparent inability to see two glasses when placed 30 inches apart and at a distance of eight feet from the animal is accounted for.

*Discrimination of Sounds.*—I endeavored to ascertain the ability of the raccoons to discriminate a high from a low tone and to form the association of being fed at the sound of the high note. The response expected of the raccoon was that he mount the high box to be fed on hearing the food signal. While pure tones should have been used it was, for practical reasons, impossible to do so. I therefore sounded the highest note, $A_1$, possible with an ordinary A French harp or harmonica, then the lowest, $A''$. For the first few trials the hand was extended toward the high box when the food signal was given and the animal fed when he climbed upon the box. When this aid was withdrawn it was found that No. 1 was practically perfect in responding to the high tone and in refusing to respond to the low one. No. 2 had not mastered the association. His record after the first few trials in which the hand signal aided him is as follows:

TABLE IV.

| | *No. 2.* High-tone, food signal. | | | *No. 2.* Low-tone, no-food signal. | |
|---|---|---|---|---|---|
| | Right. | Wrong. | | Right. | Wrong. |
| 1–50 | 37 | 13 | 1–50 | 34 | 16 |
| 51–100 | 44 | 6 | 51–100 | 38 | 12 |
| 101–130 | 27 | 3 | 101–150 | 48 | 2 |
| | | | 150–200 | 50 | 0 |

The animals had completed the visual discrimination tests before they were tried with this pitch discrimination.

*Discrimination of Forms.*—For experiments in the discrimination of forms and sizes the card-displayer already described was used. Cards of different forms or of different sizes were substituted for cards of different brightness and color. In the tests for form discrimination the animal was fed when a square card 6 x 6 inches appeared and not when a circular one 6 inches in diameter was shown. If the animal formed an association between the square card and food so that he went to the top of the high box to be fed when that card was shown and refused to go up when the circular card appeared, we may say that he discriminated. My purpose was to test the discrimination of two objects widely different for the human eye, not to test the delicacy of discrimination.

The results for form discrimination given by No. 2 and No. 1 appear below. Both animals had already discriminated differently colored cards by this method, so that attention to the cards was well established and the form test proved to be very easy.

TABLE V.

| | *No. 1.* | | | | *No. 2.* | | | |
|---|---|---|---|---|---|---|---|---|
| | Square. | | Circle. | | Square. | | Circle. | |
| | Right. | Wrong. | Right. | Wrong. | Right. | Wrong. | Right. | Wrong. |
| 1–50 | 38 | 12 | 35 | 15 | 43 | 7 | 41 | 9 |
| 51–100 | 47 | 3 | 47 | 3 | 42 | 8 | 39 | 11 |
| 101–150 | | | | | 48 | 2 | 44 | 6 |

As a matter of fact, these two cards differed in size as well as in form, but for sensation (barring judgment) I thought this circle to have more nearly the value of the square than one of exactly equal area. However, anyone who will compare two circles with radii of 3 and $3\frac{7}{20}$ inches respectively will, I think, find their visual difference very slight.

*Discrimination of Sizes.*—No. 2, No. 3, and No. 4 were tested in the discrimination of sizes by the method used in the form discrimination. Two square cards $6\frac{1}{2}$ x $6\frac{1}{2}$ and $4\frac{1}{4}$ x $4\frac{1}{4}$ inches were used. They were first shown alternately, then in varying order. The rapid learning which occurred is due to much previous training in brightness discrimination by this method. It is evident that each animal began to form the association within the first fifty trials, and that learning not to respond to the small card proceeded more slowly than learning to go up when the large card appeared. The cards were not shown simultaneously, but in succession. Thus, remembrance of the card just shown was required for a successful response. On presenting the larger card the animal was fed, if he climbed to the top of the large box.

## TABLE VI.

| | *No. 2.* | | | | *No. 3.* | | | | | *No. 4.* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Large. | | Small. | | Large. | | Small. | | | Large. | | Small. | |
| | Right. | Wrong. | Right. | Wrong. | Right. | Wrong. | Right. | Wrong. | | Right. | Wrong. | Right. | Wrong. |
| 1-50 | 47 | 3 | 44 | 6 | 29 | 21 | 33 | 17 | 1-50 | 43 | 7 | 35 | 15 |
| 51-100 | 45 | 5 | 32 | 18 | 48 | 2 | 29 | 21 | 51-100 | 43 | 7 | 31 | 29 |
| 101-150 | 47 | 3 | 39 | 11 | 44 | 6 | 38 | 12 | 202-250 | 47 | 3 | 28 | 22 |
| 151-200 | 39 | 11 | 38 | 12 | 47 | 3 | 34 | 16 | 252-200 | 44 | 6 | 35 | 25 |
| 201-250 | 49 | 1 | 47 | 3 | | | | | 20-1250 | 49 | 2 | 37 | 23 |
| | | | | | | | | | 251-300 | 48 | 2 | 48 | 2 |

### IMITATION.

Experiments were made to test whether the raccoons imitate one another and whether they would come to perform an act from seeing the experimenter do it. Briefly, I found that the animals not only do not imitate one another, but that they do not pay the slightest attention to one another except when playing, or fighting, or when biting each other gently for the sake of mutual scratching. I give an example of the experiments for the sake of criticism. The method may be inadequate. Experiments arranged so as to attract the animal's attention to the thing to be learned may still reveal imitation.

The raccoons did, in two forms of experiment, seem to acquire an impulse to do an act from seeing me do it. In one, the act was so easy that the evidence is almost worthless, but in the other the act was so difficult that it would seem to be evidence for either imitation or the presence of ideas or both. In other cases, however, the animals failed to learn from seeing me operate a mechanism.

No. 1 had learned to open Box 16, whose door was fastened by two horizontal wooden bolts, primitive barn-door latches. Throwing both of these to the right released the door; throwing one or both to the left fastened the door. The box was a difficult one to open, for having once thrown a latch to the right the chances were that the raccoon's next movement would throw it to the left.

The box had two compartments separated only by a partition of poultry wire. The imitator facing this partition was near the door so that it was *possible* for him to see the work of No. 1, in opening it. No. 4 first failed in three minutes. She was then put in the imitator's compartment while No. 1 opened the door 18 times. No. 4, however, did not see him do it. She was put in the same compartment with No. 1 and still I could never be certain that she saw his acts. She was then held and saw the experimenter open the door during several series of ten trials each. She continued to fail when left to try alone. Subsequently, I held the animal so that he certainly saw the work of the raccoon he was to imitate. When the door was opened both came out and were fed. No. 4, No. 3 and No. 2 did not learn to open the door from seeing No. 1 do it or from seeing the experimenter do it.

As a further test of imitation I taught No. 2 to claw the small block out of the opening in the top of Box 17. No. 1 was then given opportunity to learn by imitating No. 2. He did not watch No. 2's work. He was then held so that he could not fail to see it. After this he followed No. 2 to the box each time and soon learned to dive into the box as soon as No. 2 pulled out the block and get the food before No. 2 could do so. Left to open the box for himself, he did not even go to it. He was then held and saw the experimenter remove the block three times. Then he began to claw at the block while it was being removed. He did this twice more and then was perfect in the performance of the act.

No. 3 failed after four minutes to remove the block though he clawed at it somewhat. Apple was then placed in the box and he was loosed just in time to see the experimenter remove the block. He reached in and got the apple. This was repeated ten times. He then clawed out the block instantly though it had been put in tightly. No. 4, however, did as well with no chance to imitate. Evidently the act is too easy to learn to be of much value as a test of imitative ability.

The card-displayer, however, afforded a more difficult task than I would have planned for the animals deliberately. After having had some six weeks of experience in distinguishing a black from a white card and in distinguishing complementary colors, each of the four raccoons developed a tendency to reach over the front board of the apparatus and claw up the colored cards. This tendency was encouraged and finally they would claw up the right (food) card and go to the high box to be fed, or, having clawed up the wrong (no-food) card they would claw it down. The cards could not be seen until they had been lifted up and they were difficult for the animal to raise. Therefore there were many errors. So far as imitation is in question, the important point is that the raccoons did begin to do, or try to do what they had seen done by the experimenter. Before they began this they had learned to watch the cards and the movements of the trainer's hands very closely indeed. Therefore, the animals either imitated or else from their impatience to see the right card come up there sprang the idea that they themselves might make it come up. This, however, may be all there is in intelligent imitation. I stimulated their impatience by moving the cards slowly, and the clawing soon began. The whole problem, in the case of these animals, may be one of attracting their attention to the thing to be done. Perhaps seeing a thing done often enough will set free in them an impulse to do it just as being put into a box will arouse an impulse to go into it. An important question to ask is, What free impulses is the animal capable of acquiring? Thus far we have at least two: an impulse to enter a box into which it has always been lifted; and an impulse to claw up color cards which it has previously merely seen raised. Such impulses must accompany ideas acquired from the experience of being lifted in and of seeing the card raised.

This card-displayer test of imitation has an advantage over those with latches, inasmuch as the animal did not at first fail. He simply passed from seeing a thing done to doing it himself.

Since the raccoons do seem to develop a tendency to do an act they see done by an experimenter, it seems possible that were one raccoon made dependent on another for all his food he might develop a tendency to imitate the food-getting acts of the other. There is good reason to doubt, however, whether even a young raccoon can be taught to watch another. The animal's *life* depends upon his finding and getting food *before* another of his kind gets it, not *with* that other or *after* him, for nature puts but one bit of food in a place for raccoons and I should say also for chicks, dogs and cats. The bone must be seized and escaped with *before* another gets it, if another animal be near. Hence nature puts a premium on attention to the bone and punishes with hunger any tendency to watch another animal getting food. Therefore, I think it unlikely that imitation of another will ever appear in these animals in connection with the food-getting impulse. Almost all experiments so far employed in laboratories have depended on hunger as a stimulus. Perhaps a new motive should be searched for to test the presence of imitation. Such an opinion certainly seems warranted by the behavior of raccoons. I think the same is true of dogs, cats, and chicks. In monkeys, however, KINNAMAN (p. 121) elicited two examples of undoubted imitation of one rhesus by another, in connection with food-getting, and apparent cases of "instinctive imitation" were numerous. May this difference not be attributed to the fact that monkeys' live in groups or droves and search for stores of food rather than for single bits as the raccoon does?

## LEARNING FROM BEING PUT THROUGH AN ACT.

The evidence for THORNDIKE's most far-reaching conclusions concerning the mental life of cats and dogs seems to be based on their behavior in experiments in which they were put through the act to be learned. In view of his conclusions it would seem highly important that this question be tested carefully for as many of the higher animals as possible.

On page 67 of "Animal Intelligence" THORNDIKE says: "A cat has been made to go into a box through a door, which is then closed. She pulls a loop and comes out and gets fish. She is made to go in by the door again, and again lets herself out. After this has been done enough times, the cat will of her own accord go into the box after eating the fish. It will be hard to keep her out. The old explanation of this would be that the cat associated the memory of being in the box with the subsequent pleasure, and therefore performed the equivalent of saying to herself, "Go to! I will go in." The thought of *being in*, they say, *makes her go in*. *The thought of being in will not make her go in*. For if, instead of pushing the cat toward the doorway or holding it there, and thus allowing it to itself give the impulse, to innervate the muscles, to walk in, you shut the door first and drop the cat in through a hole in the top of the box, she will, after escaping as many times as in the previous case, *not* go into the box of her own accord. She has had exactly the same opportunity of connecting the idea of being in the box with the subsequent pleasure. Either a cat cannot connect ideas, representations, at all, or she has not the power of progressing from the thought of being in to the act of going in. The only difference between the first cat and the second cat is that the first cat, in the course of the experience, has the impulse to crawl through that door, while the second has not the impulse to crawl through the door or to drop through that hole. So though you put the second cat on the box beside the hole, she doesn't try to get into the box through it. The impulse is the *sine qua non* of the association. The second cat has everything else, but cannot supply that. These phenomena were observed in six cats, three of which were tried by the first method, three by the second."

On p. 73 he writes: "Presumably the reader has already seen budding out of this dogma a new possibility, a further simplification of our theories about animal consciousness. The possibility is that animals may have *no images or memories at all, no ideas to associate*. Perhaps the entire fact of association in animals is the presence of sense-impressions with which are associated, by resultant pleasure, certain impulses, and that therefore, and therefore only, a certain situation brings forth a certain act."

So definite and convincing is his evidence for this failure to learn by being put through an act in the case of dogs and cats, that

I supposed at the outset that my experiments to test this hypothesis in the case of raccoons would be few and perfectly confirmatory of THORNDIKE's view. But the behavior of the raccoons on the second and later days of my experiments soon indicated that this confirmation might not be forthcoming. It will be recalled that similar experiments of THORNDIKE's[5] on monkeys were inconclusive, and that the monkeys experimented with by KINNAMAN could not be handled. I took pains, therefore, to handle the young raccoons as much as possible, and they showed no objection to it for many months. Then one refused to be handled.

On the second day of my experiments with the female, No. 4, in Box I (button), and much to my surprise, she turned, on the thirty-third trial, and went quickly back into the box. She opened the door in six seconds, came out, was fed for a moment from the bottle and then immediately re-entered the box. Now possibly the reader is saying, "Yes, this is the phenomenon observed by THORNDIKE in cats which were pushed toward the door or held near the door." This is not the case. This young raccoon had been picked up by the nape of the neck, lifted quickly through the door and dropped on the floor of the box. When thus held the four legs of the animal hang down limp as they do in the case of a kitten carried in the mouth of its mother. This fact makes this method of holding and lifting the animal most convenient. There was no innervation of her own muscles. Four days later when tried in this box she went in on the second, third and fourth trials.

No. 3, the second raccoon tried in this box, went in himself on the twenty-second, twenty-third and twenty-fourth trials. He also had been lifted into the box on the preceding trials. On the forty-fifth and from the forty-seventh to the fifty-first trials, inclusive, he re-entered the box. On the fifty-second trial he started back but turned at the door and did not go in again that day. Subsequently, he went in regularly until his hunger began to be satisfied. During his last eighty-five trials in this box he re-entered it of his own accord eighty-two times. On the seventy-first trial, and several times thereafter, he was held near the door to make him go in but this was not done with any one of the animals until they had gone in spontaneously frequently enough to show that it was an established part of the reaction. Moreover, the hold-

---

[5] THORNDIKE, E. L. The Mental Life of the Monkeys. *Psych. Rev. Monogr. Suppl.*, vol. 3, no. 5. 1901.

ing was done simply to make them go in when their hunger was partially satisfied. Up to that time they were eager to go in, after having done so several times. These remarks apply to boxes with from one to four or five fastenings. In connection with experiments with Box 13, I several times whipped No. 3 to make him go in, for the box was very difficult to unfasten. This was done, however, only after he had gone into the box repeatedly.

If this behavior is to be used as evidence of the presence of ideas, then the reluctance of the animals to enter the boxes when they were not hungry, and when the box was difficult to unfasten is quite as significant as the fact of their getting in spontaneously at first.

No. 2 started back into Box 1 on the eleventh trial and went back into the box on the thirty-ninth, fifty-sixth, sixty-seventh, sixty-ninth and seventieth trials. The next afternoon he went into the box and came out to be fed before I could close the door. I fed him a little, and he went back. After this the usual thing was for him to go into the box when hungry. Until after the seventieth trial nothing was done to encourage No. 2 to go back. My object was to see whether the animal would turn and go in instantly entirely of his own accord. I did not even wait for him to go in; unless he returned promptly to the box, he was lifted into it.

No. 1 went into the box first on the fifty-seventh trial. After that he was held at the door six times and went in. Thereafter he went in regularly.

These results are radically different from those obtained by THORNDIKE in his experiments with cats. Since four raccoons exhibited this reaction, it is safe to conclude that any raccoon which has been lifted into a box and allowed to come out and be fed will sooner or later go in of his own accord, and further that he will go in before the one-hundredth trial and probably before the seventy-fifth trial, as my four animals did. The behavior of these animals forces one to believe that it dawns on the animal that he can hurry the matter of getting food by rushing back into the box and coming out again. The association here involved not only what the animal *had done* but also something *which had been done to it*. It may very well be doubted, however, whether lifting the animal about taught it anything. I should say rather that it had an image of the interior of the box as the starting point of the food-getting process and an idea of going back to recommence the process. This idea lost all motive power as soon as hunger was allayed.

This difference between the behavior of the raccoons and the cats, occurring as it did with Box 1, led me to modify the succeeding experiments so as to test further the animal's ability to learn without innervating its muscles. In Box 2 the door was placed six inches above the floor to see whether this would prove to be an obstacle to going back into the box. No. 4 did not begin to go in of her own accord until the fifty-first trial, but she did so very often thereafter. No. 3 went into the box on the first trial, that is, before he had ever been put into it, notwithstanding the difference between the positions of the doors and the size of the boxes. One may explain this behavior, which occurred often afterward, either by association by similarity or by inability to distinguish the differences between the two boxes. My opinion is that the open door at once suggested the usual act of going in. Probably it was the same door to the raccoon. This, however, is a crude association by similarity. "Similarity is partial identity." The differences are entirely unnoticed. No. 2 re-entered the box on the second trial; No. 1 on the fifth.

Box 3 was arranged to test further this difference between raccoons and cats. In the first place an opening in the top of the box was covered only by a loose piece of board and the plan was to put the raccoons into the box through this opening, to see whether they would learn this indirect way of entering. Then No. 4 and No. 3 were put through the act of opening the door. This was done by holding the animal, taking its paw and placing it on the string then pressing it down until the bolt was withdrawn and the door opened. No. 2 was not put through the act and No. 1 was not worked in Box 3

A low step was placed at the end of Box 3 to enable the animals to climb more easily to the top of the box. The order of procedure was as follows: The raccoon came out of a door in the front, was fed, went around to the end of the box, mounted by the step, to the top of the box and dropped through the opening into the box.

We may discuss first the act of going in. On the seventeenth trial No. 4 went in. On the eighteenth she was held on the box and went in. On the nineteenth she climbed upon the box. On the twenty-first she was put on the box and went in, and so on to the twenty-eighth trial, in which she may have been helped by the motion of the experimenter's hand in the direction of the opening. No. 3 after the fifth trial went in when placed on the box. On the eighteenth trial he re-entered the box from the floor of the room, and later he went by way of the step and the end of the box. On the twenty-seventh trial he climbed up over the front of the box and dropped into the opening in its top, thus substituting a direct for a roundabout way. No. 2 went in when put on the box after the eighth trial. From the twelfth trial he went in when put on the step, and from the twenty-second trial he went in from the floor of the room. In the extract from "Animal Intelligence" already quoted THORNDIKE says, "So, though you put the second cat on the box beside the hole, she doesn't try to get into the box through it." This description certainly does not suit the behavior of raccoons.

Having shown that raccoons learn to go into a box by being dropped in through a hole in the top, we have yet to answer the question, will the raccoon learn to operate a fastening, to perform a complicated act, by being put through the motions necessary to do the act? In order to make trial of this I decided first to put two of the animals through the act of opening cages and let two of them learn it by trial. If the average time of the first success for those put through should be shorter than the average time for those not put through, it would be fair to conclude that the putting through facilitated learning. In order to make the evidence especially strong I selected for most of the putting through experiments the two raccoons which, up to this time, had shown themselves slowest in learning the mechanisms, Nos. 3 and 4. It seems to me, therefore, that much weight must attach to the averages. The average time required for the first success in each of eleven boxes by the animals which were put through the act is 41.6 seconds; by those not put through 90.2 seconds or more than twice the former average. The results are shown in Table VII.

In Table VIII the animals which were put through *failed to escape by their own unaided efforts*, but succeeded after being put through. I have other instances of this.

It will be seen that in two of the eleven boxes the averages favor those not put through. Box 3 shows an average of 85 seconds for those put through and of but 26 seconds for those not

TABLE VII.

| | Number of Times Put Through. | Time of First Success. | Average for Those put Through. | Average for Those not put Through. |
|---|---|---|---|---|
| *Box 3. Single* | | | 85 sec. | 26 sec. |
| No. 4 | 8 | 162 sec. | | |
| No. 3 | 5 | 9 | | |
| No. 2 | none | 26 | | |
| *Box 4. Single* | | | 27 | 106 |
| No. 4 | 22 | 48 | | |
| No. 3 | 10 | 7 | | |
| No. 2 | none | 150 | | |
| No. 1 | none | 62 | | |
| *Box 5. Double* | | | 12 | 51 |
| No. 4 | 4 | 4 | | |
| No. 3 | 4 | 20 | | |
| No. 2 | none | 57 | | |
| No. 1 | none | 46 | | |
| *Box 6. Double* | | | 7 | 12 |
| No. 4 | none | 16 | | |
| No. 3 | 7 | 5 | | |
| No. 2 | none | 12 | | |
| No. 1 | none | 10 | | |
| *Box 7. Double* | | | 44 | 159 |
| No. 4 | 6 | 21 | | |
| No. 3 | 6 | 27 | | |
| No. 2 | none | 22 | | |
| No. 1 | none | 296 | | |
| *Box 8. Triple* | | | 24 | 39 |
| No. 4 | 6 | 24 | | |
| No. 3 | 6 | 25 | | |
| No. 2 | none | 62 | | |
| No. 1 | none | 16 | | |
| *Box 9. Four Latches* | | | 18 | 37 |
| No. 4 | 6 | 16 | | |
| No. 3 | 6 | 20 | | |
| No. 2 | none | 29 | | |
| No. 1 | none | 45 | | |
| *Box 11. Five Latches* | | | 34 | 24 |
| No. 4 | 6 | 30 | | |
| No. 3 | 6 | 39 | | |
| No. 2 | none | 36 | | |
| No. 1 | none | 12 | | |
| *Box 12. Six Fastenings* | | | 78 | 199 |
| No. 4 | 6 | 134 | | |
| No. 3 | 6 | 23 | | |
| No. 2 | none | 364 | | |
| No. 1 | none | 34 | | |

TABLE VIII.

| | FAILED BY OWN EFFORTS AFTER. | NUMBER TIMES PUT THROUGH. | TIME REQUIRED FOR FIRST SUCCESS. | AVERAGE FOR THOSE PUT THROUGH. | AVERAGE FOR THOSE NOT PUT THROUGH. |
|---|---|---|---|---|---|
| *Box 10. Thumb-latch* | | | | | |
| No. 1 | 840 sec. | | | | |
| No. 1 | 90 | | | | |
| No. 1 | 75 | 3 | 6 sec. | 10 sec. | |
| No. 1 | 120 | 1 | 6 " | | |
| No. 4 | | 6 | 18 " | | |
| No. 2 | | none | 30 " | | 30 sec. |
| *Box 14. Hook* | | | | | |
| No. 4 | 600 | 9 | 231 | 117 | |
| No. 1 | 1920 | 5 | 3 | | |
| No. 3 | | none | 545 | | 310 |
| No. 2 | | none | 75 | | |

put through. This is due to No. 4 alone, however, for No. 3 (put through) made a record of 9 seconds, while No. 2 (not put through) made a record of 26 seconds. Box 11, with its five fastenings, gave an average of 34 seconds for those put through, as against 24 seconds for those not put through. This is due to No. 1's remarkably short time, 12 seconds, on the first trial, and to No. 3's difficulty in learning the box. The full record of No. 3's learning makes Box 11 give rather conclusive evidence in favor of putting through. After being put through six times No. 3 succeeded with Box 11 eighteen times consecutively. The next morning he failed after twenty-five minutes to pull one of the loops, though he worked the other fastenings. Although he was evidently already hungry and worked hard to escape he was left untried for two hours to see whether increased hunger would help him. When next tried he failed after eleven minutes, was put through ten times and succeeded in forty seconds, then in forty-four, then in twenty-nine, and so on. The next morning he failed after seven minutes, was put through six times, then succeeded in twenty-three seconds. The next morning he failed in five minutes, was put through twice and then succeeded in thirty seconds. The next morning he failed on the same loop, was put through once and succeeded always thereafter, steadily reducing his time. Now this is, in many respects, the poorest record for No. 3 or for any other of the raccoons and I fancy the reader is saying, "This one case outweighs all your averages. Do you not see that the animal was hindered rather than helped in learning by being put through?" The answer is, of course, why should not his eighteen consecutive successes, unaided after the first six trials, have stamped in the reaction? Each morning he failed once more (he almost always failed on loop 1, a fastening he had already learned). He failed, also, no matter how long I waited for him. But *he never failed immediately after he had been put through, and each of his successes following the putting through was quick.* The fact is the box was very complex for him, he would forget a fastening, be put through, then not fail again that day. The next day the difficulty would reappear. He was very slow to learn this box, but remembered it longer than did any of the others. The point I would emphasize is simply that putting through after a failure certainly and always resulted in making the next trial a success. It seemed, as we say of human beings, to refresh his memory. Would he have failed as frequently and during so many days had he been forced to learn by trial and error, not obtaining food at all until he succeeded, be it a day or a week? I think he would not have failed as frequently after the first success. No doubt the putting through caused him to depend upon it. I do not believe that putting through has nearly so much stamping-in power as a self-innervated movement. It has not for man. A man may be told how to make a shot at billiards but only practice in making the shot will fix it. A player having made the shot once, as directed, may at that time succeed. In later trials he will make it sometimes very awkwardly. So with our animals. Often the first success does not require the longest time either for those put through or for those which innervate their own muscles. These short first times and longer later ones are sufficiently frequent to show a marked difference between the learning of dogs and cats and that of raccoons. I think, finally, that putting through helps a raccoon to succeed in trials immediately following the experience of being put through, and that this is a mental effect. It establishes a transient association. Trial and error forms more stable and permanent associations—a reflex affair simply.

The description of No. 3's learning in Box 11 should make it clear that the averages in that box deserve but little weight. They differ by only ten seconds. But, however that table be counted, the averages and the number of individual cases in favor of learning by being put through are too widely different from those against it to be ascribed to chance. The experiments from which these data are taken were continued for three months.

One who observed the experiments closely might state what appears at first to be a very strong argument against our conclusions. For example, in Box 5, which had two fastenings, I called the order in which the animal was put through the two "direct," the other possible order "reverse." No. 4, who was put through, did the acts in the reverse order roughly two-thirds of the times, and No. 3 probably three-fourths of the times. I *did not* succeed in establishing the order in which I had put the animal through. This is a serious objection until we compare it with the behavior of the animals which were not put through. Let us examine the records of No. 2 and No. 1 for July 19, 1905, calling that order, "direct" in which the animal attacks the fastenings for three consecutive times. No. 2, on the morning of that date, followed the direct order eleven times after he established it. In the afternoon he did it in the reverse order thirteen out of fourteen trials. I will quote from my record of his work the next morning. "Direct, reverse, direct, reverse, direct, reverse, reverse, reverse, direct, reverse, direct, reverse, reverse, direct, reverse, reverse, reverse." This is typical. On the morning of July 19, No. 1 did the act eleven times in the direct order and five in the reverse. In the afternoon twice in the direct and seven times in the reverse order. The fact is the raccoons never mechanize the order of their performances into a settled routine. Therefore if at this point of study I were asked the question, Did the animals perform the same act you put them through? I should answer, they did and they did not. They were put through most of these acts with one forepaw. They did the act with that paw, with the other forepaw and with both forepaws and exactly the same is true of those who learned the fastenings by trial and error. The question, however, may be changed to, Can the animal be made to learn the act you put him through and to employ no other? Yes, it happens that this can be easily done with these animals.

A more decisive test of the value of putting through would be, of course, one which answers the question, Does the raccoon, by being put through an act, learn to operate a mechanism which it had failed to learn by its own efforts?

No. 1 in his first work in Box 10 failed because he worked two slats loose and kept attacking them. He first failed in fourteen minutes; was put through, then failed in one minute and thirty seconds; was put through and failed in one minute and fifteen seconds and was put again through. He then did the act in six seconds. He afterward failed once, was put through and did the act in six seconds. This is, as shown above, the usual condition. The putting through helps to a quick success but does not insure permanency unless repeated more times than a reflex performance.

Box 14 was most difficult for it was fastened with a horizontal hook which had to be lifted vertically, and the raccoon cannot well lift an object vertically with his paw unless he can stand directly above it. There remained but three possible ways to lift the hook, namely, with the teeth, with the nose, or with the back of the head. The latter was done but three times in all; I think this was because in this case the animal could not see the hook become free and fall. It was really a quick and convenient way of lifting the hook. While No. 3 and No. 2 succeeded in this box, the other two raccoons failed. No. 4 failed after *ten minutes* of steady clawing. She was put through ten times by lifting the hook with her nose. She then lifted the hook with her nose after three minutes fifty-one seconds, again in sixty-one seconds, then in twenty-three, then in five, four, five and one seconds successively. Before being put through No. 4 did not attack the latch directly. It was a black hook, the box was of rather dark wood and all preceding latches had been more conspicuous both in position and color. After being put through she worked directly at the latch. If one objects that No. 4 should have succeeded in less than three minutes, I can only reply that the hook was a difficult fastening, that this is the first time the raccoons had to learn to work with the nose and that I am quite willing to grant that little or no *skill* comes from putting through. Finally, let me add that No. 4 always worked the latch with the nose, by the act she had been put through.

No. 2 also failed on the horizontal hook. To make it a certain failure I waited thirty-two minutes while he worked steadily. I put him through five times by raising the hook with his nose. He then succeeded in three and four-tenths seconds, then in seven and two-tenths, and so on. Supported by the averages of the table above, these two examples make it certain that raccoons *can learn* *an act from being put through it, even though they have failed to learn it by their own efforts.* My own opinion is that No. 1 learned the exact act by being put through. No. 4, it is true, *may* have learned only the place to attack. To urge this objection, however, amounts to saying that the animal must have got some idea or image of the place or hook from being put through, for surely no reflex act is established in an animal whose muscles are limp. Had I not held my hand beneath her muzzle she would have let it hang down and it would not have raised the hook. So in this case especially the act of putting the animal through with uninnervated muscles gave her a motive or impulse to innervate the muscles. Personally I should judge that the hook lifting with a click and noisily falling, not more than an inch in front of the raccoon's eyes, was fully as well attended to as the place of attack. No. 1 also did not vary once from the act of lifting the hook with his nose. This is important when we compare it with the work of those not put through. I record in Table IX the trials and methods of lifting the hook of No. 2 and No. 3.

TABLE IX.

*No. 2.*

1st half-day.

1. Done with mouth.
2. Done with mouth
3. Done with mouth
3. Done with mouth.
4. Done with mouth.
5. Done with mouth.
6. Done with mouth.
7. Done with nose.
8. Done with mouth.
9. Done with mouth.
10. Done with mouth.
11. Done with mouth.
12. Done with nose.

13 to 18 incl. Done with mouth.

2d half-day.

1. Done with mouth.
2. Done with side of nose.

3 to 11 incl. Done with mouth

12. Done with nose.

13 to 15 incl. Done with mouth.

16 to 18 incl. Done with nose.

19. Done with mouth.
20. Done with nose, and always so thereafter.

Total with mouth, 30 times.

Total with nose, 8 times.

*No. 3.*

1. Done with foreleg (not paw).
2. Done with head.
3. Done with head.
4. Done with head.
5. Done with nose, and continued in this way.

It is evident, therefore, that the best method for the animal is to lift the hook with its nose. I have now shown why we should change the question, Does the animal learn the act you put him through? to the question, Can he be made to do so? If the act which he is put through is the one which will remain the easiest and most convenient for him throughout the tests, irrespective of his position in the box, he will never vary from it. If not, he will employ your act when his position makes it convenient and he is looking at the latch you began with. He will also vary from it very often but not a whit more often than a raccoon not put through will vary from the act he seems to establish in his early trials. Moreover, an animal may begin a new way sometimes after a hundred or more trials, for example, No. 4 combined acts 1 and 6 in Box 13 after several hundred trials; No. 3 combined them much earlier; No. 2 after mounting the platform in Box 13 many times took to lifting it with both paws. When it was dropped the jerk in addition to the weight of the platform would raise the bolt. This was an awkward method and, while it occurred almost consecutively during three days' work and now and then for some time longer, it was gradually relinquished.

It would seem that enough experimental evidence has been presented to show that the raccoons do learn without innervating their own muscles. But the opposite condition as found by THORNDIKE in cats, namely, that they learn by "trial and error" only, has been made to support so important conclusions concerning the mental life of animals, that I shall risk taxing the reader's patience with a further recital of experimental tests.

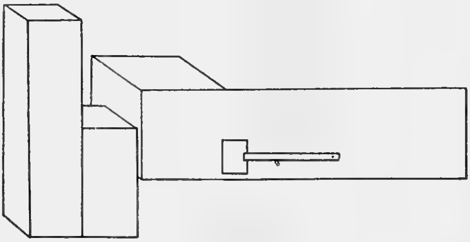


FIG. 2.

In these experiments I used the card-showing device already described, but I placed a lever holding a color on the front side of the apparatus so that the animal might learn to lift it himself. This could be done either by the nose or the paws. It was easiest at the beginning of the ascent to raise the lever with the nose but hard to elevate it thus completely. It required a vigorous toss of the head to make the lever reach the point where it would not fall back. On the other hand, while difficult to start with the paws, it was easy to finish the ascent by that method. The disadvantages of these ways of lifting the lever were, therefore, nearly equal. Can one raccoon be taught to lift the lever with his nose, another with his paws, thus proving that more than one kind of reaction can be taught the animals by putting them through? And can they be put through the acts enough times to establish the habit in addition to what has been described as an apparent mental effect which is readily forgotten?

All the raccoons were first given trials to determine whether they would hit upon the act of raising the lever. All came to the apparatus and watched it closely. Previous experience had aroused their interest. None, however, lifted the lever nor did I expect it, for the animal was free alone in the room, and while all the individuals clawed at colors back of the board none had ever done so in frontof it.

On May 24, 1906, No. 1 was put through sixty times by lifting the lever with his nose. He was then given an opportunity to do so unaided. If he failed within approximately thirty seconds, the lever was raised and he was fed. This was done fifteen times. The seventh time he came and looked at the card when it was down, on the ninth and fourteenth he pushed at it with his nose, and on the eleventh with his paws. Although he had not mastered the performance he seemed to have made a slight approach toward it. The next day he was put through ninety-five times and succeeded instantly in performing the act on the ninety-sixth. On the ninety-seventh, ninety-eighth, one hundredth, one hundred-seventh and one hundred-tenth trials he failed, but he succeeded in all the other trials between the ninety-sixth and one hundred-tenth (fourteen in all), and always after the one hundred-tenth. On July 11, without practice in the meantime, he was perfect in the performance of the act. No. 3 learned as did No. 1, although more slowly. He did not fail after his first success, although at first, for ten trials, he lifted the lever only half way up. These ten attempts I rewarded but later he was forced to give the lever a strong toss to get food. In the cases of both No. 1 and No. 3 the movement they were put through was the one they followed uniformly.

On June 1, 1906, No. 2 was put through the act of lifting this lever with his paw one hundred times. He then did the act with his paw forty-five times in succession. On June 7, he did it fifty times without error and on July 11 he was still perfect although without practice meanwhile. As No. 2 pursued one method throughout, and No. 1 and No. 3 the other, it cannot be said that our only crucial tests consist of reactions with the nose which are so forced and unnatural as to be poor evidence.

As to the establishment of a habit, the records are ambiguous. No. 2 was as perfect after being put through one hundred times as he would have been after eight or ten accidental successes. The other two, with more experience, were less perfect. They did not learn the toss I gave the lever, but expected food for raising it only a trifle and letting it drop back. Withholding the food brought the complete reaction.

I must explain how the raccoons showed that they expected food after the abortive performances. On raising the lever the animal stood with his forepaws on top of the front board to be fed. After every abortive effort he would take this position, then, as food was not forthcoming, he would drop to the floor and dive under the lever again with his nose. All the animals added to this reaction the act of clawing the lever down into the horizontal position so that it might be raised again. The experimenter merely had to feed the animal each time the lever was raised, and the work thus became very rapid.

Let us summarize this long section:

(1) All the raccoons began, of their own initiative, to run back into boxes into which they had hitherto been lifted.

(2) All learned to go up to the top of a box and drop through a hole into the box after having been lifted into the box repeatedly.

(3) All, after having learned to go to the end of a box, up a step and thence to the top of the box, by being lifted through these several stages of the ascent, learned to abbreviate the act by climbing directly up the front to get to the hole in the top of the box.

(4) No matter how well the animal had learned the through-top reaction, if the front door, out of which he had just come, was not closed behind him he would dodge back through that as the quickest way to re-enter the box.

(5) All four raccoons learned to undo a fastening by being put through the act. They did not in general duplicate the act they were put through, but neither did they in general duplicate the act of their first success, or of their first three consecutive successes, when these were attained by their own efforts.

(6) They could be made to duplicate the exact act they were put through by the arrangement of apparatus so that other acts were more difficult. The duplication was then perfect in all trials.

(7) The average time required for the first success after being put through is very much less than the average time for the first success by trial and error. This was true in nine out of eleven boxes and with the color showing device.

(8) Finally, the animals learned acts by being put through them which they repeatedly had failed to learn when unaided. In all these cases the act was a duplicate of that which they had been put through.

### ON THE PRESENCE OF MENTAL IMAGES.

It would seem that nine-tenths of the experimental evidence for the absence of ideas in dogs and cats comes from their inability to learn from being put through. The experiments were almost identical with some of those described above. If inability thus to learn is evidence against the presence of ideas, then ability to do so should be equally strong evidence for it. We are, therefore, already embarked on the discussion of the presence of ideas in raccoons. It seems to me that animals which, so far as we know at present, are utterly unable to learn save by innervating their own muscles must be devoid of ideas or at least "of a *stock* of images which are motives for acts." This conclusion of THORNDIKE'S is, I think, of the utmost value to those who experiment with animals, and the evidence against it in the case of cats is meager in the extreme. Therefore, I must first urge the reader to compare point by point the behavior of cats and raccoons in put-through experiments, and to note *the radical difference at every point.*

We may now consider what further evidence of the presence of mental images is furnished by the raccoons and what behavior of theirs seems to show a lack of images.

*Recognition of Objects.*—Some of the observations of this are commonplace enough. First, on the fifth day after I received the raccoons one of them climbed to a box, then to the top of a barrel on which the bottle of milk had been placed. When lifted down he at once repeated the performance. A day or so later, another, No. 3, recognized the bottle at a distance of two feet and went to it. He was given milk, and went to the bottle again. This bottle was small and round and was almost completely covered by the hand of the experimenter when he was feeding a raccoon. Were it the whole situation the animal was reacting to, why should he not have come to me, the source of all his food, instead of making for the bottle as soon as he saw it. The act in No. 3's case was far too definite to be an accident. I think that he recognized the red rubber nipple. All of the animals now go directly to the bottle if it is set down at all, so it must be hidden. I varied the experiment by lowering the bottle into the room through a window when the raccoons were lying at rest in a remote corner. Within a minute all were clinging to the bottle and struggling to get at the nipple. Next I lowered a small piece of wood, the size of the nipple and wrapped with red cloth to appear like the nipple. All came to it. Two tried to suck it. At first they seemed unable to distinguish it from the nipple. Perhaps this indicates that they do not rely greatly on the sense of smell. When tried thus again they merely played with the piece of wood.

When working with Box 12 (six fastenings), No. 4 refused to go into the box. She was switched twice to make her do so. After this, showing her the whip would make her go in.

A case of direct searching for the bottle may now be mentioned. On being released from the large cage in which they were confined during experiments, No. 4 went directly toward the corner of the room where she had some days before found the bottle. The total distance was ten feet, but she could not have seen the bottle until she came around a box within two feet of it. All the other raccoons were seen to do this.

No. 3 was reluctant to go into a complicated box and he formed the habit of biting when I attempted to lift him into it. I held him and thrust a finger down his throat, then whipped him. For five days afterward he would growl, snap at and retreat from me though still on good terms with my assistant, Mr. ERWIN.

*Forgetting.*—After three days without practice in Box 2, No. 4 seemed almost to have forgotten how to work it. There was no directness in her movements and her time records were poor. A period no longer than three days should show no influence of this sort on a well established reflex, and all records agree, I believe, in indicating that a period of some weeks or months would not suffice to show any great falling off in the skill of dogs and cats.

In complicated boxes all the raccoons had periods of forgetting one fastening only. Sometimes this fastening was forgotten during two or three days. Often my notes read as follows. "Aug. 5, Box 11, Dolly (*i. e.*, No. 4), forgot loop 2 today in three out of four consecutive trials. Jack (*i. e.*, No. 1), forgot button 1 almost invariably *except when he pulled loop 1 first. In those cases he turned button 1 next.*" Does this not give us an important distinction between a reflex and an association? The reflex has but one cue, an association many. Jack did not forget button 1 when he pulled loop 1 first. This had become partly habit because I had built the box up from two fastenings and when it had two he usually pulled the loop first, then turned button 1. Later when I was reviewing Box 13 after periods of one hundred forty-four and one hundred forty-seven days respectively, each of the animals (except No. 3) failed on some particular latch or two latches, not on all, nor on one latch in one trial and another in another. If they had settled down to a routine order of working this box, I venture to say that not one of them would have failed after two hundred days or longer. The recall(?) in this case would have been, like that of a boy in swimming for the first time since the preceding summer, perfect. No. 3's work gives evidence of this. He alone gave a pair of duplicate performances in Box 12 (six fastenings). Thus, on August 18, in the twelfth trial he worked the fastenings in the following order:

(12) 5–2′–2–5–6 & 1′–5–1–5[7]
(13) 5–2′–2–5–6 & 1′–5–1–5.

The eighth and ninth trials were almost duplicates and there were other partial duplicates. After one hundred forty-seven days without practice No. 3 alone escaped from Box 13, which was Box 12 with one added fastening. I attribute his success entirely to the superior mechanization of his performance. KINNAMAN says of monkeys, "When the group consisted of two or three fastenings the monkey soon adopted a regular routine which he rarely failed to follow." I infer from this that the monkey did not do so with more than three fastenings. The raccoons did not with only two fastenings. I have show that No. 2 followed

---

[7] "6 & 1′" means both latches simultaneously.

one order predominantly in the morning, and the reverse in the afternoon of the same day, and in general with two fastenings the two orders appeared alternately. Consequently I should say that the monkeys are superior to the raccoons as habit-formers. The raccoons operated almost as complex mechanisms, but they could not reduce the performance to routine. Finally, if the natural history books are to be believed, trappers, in order to ensnare the raccoon depend not on his habits but on his instincts. The trap is not put where he habitually enters the stream, for he enters all along it; instead a bright swinging object is hung over the trap so that in reaching for it he steps on the trigger. Finally: a corollary of the proposition that there are two types of learning, namely, learning by trial and error and learning by means of ideas, should be that there are two types of forgetting, distinguished especially by their time intervals. This, our records seem to show when compared with those for dogs and cats.

*Variability.*—In addition to having no fixed order for groups of fastenings, the raccoon changes his method of reacting to a single fastening. I have shown that which paw he uses depends on his position with regard to the latch to be unfastened (*cf.* p. 225). As already stated, No. 2, who had learned perfectly to lift the horizontal hook with his mouth finally changed to lifting it with his nose. Finally, raccoons which have done two acts separately hundreds of times may suddenly come to do them simultaneously. No. 3 and No. 4 depressed the platform and pulled loop 1 in Boxes 12 and 13 at the same time. Others occasionally worked the thumb-latch and a button at once, and sometimes two buttons were depressed simultaneously.

*Association by Similarity.*—If a latch similar to another be added to a group of fastenings, but in a different place, it may be attacked and worked first. I cannot say certainly that this is untrue of a dissimilar fastening for, while it was not the fact with the horizontal hook, the wooden plug or the platform as a platform, it would probably have occurred with the thumb-latch had I not first used it singly. The vertical cord leading down to the platform was jumped at directly and vigorously pulled by No. 1 as soon as he saw it, as if he thought it another loop; later he learned to jump upon the platform. He also worked a second barn-door latch before the first one, with which he was familiar. The second was two inches above the first. All the animals would pull a second loop with one direct pull, though it was in a different part of the box, and the same is true of a second button placed on the opposite side of the door from the first. Now, no one can meet the argument that this is not the noticing of similarity but a failure to notice differences and I have said above that Jack attacked the platform cord "*as if* he thought it another loop." We may ask, however, Why he did not so attack the horizontal hook or the wooden plug? It will not do to reply that they were in new places. It may answer to say that they were more difficult, but even then they should have been *attacked*, by one of the raccoons first, even if unsuccessfully. All this is no doubt inconclusive. I may say, however, that the raccoons did not give the same experimental warrant for this dialectic reply that cats do. That is, unlike cats, they did *not* paw at the place where the loop had been nor did they claw at the loop or button when the door was open. I tried moving the loop from place to place in the boxes. Not once even did they claw where it had been; instead they attacked it at the new place with one direct movement. I removed from the box one loop and then another. Each of the raccoons would come to the place where the loop had hung and look up through the slats in the top of the box. Once I had left the loop lying on the top. It was seen by the raccoon, clawed back into the box, and then pulled. With each of the boxes I tried leaving the door open. The raccoons came directly out with no movements in the direction of the fastenings.

*Reluctance and Expectancy.*—All of the raccoons when hungry were eager to re-enter a box of two, three, or four fastenings. They could escape from these quickly. But they were very reluctant, even when hungry, to enter a box of five, six or seven fastenings. The small piece of meat they received as a reward seemed to have its effect eclipsed by the memory of the difficulty of escape. I regularly had to put them in Box 13, though they knew the way. Sometimes they resisted strongly by laying hold of the sides of the door and sometimes by snapping at the hand of the experimenter at the moment they were dropped into the box.

No raccoon would willingly re-enter a box of from one to four fastenings after his hunger was satisfied. One may say that in this case the sensations of satiety and weariness did the work, yet no one who saw the animals resist being put into a box failed to credit them with a rather distinct memory of the difficulty of escape.

In common with other animals, the raccoon expects food when he has done the thing which usually brings him food. All would come and look up at me on escaping from the box. I tried to test this at some length. An inclined plane of poultry wire was made and No. 3 was fed when he climbed to the top of it. After a few trials the plane was extended twenty-eight inches. When he reached the former terminus he stopped and looked at the experimenter. The plane was again lengthened with the same result. He always failed to go beyond the old point on the first trial, but on the second he would pause at that point, look about and then go on.

*Varying Means to the Same End.*—While No. 3 was on top of Box 16 a piece of apple was dropped through the top. He started down the back side of the box to get it. The door at the back was closed so he came slowly around the long cage into the front door, through which he had never entered before but through which he had escaped, and got the apple. This was repeated. He was fifteen seconds coming around the cage, but three or four seconds were wasted in trying to reach through the wire to get the apple. When this was repeated again, he was twenty seconds coming around but did not reach through, as the apple was too far from any side of the cage for him to reach it. In this case he certainly would have entered the cage at the back had the door been open. As it was closed, he came around to the front door. Furthermore, in the third repetition, he would have tried to reach the apple through the wire had it not been too far away.

In the above examples No. 3 may have seen the apple all the time, though this is doubtful. Box 17 was such that food placed in it could not be seen from outside. It was ten inches square and four inches high, with closed sides. A three inch square was sawed out of the top. This piece could be put in place again thus closing the opening. A staple was fixed in the center of the piece sawed out, so that it might be clawed out and away from the opening, which it fitted closely.

The plan was to throw bits of apple into the box through the opening in its top, allow the raccoon to reach in and get the apple several times, then cover the opening with the piece which had been sawed out. After this had been done with No. 4 she *instantly* clawed out the block. She seemed to work as if actuated by a thought of apple in the box. It was not done by random clawing, nor could she smell or otherwise perceive the piece of apple in the box. Her work was based entirely on the former experiences of having found apple in the box when open. No. 3 clawed directly at the block but failed to dislodge it; tried once more and succeeded.

I now varied the experiment by using Box 18. This was large and had a square sawed out of the top large enough to permit the animal to crawl through the top. No. 1 secured food twenty-five times by going through the top. The box had no bottom and instead of resting directly on the floor it rested on a row of bricks. Removing one of these made an opening under the lower edge of the box through which the raccoon might crawl. The opening in the top was now closed and nailed fast. No. 1 was freed, went to the top of the box and tried to claw out the block. He then walked about the room then tried the block again. He then went to the opening made by removing the brick, stopped a moment, then crawled in. Total time, 100 seconds. Thus No. 1 learned to go in by either the upper or lower opening, but when the one through which he had been fed last was closed, he would hesitate a moment, then go to the other. Finally the side opening was closed and over the opening in the top was placed end-wise a cylinder eighteen inches high made of a roll of poultry wire. No. 1 was freed. He walked around the roll of wire which thus fenced in the opening in the box. He then climbed up the outside of this roll and down the inside of it, into the box. The time from his release until he entered the box was thirty seconds. No. 4 went directly into the lower opening at the first trial; time, seven seconds. No. 2 failed to go in through the roll of poultry wire. Thus all but he turned almost directly from the opening, which they knew and found closed, to another opening and entered through that one. They could not see the apple for it was dark inside the box, nor could they smell this particular piece of apple for the room was full of the odor of apple. It seems to me that they must have retained an image of "apple-there." I should not urge this point, however, if I did not think that the following experiments give substantial evidence of the presence of visual images.

In concluding the description of experiments in discriminating cards of different colors and intensities, I pointed out that successful reactions demand that the raccoon compare a color which has just *disappeared* with one now present. Either this or else the animal must keep track of the number of times the colors are shown, going up every other time when the colors appear alternately, every third and fourth time when they appear by twos , etc. This second explanation violates the law of parsimony, of course, and was eliminated by the fact that I secured series of perfect reactions when the colors were shown at random. When I changed for the first time from alternate showing to twos, or from twos to threes, there resulted confusion and errors quite sufficient, I think, to show that the animals distinguish one movement from two or two from three (a species of counting). As this was of no avail when the colors were shown at random, I also believe that the animal must have retained some sort of image or visual impression of the absent color and reacted to it. The experiment now took a form which shows this more clearly. Spontaneously several of the raccoons had been clawing the "no-food" card down and sometimes they clawed the "food" card up. Finally, all but No. 4 became fairly proficient in this. I quote one of the records made by No. 1 (Jack), after much training.

TABLE X.

| Trial. | Green. | Red. | Remarks. |
|---|---|---|---|
| 1 | * | — | He clawed green up and was fed. |
| 2 | * | — | He clawed green up and was fed. |
| 3 | * | — | He clawed green up and was fed. |
| 4 | * | — | He clawed green up and was fed. |
| 5 | * | — | He clawed green up and was fed. |
| 6 | * | — | Put red up, looked at it, then put it down, then put green up. |
| 7 | * | — | Put red up, then put green up. |
| 8 | * | — | Put red up, then put it down. |
| 9 | * | — | Leaving red up, he put green up. |
| 10 | * | — | Put red up and left it up, then put green up. |
| 11 | * | — | Put red up, then down, then put green up. |
| 12 | * | — | Put red up and left it up, then put green up. |
| 13 | * | — | Put red up and left it up, then put green up. |
| 14 | * | — | Put red up, then down, then put green up. |
| 15 | * | — | Put green up. |
| 16 | * | — | Put red up and left it up, then put green up. |
| 17 | * | — | Put red up and left it up, then put green up. |
| 18 | * | — | Red up, then down, then green up. |
| 19 | * | — | Put red up then green up. |
| 20 | * | — | Put red up and down twice, then green up. |
| 21 | * | — | Green up. |
| 22 | * | — | Green up. |
| 23 | * | — | Red up, then down, then green up. |
| 24 | * | — | Put green up. |
| 25 to 30 incl. | * | — | Put green up. |

"April 19, 1906, Jack. Apparatus, card-displayer as usual. Colors green and red. Fed at green. Green in front and shown first. It is to be shown three times and Jack fed if he responds; then red is to be shown three times and he will not be fed. This order to be maintained except when Jack interrupts it by clawing up colors."

No. 2, No. 3 and No. 4 also made very fair records, but never quite so good as those of No. 1.

When the animal thus reacts perfectly to red and green, and in addition busies himself in clawing the red card down and the green card up, surely his discrimination of the two is perfect. Now we are forced to ask, *Why should he put the red card down if it did not fail to correspond with some image he had in mind,* and why when he put the green up should he leave it up and go up on the high box for food *if the green did not correspond with some image he had in mind?*

The reader may ask why the animal did not always claw up the right card if he knew the right one. The colors could not be seen when the cards were down behind the front of the displayer, nor could I place them where they would be seen, else as soon as the green card was exposed the animal would go up for food repeatedly without further clawing.

Using the card displayer, I now arranged two situations which were identical so far as present sense stimuli were concerned. The only difference was one which had to be remembered, for a moment at least. Three levers were placed on the displayer. One on being raised displayed white, another orange, another blue. The plan was to display white, orange and blue consecutively, then display the same blue three times. I fed the animal if he climbed upon the high box on being shown the series white, orange, blue, and did not feed him after the series, blue, blue, blue. No. 1 was taught to react properly in this experiment. I then changed the two series to white, blue, red, food; and red, red, red, no food.

This I taught to No. 2, No. 3 and No. 1. The records of their learning, in groups of fifty trials each, appear below. The later records show that there was almost complete mastery of the situation, though I never *completely* inhibited the animals' tendency to start up on seeing white or blue which were precursors of the red which meant food. Thus the animals all anticipated red on seeing its precursors, which in itself seems good evidence of ideation. Many times, however, they turned back after starting at blue or white and looked for the red, then climbed up once more, thus showing that the red was not a neglected element of the situation but an expected color which they generally waited to see, but sometimes were too eager to wait for. Because of this frequent turning back and waiting for red, I am certain that going up to white and blue in the later trials was due to expectation of red to follow. Not so in the earlier trials with No. 2 and No. 3. Their numerous early errors at blue were due to the fact that they had heretofore been trained with two colors, hence they went up most frequently at the second. Although in the case of the two-color training the colors were presented in varying order, the food color must always appear next after the no-food signal so that the one, two, relation was deeply fixed. Furthermore, at the beginning of the two-color tests the "food" and "no-food" signals were given alternately. No. 1, on the other hand, had been previously trained with three colors and now although blue, his former food signal, was placed second as a no-food color, he made the mistake of reacting to it only ten times in the first fifty because *it was not third*, while he did go up to the final "no-food" red twenty-seven times *because it was third*. It seems certain, therefore, that raccoons are able to learn to distinguish one object or movement from two and two from three, a species of counting not differing from that which anthropologists ascribe to primitive man (see Table XI).

In the fourth group of fifty trials it will be noticed that No. 1 failed to respond four times, while two is the maximum number of preceding failures in any group of fifty. This occurred because in this and succeeding groups I gave each series of colors twice The previous alternate showing of each series caused hesitation and failure to go up. I think his behavior also distinctly showed doubt. In the same group of reds he stayed down 37 times, while in the next group he stayed down only 28 times. May not the difference of 9 trials be ascribed to his uncertainty? It will be seen that this change of order increased his mistakes in reacting to white, blue, and the first two reds. All the mistakes accredited to first red after the one hundred-fiftieth trial are reactions to the fourth red which, of course, had to be recorded as occurring as the first red of a second series. All this, I think, shows that introducing the new order, each series twice, was puzzling to the animal and caused him to react to the fourth red and to increase the number of "no reactions."

Finally, every doubtful case was recorded against the animal; thus if a raccoon started up just as red, after white and blue, came into view, it was counted as a response to blue unless the experimenter *saw* the animal look at the red. Therefore, the animals might now learn three new cards more quickly. Their previous training on the other hand made them very attentive to the cards and was greatly in their favor. Untrained raccoons probably could not do nearly so well, but these undoubtedly did a trifle bet-

TABLE XI.

| Experiment. | White. | Blue. | Red. | Failed. | | Red. | Red. | Red. | Perfect. |
|---|---|---|---|---|---|---|---|---|---|
| | | | | *No. 1.* | | | | | |
| 1–50 | 2 | 10 | 36 | 2 | | 6 | 9 | 27 | 8 |
| 51–100 | 0 | 5 | 43 | 2 | | 3 | 8 | 34 | 5 |
| 101–150 | 1 | 5 | 43 | 1 | | 1 | 3 | 23 | 23 |
| 151–200 | 0 | 2 | 44 | 4 (shown twice) | | 0 | 6 | 7 | 37 |
| 201–250 | 0 | 2 | 43 | 5 (shown twice) | | 1 | 10 | 11 | 28 |
| 251–300 | 3 | 5 | 39 | 3 (shown twice) | | 1 | 9 | 8 | 32 |
| 30–350 | 0 | 13 | 36 | 1 (shown twice) | | 7 | 6 | 8 | 29 |
| 351–400 | 0 | 1 | 49 | | | 2 | 2 | 2 | 44 |
| | | | | *No. 2.* | | | | | |
| 1–50 | 11 | 20 | 19 | | | 3 | 18 | 28 | 1 |
| 51–100 | 4 | 22 | 23 | 1 | | 6 | 16 | 25 | 3 |
| 101–150 | 2 | 29 | 19 | | | 2 | 30 | 17 | 1 |
| 151–200 | 5 | 34 | 11 | | | 1 | 10 | 26 | 13 |
| 201–250 | 2 | 5 | 41 | 2 | | 2 | 7 | 32 | 9 |
| 251–300 | 4 | 21 | 25 | | | 3 | 9 | 17 | 21 |
| 301–350 | 2 | 7 | 41 | | | 3 | 4 | 21 | 22 |
| 351–400 | 5 | 23 | 22 | | 351–381 | 0 | 0 | 0 | 30 |
| 401–450 | 9 | 7 | 32 | 2 | | | | | |
| 451–500 | 7 | 15 | 28 | | | | | | |
| 501–540 | 6 | 8 | 25 | 1 | | | | | |
| | | | | *No. 3.* | | | | | |
| 1–50 | 11 | 19 | 19 | 1 | | 10 | 20 | 19 | 1 |
| 51–100 | 10 | 18 | 22 | | | 10 | 18 | 22 | 0 |
| 101–150 | 6 | 16 | 27 | 1 | | 4 | 25 | 15 | 6 |
| 151–200 | 5 | 14 | 30 | 1 | | 0 | 8 | 19 | 23 |
| 201–251 | 2 | 19 | 25 | 4 | | 3 | 7 | 12 | 28 |
| 251–300 | 1 | 18 | 31 | | | 2 | 4 | 10 | 34 |
| 301–350 | 3 | 8 | 36 | 3 | 301–327 | 0 | 0 | 2 | 25 |
| 351–400 | 2 | 5 | 43 | | | | | | |
| 401–426 | 3 | 1 | 22 | | | | | | |

ter than the records indicate. The point at issue, however, is not the rate of learning, but merely the question whether these animals did learn to discriminate two situations in which *the present sense stimuli* were identical, namely, two red cards. I set as an arbitrary standard of mastery twenty-five successive perfect responses. More than this was attained with No. 1, giving each series once, and again giving each series twice. I attained it for the series of reds with both No. 2 and No. 3, and so nearly attained it with the other series that no doubt remains of their practical mastery of the situation.

This appears more clearly if we realize that had the animal climbed up at every card of the white-blue-red series, he would have made one hundred mistakes and only fifty correct responses in fifty trials. Yet the animal was very eager to go up on the box. All the food he ever had when colored cards were shown he received at that place. With this chance for mistakes the record seems conclusive.

Does the method of the experiment warrant the claim that the animal *retains* an image of the cards which just preceded red? For No. 1, success meant first, that he respond to red preceded by white and blue, now both out of sight, and that he refuse to respond to red preceded by two reds, now both out of sight. Later he must refuse to respond to six reds in succession, but continue the old response to white-blue-red now given twice in succession. Certainly no counting can enter here. The other two learned the alternate order as rapidly as No. 1 in the light of his previous three-color training. Therefore his work is typical.

The behavior of all three animals happens to be more conclusive than the records of their learning, for each one, on seeing the first red, would drop down from a position with both forepaws on the front board to stand on all fours on the floor in front of it and merely glance up at the succeeding reds. As soon as the white appeared, however, the animal would lean up against the front board, claw down the white and the blue but *never the final red.* Moreover he kept his eyes directed on the point at which these colors appeared and promptly clawed them down. Now does not the law of parsimony demand that these reactions be explained as due to visual images with which the animal compared the appearing card? The turning back and looking for the final color, when the impulse to start up is strong, and the few failures to respond at all, in most of which the animal seemed not to have remembered what colors had preceded the red, suggest that it does.

It may still be objected, that retaining an image while you raise three or even six colors is hardly retention at all, so short is the time. Of course the fact that the animals made steady and rather uniform progress for six days would show that the impression was not effaced in twenty-four hours. No. 1, however, was given a review of his first three-color work after an interval of eighteen days. He did not respond to the three blue cards at all and made but one mistake in twenty trials to the series white-orange-blue, though he did *start* up at orange six times. The visual images of the colors must therefore have been retained for eighteen days with sufficient clearness to permit successful responses. As No. 1 does not differ from the others in memory power this result may be accepted as typical. We are, therefore, forced to believe that the raccoon retains visual images.

## SUMMARY.

1. In the rapidity with which it forms associations the raccoon seems to stand almost midway between the monkey and the cat, as shown by the numerical records for those animals. In the complexity of the associations it is able to form it stands nearer the monkey.
2. Long practiced motor associations show a good degree of permanence; others are very transient. The raccoon presents two types of learning and two types of forgetting.
3. The raccoon discriminates forms, sizes, and tones. It also discriminates cards of different colors and intensities, but it probably responds to the latter quality alone.
4. I have no evidence that the raccoon imitates its fellows. Long attention to the experimenter's movements apparently arouses in the animal an impulse to attempt the act itself, but this impulse may be entirely spontaneous.
5. The raccoon certainly learns various acts from being put through them (see summary, p. 248).
6. My experiments indicate the presence of visual images.

# THE EGG-LAYING APPARATUS IN THE SILKWORM (BOMBYX MORI) AS A REFLEX APPARATUS.

BY

ISABEL M'CRACKEN.

(*From the Physiological Laboratory, Stanford University.*)

WITH ONE FIGURE.

The earliest investigators of the nervous system of Arthropoda (ALEXANDER VON HUMBOLDT, 1797, TREVIRANUS, '32, BURMEISTER, '32) established several facts in regard to the functions of the nervous system in insects.

1. That the nerves of insects are as sensitive to electrical and chemical stimuli as those of vertebrates.
2. That correlated movements are not impossible after the head has been snipped off (walking, swimming, etc.), although frequently requiring external stimuli to initiate the movement.
3. That removal of an eye, a feeler or half of the brain causes circular movements toward the sound side.

These writers, however, looked upon the brain as the instigator and controller of the functions of the nervous system and traced the motions after decapitation to the irritability of muscles alone. Not until NEWPORT[1] investigated the anatomy of the nervous system of *Sphinx ligustri* did investigators begin to assume functional independence for the ganglia of thorax and abdomen in insects. Later investigators, notably FAIVRE ('56), WARD ('79), STEINER ('87), and others, found the thoracic as well as the supra- (the brain) and sub-œsophageal ganglia to be centers of movement, and the abdominal ganglia to be respiratory centers at least. FAIVRE claimed for the brain and for the sub-œsophageal ganglia certain characteristic functions analogous to those of the brain of vertebrates—for the brain, will and directive power, and for the sub-œsophageal ganglion coördination of movement.

---

[1] NEWPORT, GEORGE, 1834. On the Nervous System of *Sphinx ligustri*. *Philosophical Transactions*, p. 389.

Bethe[2] ('97) gives a review of the work of these investigators and, in a series of careful experiments upon several species of insects and other Arthropoda, discredits some of the previous assumptions, notably those of Faivre, verifies many of the facts and establishes certain theories. His experiments point to the following conclusions: That the brain besides being the central ending of certain peripheral nerves (nerves to the antennæ, eyes, etc.) is an inhibitory center and exercises a tonus upon the musculature; that the influence of each half of the brain and sub-œsophageal ganglion is felt mainly in the extremities of the same side. He showed that the decapitated insect in several species is still in a condition to perform all of its characteristic movements, except that there is a certain awkwardness and feebleness in these activities. Bethe also adduced evidence (in Hydrophilus and Astacus) showing the independence of the thoracic ganglia.

The present work deals with the behavior of the egg-laying apparatus of the silkworm (Bombyx mori) in the normal, decapitated and dethoraxed insect.

It was not a matter of surprise to find the reproductive system in the silkworm functioning through the ganglion with which it is intimately connected. It was, however, of much interest to observe the accurate response in every part of the system throughout a long period of time after severance of head or head and thorax, the conditions under which this response took place and the coördinate movements in other parts of the body.

## THE REPRODUCTIVE SYSTEM.

In the female silkworm, the paired ovaries consist each of four elongated tubes, the ovariole tubes (Fig. 1, *O.t.*), having an expanded length of about 36 mm. The terminal filaments of these ovarioles or egg chains are united by a common filament to the dorsal wall of the abdomen. These series of four ovarioles unite in a short common oviduct about 2 mm. in length (Fig. 1, *Od.*). The two oviducts unite in a common vagina, an elongated chamber with a length of about 6 mm. The vagina passes as a single tube to the extremity of the body, where it culminates at the surface in an ovipositor consisting of a short muscular tube terminated by

---

[2] Bethe, A., 1897. Vergleichende Untersuchungen über die Functionen des Centralnervensystem der Arthropoden. *Pflüger's Archiv der Physiologie*, Bd. 68, pp. 449–544.

two lips covered with short hairs (Fig. 1, *Ov.*). The ovipositor when not functioning is shielded by chitinized plates, two dorsolateral and one ventral (Fig. 1, *D.pl.* and *V.pl.*[1]). Upon the dorsal and lateral walls of the ovipositor, also shielded by the dorsolateral plates, are certain extensible glands, the alluring glands, which serve to attract the male at mating time. There are three other essential parts to the system, as follows: A pair of colleterial or cement glands (Fig. 1, *Col.gl.*) open by a common duct into the vagina through its dorsal wall posteriorly. These glands secrete a fluid that flows into the vagina and accompanies the fertilized egg through the ovipositor, firmly fixing the egg to a surface, by hardening as it is exposed to the air. The bursa copulatrix, a large sac-like organ (Fig. 1, *B.c.*) and the spermatheca with its spermathecal gland (Fig. 1, *Sp.*) open separately (seemingly) by means of ducts into the vagina, the latter a little forward of the former. The mechanism of the intimate connection that must exist between the internal opening of the bursa and the opening of the spermatheca was not determined. The bursa copulatrix

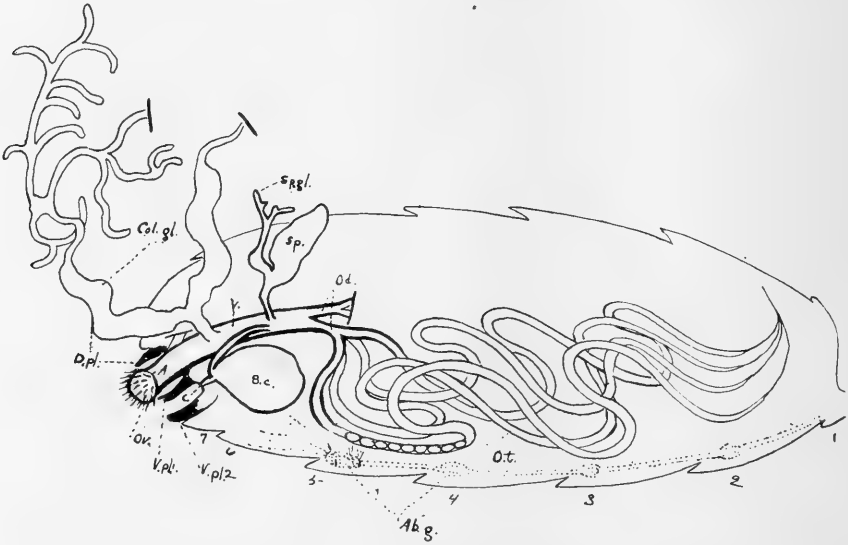


FIG. 1. Anatomy of the Reproductive System (Bombyx mori). *Ov.*, ovipositor; *V.*, vagina; *Od.*, oviduct; *O.t.*, ovarioles; *Bc.*, bursa copulatrix; *C.*, copulatory pore; *Col.gl.*, colleterial glands; *Sp.*, spermatheca; *Sp.gl.*, spermathecal gland; *D.pl.*, dorsal plate; *V.pl.*[1], 1st ventral plate; *V.pl.*[2], 2d ventral plate; *Ab.g.*, abdominal ganglia (*2, 3, 4, 5*); *A*, position of the "alluring glands."

communicates immediately (there being but a very minute intervening canal) with the outside through a separate opening, the copulatory pore (Fig. 1, *c.*). This is situated on the ventral surface of the abdomen, ventrad of the ovipositor, in a recess between two chitinized plates, the one subtending the ovipositor, the other ventrad of this one (Fig. 1, *V.pl.*[1] and *V.pl.*[2]). The opening is controlled by sphincter muscles. The communicating tube between the bursa and vagina is long (2½ mm.), narrow and direct. The communicating tube between the spermatheca and vagina is comparatively long, the spermathecal gland (Fig. 1, *Sp.gl.*) opening at the base of the spermatheca at its adjunct with the spermathecal duct.

At the time the adult leaves the cocoon, each ovariole or egg chain contains from fifty to sixty fully formed eggs. (Dissection of one abnormal individual showed six ovarioles upon each side instead of the normal number of four.)

In the functioning of the reproductive apparatus (primary and accessory glands and ovipositing apparatus), therefore, the following must take place:

(*a*) The sperm is received into the bursa copulatrix and passes through a considerable distance into the spermatheca.

(*b*) From the spermatheca, surrounded by a fluid secreted by the spermathecal gland, the sperm passes into the vagina.

(*c*) Eggs pass down the ovarial tubes (ovarioles) enclosed by a shell secreted by certain glandular cells in the ovarioles, and reach the vagina.

(*d*) Becoming fertilized and surrounded by fluid secreted by the colleterial glands, the egg is passed on by the vagina to the ovipositor.

(*e*) Finally, the lips of the ovipositor open and each egg is accurately placed by the side of another. In egg placing, the sensory surface of the ovipositor is moved with dorso-ventral and lateral movements, from right to left or left to right, avoiding each previously placed egg. When the full quota of eggs have been placed, they lie in several concentric rows, in a semi-circular area (sometimes circular) about a center within which the moth has been turning from side to side.

The posterior abdominal ganglion (Fig. 1, *Ab.g.*) is situated in the fifth abdominal segment. The seven paired nerves of this ganglion are distributed as follows: Nerves *1* and *2* to the muscles and skin of the fifth abdominal segment. Nerves *3* and *4* to the muscle and skin of the sixth abdominal segment. Nerves *5*, *6* and *7* to the reproductive organs and muscles of the last abdominal segment. A certain neurone of the fourth nerve ends in the walls of the oviduct. Neurones of the fifth and sixth nerves end in the muscles controlling the anal opening and ovipositor, extensors and retractors, and opening of the bursa. Neurones of the seventh nerve are distributed to the ovipositor, to the walls of the colleterial gland, to the vagina and to the rectum.

The silkworm takes no food in the adult stage, although living from ten to twenty days in a strong, vigorous condition. The female moves about but little. The mating instinct, to the end of egg fertilization and preservation of the species, is the only conspicuous adult instinct exhibited. The reflexes connected with reproduction are the only apparent spontaneous reflexes exhibited. No difficulties are encountered in experimenting with these insects in the way of disturbing influences from fright, hunger or efforts to get away.

While not attempting in this series of experiments to cover completely the ground of the functioning and nervous control of the reproductive system, much interesting data was obtained relative to its behavior.

## NORMAL BEHAVIOR.

Adults leave the cocoon under normal conditions between 7 and 8 a. m. The female at once extends the alluring glands. If a male is near, mating takes place at once. The mated pair remain almost continuously in copula from twenty-four to thirty-six hours, after which, for the next twelve to seventy-two hours there are intermittent periods of egg laying. Within two to five days after issuing, one to three days after mating, a female will have oviposited her full quota of eggs. There is no regularity with reference to total number of eggs oviposited by individuals. These range in normal healthy individuals from three hundred to considerably over five hundred eggs in the races used for this work.

In the unmated insect, as in the mated, there is no regularity as to the number of eggs oviposited, but eventually the full quota of eggs are placed.

## NATURE OF THE EXPERIMENTS.

The following experiments were inaugurated to determine if possible the innervating center of the reproductive apparatus; the extent to which this primary reflex was augmented by removal of the brain; and the degree of correlation between this and other reflex centers.

After severing the head from the body in the silkworm moth, there is no loss of blood, and the moth shows no signs of inconvenience. The insect rests placidly upon the table. There is no restlessness. No spontaneous movements occur if the sensory surfaces are carefully protected from stimulation. The alluring glands remain retracted beneath the anal plates. A stimulation brought to bear upon the abdomen, however, by pressure with the fingers or rubbing with the pencil, starts a definite and invariable response in the reproductive machinery. All the coördinated reflexes that are involved in the placing of an egg follow.

This investigation began July 1, 1906, when the last of the first generation of the season were maturing. It was continued throughout the greater part of July and resumed August 30 with a larger number of moths, when the second generation was coming to maturity. Practically the same results were obtained in each lot.

The investigation progressed under fifteen series of observations. The condition of each series was as follows:

SERIES 1. Moth unmated, not decapitated, not stimulated, hence a normal unmated moth. Table I.

SERIES 2. Mated, not decapitated, not stimulated—a normal mated moth. Table II.

SERIES 3. Not mated, not decapitated, but stimulated at intervals previous to normal time for ovipositing.

SERIES 4. Mated, not decapitated, stimulated previous to normal time for ovipositing.

SERIES 5. Not mated, decapitated, not stimulated.

SERIES 6. Mated, decapitated, not stimulated.

SERIES 7. Not mated, allowed to oviposit a group or so of eggs, than decapitated and not stimulated.

SERIES 8. Mated, allowed to oviposit a group of eggs, then decapitated, not stimulated.

SERIES 9. Decapitated, afterward mated, mate removed, moth not stimulated.

SERIES 10. Not mated, decapitated, stimulated one to several days after issuing. Table III.

SERIES 11. Mated, decapitated and stimulated one to several days after issuing. Table IV.

SERIES 12. Decapitated, afterward mated, mate removed, moth stimulated. Table V.

SERIES 13. Mated (or unmated), dethoraxed and not stimulated.

SERIES 14. Mated, dethoraxed, stimulated. Table VI.

SERIES 15. Dethoraxed, stimulated, then commissures connecting each abdominal ganglion cut consecutively from anterior to posterior.

A large number of moths were under observation in each series (from ten to forty) and care was exercised to obtain healthy moths from well-fed larvæ.

Tables I and II give the following data in regard to fourteen of the individuals (seven in each series) under observation in Series 1 and 2; length of life, number and frequency of groups of eggs oviposited and total number of eggs oviposited. Nearly all of these moths issued upon the same day (at most one or two days apart), hence under practically the same general environmental conditions of temperature, etc. The data here recorded are typical of that for all the individuals observed in these series. Individuals in Table I (Series 1) are *normal unmated moths*; in Table II (Series 2) are *normal mated moths.*

The average length of life of moths in each series is thirteen or fourteen days, average number of eggs in Series 1, 411, in Series 2, 421. The unmated moth, therefore, lives as long as the mated moth, and each oviposits the full quota of eggs, as comparison of the two tables shows. The essential difference in behavior in the two series is indicated in the total number of egg-laying periods and in the difference in number of eggs placed during any one period by a single individual. In Series 1 (unmated moths) the egg-laying period averages eight days, a maximum of ten days, a minimum of six days. In Series 2 (mated moths) the egg-laying period averages three days. Only occasionally is the egg-laying period extended into the fourth day.

In No. 7 (Table II), for some unaccountable reason, the moth, while ovipositing the normal number of eggs in the three-day period, did not begin to oviposit until she was six days old. This is unusual.

In unmated moths, during the long periods intervening between the egg-laying periods, the alluring glands are almost constantly extruded. In mated moths, remating ensues in the intervening periods.

*Series 1. Normal unmated moths.*

TABLE I.

| No. 1.<br>Issued Sep. 3.<br>Died Sep. 18. | | No. 2.<br>Issued Sep. 3.<br>Died Sep. 12. | | No. 3.<br>Issued Sep. 3.<br>Died Sep. 18. | | No. 4.<br>Issued Sep. 3.<br>Died Sep. 17. | |
|---|---|---|---|---|---|---|---|
| Oviposited. | No. of eggs. | Oviposited. | No. of eggs. | Oviposited. | No. of eggs. | Oviposited. | No. of eggs. |
| Sep. 5 p.m. | 7 | Sep. 4 p.m. | 38 | Sep. 4 p.m. | 4 | Sep. 5 p.m. | 3 |
| 6 a.m. | 34 | 5 p.m. | 36 | 5 a.m. | 14 | 6 a.m. | 25 |
| 7 p.m. 1.30 | 104 | 6 p.m. | 92 | 6 a.m. | 19 | 7 p.m. | 50 |
| | | 7 p.m. | 132 | 7 p.m. | 35 | 8 a.m. | 26 |
| 7 p.m. 4.30 | 34 | 8 p.m. | 32 | 8 p.m. | 20 | 9 a.m. | 35 |
| | | 9 a.m. | 180 | 9 a.m. | 19 | 10 p.m. | 70 |
| 8 p.m. | 50 | 10 p.m. | 88 | 9 p.m. | 36 | 11 p.m. | 42 |
| 9 a.m. | 100 | 11 p.m. | 32 | 10 p.m. | 34 | 12 p.m. | 130 |
| 10 p.m. | 150 | | | 11 p.m. | 36 | 13 p.m. | 34 |
| | | | | 12 p.m. | 3 | 16 p.m. | 21 |
| Total | 479 | Total | 630 | Total | 214 | Total | 436 |

TABLE I—*Continued.*

| No. 5.<br>Issued Sep. 3.<br>Died Sep. 16. | | No. 6.<br>Issued Sep. 3.<br>Died Sep. 19. | | No. 7.<br>Issued Sep. 5.<br>Died Sep. 15. | |
|---|---|---|---|---|---|
| Oviposited. | No. of eggs. | Oviposited. | No. of eggs. | Oviposited. | No. of eggs. |
| Sep. 5 p.m. | 16 | Sep. 5 p.m. | 4 | Sep. 6 p.m. | 2 |
| 6 p.m. | 72 | 6 p.m. | 20 | 7 a.m. | 28 |
| 7 p.m. | 56 | 7 a.m. | 96 | 8 p.m. | 52 |
| 8 a.m. | 7 | 8 p.m. | 94 | 9 a.m. | 16 |
| 8 p.m. | 44 | 9 a.m. | 68 | 10 p.m. | 78 |
| 9 a.m. | 35 | 10 p.m. | 17 | 11 p.m. | 120 |
| 10 p.m. | 38 | | | 12 p.m. | 38 |
| 11 p.m. | 58 | | | | |
| 12 p.m. | 21 | | | | |
| 13 p.m. | 6 | | | | |
| Total | 353 | Total | 299 | Total | 334 |

In the unmated moth, the ovipositing apparatus appears therefore to be under an inhibitory influence that is removed in the mated insect, in which the necessity for it is also removed. The question arises, Does the excitement or activity of the mating instinct have an inhibitory effect upon the egg-laying apparatus, or does the presence of the sperm in the receptive organs of the mated insect incite the reproductive mechanism to the greater functional activity? This ability to prolong the egg-laying period through several days is an apparent adaptation to a condition that might exist amongst wild forms, but for which there appears to be no necessity in this domesticated species under its normal conditions of commercial breeding; that is, an adaptation either to a scarcity of males or a late issuance of males in a particular area.

*Series 2. Normal mated moths.*

TABLE II.

| No. 1.<br>Issued Sep. 3.<br>Mated Sep. 3 p.m.<br>Died Sep. 12. | | No. 2.<br>Issued Sep. 3.<br>Mated Sep. 3.<br>Died Sep. 15. | | No. 3.<br>Issued Sep. 3.<br>Mated Sep. 3.<br>Died Sep. 15. | | No. 4.<br>Issued Sep. 3<br>Mated Sep 3.<br>Died Sep. 11. | |
|---|---|---|---|---|---|---|---|
| Oviposited. | Eggs. | Oviposited. | Eggs. | Oviposited. | Eggs. | Oviposited. | Eggs. |
| Sep. 6 a.m. | 160 | Sep. 5 p.m. | 75 | Sep. 6 a.m. | 212 | Sep. 5 a.m. | 100 |
| 7 a.m. | 64 | 6 a.m. | 90 | 7 p.m. | 120 | 6 a.m. | 180 |
| 8 p.m. | 250 | 7 p.m. | 200 | 8 a.m. | 16 | 7 a.m. | 200 |
| Total | 474 | Total | 365 | Total | 348 | Total | 480 |

TABLE II—*Continued*.

| No. 5.<br>Issued Sep. 4.<br>Mated Sep. 4.<br>Died Sep. 10. | | No. 6.<br>Issued Sep. 2.<br>Mated Sep. 3.<br>Died Sep. 15. | | No. 7.<br>Issued Sep. 3.<br>Mated Sep. 3.<br>Died Sep. 12. | |
|---|---|---|---|---|---|
| Oviposited. | Eggs. | Oviposited. | Eggs. | Oviposited. | Eggs. |
| Sep. 5 p.m. | 100 | Sep. 4 p.m. | 180 | Sep. 9 a.m. | 110 |
| 6 | 140 | 5 a.m. | 200 | 10 p.m. | 32 |
| 7 | 160 | 6 p.m. | 160 | 11 p.m. | 300 |
| Total | 400 | Total | 440 | Total | 442 |

Having determined that eggs were oviposited in neither mated nor unmated moths until twelve to twenty-four hours had elapsed after issuing, an effort was made to induce early ovipositing by means of external stimuli. In unmated insects (Series 3) and in mated insects from which the males had been early removed (Series 4) the abdomen was stroked with pencil or finger for a few seconds, or gently pressed, at various times during the period previous to the normal time for ovipositing. (This, and the rubbing of the abdomen by the male, had been previously found to be effective stimuli in inducing ovipositing in decapitated moths.) This stimulation met with no response, but ovipositing beginning at the normal time was continued from one to three days (rarely four) in the mated insect and from seven to ten days in the unmated insect. If it is true that the brain in insects may be looked upon as a reflex-inhibitory center, then, as set forth by BETHE with reference to various movements, here the ovipositor fails to respond to a stimulus that is unfailing in a moth with brain removed, because of this inhibitory influence.

In normal moths, whether mated or unmated, the rate of ovipositing is irregular. The following shows the time rate for three unmated moths.

This in general shows the variation observed in time rates in all moths in which time rate data were taken. (Figures indicate seconds elapsing between each successive egg.)

A—10, 5, 7, 5, 6, 4, 5, 9, 7, 6, 6, 5, 6, 6, 11, 6, 4, 6, 6. Av., 1 per 6 sec.
B—7, 10, 10, 14, 5, 2, 9, 11, 9, 43, 7, 9, 9, 4, 6, 9, 8, 21, 8, 62, 9. Av., 1 per 11 sec.
C—1, 8, 47, 7, 18, 8, 71, 84, 11, 19, 8, 9, 7, 22, 11, 10, 12, 9, 15, 10. Av., 1 per 16 sec. The average for all insects timed was from 9 to 12 sec.

Unfortunately time rates were not secured from day to day for the same individuals amongst normal moths, as in experimental groups. The irregularity in the rate is due to some extent at least to the manœuvers of the ovipositor in (apparently) seeking a favorable spot to place the egg. The movements of the ovipositor previous to the placing of the egg have the appearance of an intentional effort to avoid placing one egg upon another. This movement was later studied in dethoraxed moths.

After having determined the behavior of the egg-laying apparatus in the normal insect, twenty unmated moths and about forty moths that had been previously mated were decapitated for Series 5 and 6.

These were isolated in individual boxes to avoid the possibility of stimulation by contact. The average length of life in the former was fourteen days, the average length of life in the latter was thirteen days, showing thus no great deviation from that of the normal insect. No unmated moth oviposited at all. Amongst the forty mated moths but three produced any eggs, one of these producing one, one producing four, and one producing six eggs. In the latter case the eggs were produced immediately after the moth had been lifted by the wings, consequently after having been submitted to stimulation to that extent. In the other two cases no stimulation was known to have taken place. From the fact that such a large number of unstimulated moths failed to produce any eggs after decapitation, and from later results with stimulated insects, it seems that spontaneous egg production under this condition is exceedingly rare.

Furthermore, in neither mated nor unmated insect was there any extension of the alluring glands, nor was any stimulation such as pressure, rubbing of the abdomen by the male, etc., sufficient to induce an extension of these glands. Whether this was due primarily to the fact that these were deprived of their innervating center through loss of the head (the brain) or whether the loss of antennæ alone would have brought about the same result, was not determined. Probably the nature of the stimulus was also inadequate. The behavior of the alluring glands demands special consideration and was not taken up in this investigation.

In Series 7 and 8 the moths (about twenty in each case) were either mated or left unmated, and permitted to oviposit normally a small group of eggs. Then the head was removed by a sudden snip with a sharp scissors. In no case did ovipositing continue, nor were any more eggs produced throughout the life of the insect, although moths in the series lived for an average of twelve days.

In Series 9 the moths were first decapitated; later, although there had been no extension of the alluring glands, there was apparently no difficulty in the way of mating. In every case (about twenty females were observed), the males that were walking about upon the table, vibrating their wings in the air, found the headless females and upon contact of the two bodies and after a little manœuvering on the part of the male, by way of circling about and rubbing the body of the female partly for the purpose of orientation, mating invariably took place without difficulty.

After separation, if the male was left in the mating box with the female, the full quota of eggs were always oviposited by the headless female. If, however, the male was removed immediately upon separation, no eggs followed. In the former cases, therefore, eggs were no doubt brought about by stimulation of the abdomen by the movements of the male. In several observed cases this was true. While ovipositing was in progress, mating could not take place, since the extrusion of the ovipositor served as an efficient barrier. The continual rubbing of the abdomen of the female by the male, that followed failure to mate, served, however, as a continual stimulation until all the eggs were oviposited.

Eggs produced under this condition are fertilized and accompanied by the cement secretion of the colleterial glands, which secures them to the surface, as in the normal insect. The ovipositor places the eggs accurately one by the side of another. The legs assist the movements of the ovipositor by carrying the body to the left or right, as demanded, in order to avoid placing one egg upon another, when the movements of the ovipositor alone are inefficient. This shows that the whole system is in perfect functional condition—as shown even more conclusively later.

In Series 10 and 11 the moths were either unmated (Series 10, Table III) or mated (Series 11, Table IV), afterward decapitated and stimulated at various intervals as indicated in the tables, by pressure upon the abdomen with the fingers. In some cases moths were stimulated every five or ten minutes during a certain period, in others once a day only for several days in succession, in still others both methods were employed. The result is the same in each case. In no case were eggs produced except as a result of stimulation. In very rare cases only did stimulation fail to bring a response in the way of a group of eggs. In such cases the ovipositor responded by becoming extruded, the failure of the appearance of the egg was due apparently to failure of the transportation of the egg along its path from ovariole to ovipositor. Failure was more apt to occur when the young moth was stimulated; that is, stimulation taking place before the normal time for egg laying in the normal insect. This appears to indicate that the inhibition of the egg-laying reflex was not completely removed with removal of the head.

The time elapsing between the stimulation and the response was sometimes inconsiderable, and sometimes of many seconds' duration. In several cases, eggs followed after one second; in a few cases not for fifty seconds; usually, however, in from six to twelve seconds. The time-rate of egg-placing was no greater and no more irregular than that in normal insects, as the following examples will show (figures indicate time, in seconds, between the placing of eggs).

A—14, 8, 8, 12, 12, 8, 8, 12, 16, 10, 7, 6, 9, 8, 6, 8, 12, 7, 9, 8. Av., 1 per 9 sec.
B—6, 12, 6, 12, 17, 5, 14, 15, 12, 7, 6, 9, 11, 4, 9, 9, 9, 39, 14, 6. Av., 1 per 11 sec.
C—14, 6, 7, 5, 5, 8, 7, 5, 6, 5, 5, 6, 5, 7, 6, 18, 14, 5, 5, 6. Av., 1 per 7 sec.

*Series 10. Moths not mated, decapitated and stimulated.*

TABLE III.

| No. 1.<br>Issued Sep. 8<br>Decap. Sep. 8 a.m.<br>Died Sep. 19. | | No. 2.<br>Issued Sep. 8.<br>Decap. Sep. 8 a.m.<br>Died Sep. 18. | | No. 3.<br>Issued Sep. 8.<br>Decap. Sep. 8 a.m.<br>Died Sep. 15. | | No. 4.<br>Issued Sep. 8.<br>Decap. Sep. 8 a.m.<br>Died Sep. 16. | |
|---|---|---|---|---|---|---|---|
| Stimulated. | No. of eggs. | Stimulated. | No. of eggs. | Stimulated. | No. of eggs. | Stimulated. | No. of eggs. |
| Sep. 8 p.m. 4 | 0 | Sep. 8 p.m. 4 | 0 | Sep. 8 p.m. 4 | 6 | Sep. 8 p.m. 4 | 8 |
| 8 p.m. 9 | 0 | 8 p.m. 8 | 4 | 8 p.m. 9 | 13 | 8 p.m. 9 | 3 |
| 9 p.m. 9 | 3 | 8 p.m. 9 | 10 | 8 p.m. 9.15 | 3 | 9 p.m. 9 | 12 |
| 12 p.m. 10 | 10 | 9 p.m. 2 | 13 | | | 12 p.m. 3 | 4 |
| 13 a.m. 8 | 16 | 12 p.m. 9 | 14 | 9 p.m. 2 | 8 | | |
| 13 a.m. 10 | 8 | | | 12 p.m. 9 | 8 | | |
| 13 p.m. 4 | 12 | | | | | | |

TABLE III—*Continued.*

| No. 5.<br>Issued Sep. 8.<br>Decap. Sep. 8 a.m.<br>Died Sep. 19. | | No. 6.<br>Issued Sep. 8.<br>Decap. Sep. 8 a.m.<br>Died Sep. 18. | | No. 7.<br>Issued Sep. 8.<br>Decap. Sep. 8 a.m.<br>Died Sep. 18. | |
|---|---|---|---|---|---|
| Stimulated. | No. of eggs. | Stimulated. | No. of eggs. | Stimulated. | No. of eggs. |
| Sep. 8 p.m. 4 | 12 | Sep. 8 p.m. 4 | 10 | Sep. 12 p.m. | 25 |
| 9 p.m. 4 | 0 | 8 p.m. 5 | 6 | 13 p.m. 4 | 20 |
| 9 p.m. 9 | 11 | 8 p.m. 9 | 6 | 13 p.m. 9 | 15 |
| 12 p.m. 2 | 11 | 17 p.m. 5 | 130 | 14 p.m. 4 | 4 |
| 12 p.m. 9 | 9 | 17 p.m. 9 | 18 | | |

*Series II. Moth mated, afterward decapitated and stimulated at intervals.*

TABLE IV.

| No. 1.<br>Issued Sep. 4 a.m.<br>Mated Sep. 4 p.m.<br>Decap. Sep. 5 p.m.<br>Died Sep. 18. | | No. 2.<br>Issued Sep. 4 a.m.<br>Mated Sep. 4 p.m.<br>Decap. Sep. 5.<br>Died Sep. 18. | | No. 3.<br>Issued Sep. 4 a.m.<br>Mated Sep. 4 p.m.<br>Decap. Sep. 5 p.m.<br>Died Sep. 16. | | No. 4.<br>Issued Sep. 4 a.m.<br>Mated Sep. 4 p.m.<br>Decap. Sep. 5 p.m.<br>Died Sep. 14. | |
|---|---|---|---|---|---|---|---|
| Stimulated. | No. of eggs. | Stimulated. | No. of eggs. | Stimulated. | No. of eggs. | Stimulated. | No. of eggs. |
| Sep. 6 p.m. 3 | 4 | Sep. 5 p.m. | 10 | Sep. 9 a.m. 11 | 6 | Sep. 10 p.m. 8.30 | 6 |
| 6 p.m. 3.10 | 204 | 9 a.m. | 11 | 9 a.m. 11.35 | 37 | 10 p.m. 8.35 | 30 |
| 6 p.m. 3.45 | 52 | 10 p.m. | 21 | 9 a.m. 11.45 | 63 | 10 p.m. 8.40 | 12 |
| 6 p.m. 3.55 | 33 | 11 p.m. | 16 | 9 a.m. 12 | 33 | 10 p.m. 8.45 | 20 |
| 6 p.m. 4.05 | 22 | 12 p.m. | 21 | 9 p.m. 12.15 | 45 | 11 p.m. 5.30 | 13 |
| 6 p.m. 4.15 | 39 | 13 p.m. | 10 | 9 p.m. 12.20 | 41 | 12 p.m. 8.30 | 6 |
| 6 p.m. 4.35 | 27 | (all fertile) | | 9 p.m. 12.30 | 15 | 12 p.m. 8.45 | 12 |
| 6 p.m. 4.45 | 40 | | | 9 p.m. 12.45 | 22 | (all fertile) | |
| 6 p.m. 5 | 25 | | | 10 p.m. | 9 | | |
| 6 p.m. 5.15 | 39 | | | 11 p.m. | 63 | | |
| 6 p.m. 5.30 | 7 | | | 15 p.m. | 13 | | |
| 6 p.m. 5.35 | 7 | | | | | | |
| 6 p.m. 5.45 | 5 | | | | | | |
| 6 p.m. 7 | 3 | | | | | | |
| Total (all fertile) | 507 | | | Total (all fertile) | 349 | | |

TABLE IV—*Continued.*

| No. 5.<br>Issued Sep. 8 a.m.<br>Mated Sep. 8 a.m.<br>Decap. Sep. 8 p.m.<br>Died (?) | | No. 6.<br>Issued Sep. 8 a.m.<br>Mated Sep. 8 a.m.<br>Decap. Sep. 8 p.m. 5.<br>Died Sep. 15 | | No. 7.<br>Issued Sep. 10 a.m.<br>Mated Sep. 10 a.m.<br>Decap. Sep. 10 p.m.<br>Died Sep. 20. | |
|---|---|---|---|---|---|
| Stimulated. | No. of eggs. | Stimulated. | No. of eggs. | Stimulated. | No. of eggs. |
| Sep. 8 p.m. 5.30 | 6 | Sep. 10 p.m. | 8 | Sep. 10 p.m. 9.30 | 24 |
| 8 p.m. 7.30 | 17 | 11 p.m. 8 | 44 | 11 p.m. 7 | 12 |
| 8 p.m. 8.30 | 6 | 11 p.m. 8.10 | 44 | 11 p.m. 7.05 | 3 |
| 9 p.m. 9 | 8 | 11 p.m. 8.25 | 59 | 11 p.m. 7.10 | 50 |
| 12 p.m. 9 | 15 | 13 p.m. 7 | 12 | 11 p.m. 7.30 | 56 |
| (all fertile) | | 13 p.m. 7.15 | 13 | 11 p.m. 8 | 32 |
| | | 13 p.m. 7.30 | 55 | 11 p.m. 8.15 | 34 |
| | | (all fertile but two) | | (all fertile) | |

Inspection of Tables III and IV shows that the number of eggs oviposited in each group; that is, after each successive stimulation, is also variable, being, however, on the average no less variable on the first day than several days later.

The strength of the stimulus, as employed, not being measurable, the connection between this and the response was not determined but is conceivably a potent, though probably not a controlling, factor in determining the character of the response.

The same relative variability prevailed from day to day and from group to group upon the same day as to number of eggs in a group in both normal and decapitated (stimulated) moths, due probably to variability in strength of stimulus and other unknown conditions. On the whole, unmated moths oviposited fewer eggs at any one time than the mated moth, as in the normal insect. This suggests a connection between activity of the reproductive mechanism and the presence of sperm in the female receptacle. The average time rate of egg placing in the decapitated moth varies from group to group upon the same day and from day to day as the following examples show.

### SERIES II.

A issued Sept. 22, a. m., mated Sept. 23, p. m. 4, decapitated Sept. 24, p. m. 1.30. Time rate of ovipositing after stimulation.

1st group, Sept. 24, p. m. 5.35—14, 6, 9, 8, 20, 7, 21, 11, 20, 20, 8, 7, 8, 17, 15, 8, 8, 8, 9, 37, 67. Av. of 1 per 15 sec.

2d group, Sept. 24, p. m. 5.45—3, 21, 11, 9, 25, 10, 10, 12, 7, 8, 9, 10, 15, 11, 24, 8. Av. of 1 per 12 sec.

3d group, Sept. 24, p. m. 8.15—4, 11, 23, 30, 20, 7, 13, 15, 14, 11. Av. of 1 per 14 sec.

B issued Sept. 4, a. m., mated Sept. 4, p. m., decapitated, Sept. 5, p. m. 1.30. Time rate of ovipositing after stimulation.

1st group, Sept 10, a. m. 8.30—3, 16, 25, 6, 14, 9, 3, 25, 16, 27, 6, 20, 9, 11, 8, 10, 9, 36, 15, 15, 7, 21, 7, 13, 11, 15, 13, 12, 8, 15. Av. of 1 per 10 sec.

2d group, Sept. 10, a. m. 8.35—58, 7, 13, 15, 9, 13, 9, 25, 13, 7, 9, 15, 9. Av. of 1 per 15 sec.

3d group Sept. 10, a. m. 8.40—18, 8, 18, 7, 20, 33, 17, 15, 9, 16, 19, 14, 13. Av. of 1 per 17 sec.

4th group, Sept. 10, a. m. 8.45—20, 7, 29, 17, 10, 13, 14, 14, 14, 14, 15, 6, 27, 10, 9. Av. of 1 per 14 sec.

5th group, Sept. 11, p. m.—20, 6, 12; 27, 11, 14, 9, 35, 29, 25, 39. Av. of 1 per 19 sec.

6th group, Sept. 12, a. m.—3, 39, 37, 26 6, 3, 26, 17, 27, 35, 23, 24, 24. Av. of 1 per 24 sec.

C issued Sept. 4, a. m., mated Sept. 4, p. m. 4, decapitated Sept. 5, p. m., 1.30. Time rate of ovipositing after stimulation.

1st group, Sept 9, 11.35—7, 5, 11, 14, 6, 7, 6, 4, 5, 4, 4, 5, 9, 5, 6, 16, 5, 6, 6, 6, 5, 5, 5, 6, 5, 5, 4, 4, 5, 6, 5, 4, 9, 7, 4, 9, 4, 29, 1. Total, 34 eggs, 1 per sec.

2d group, Sept. 9, 11.45—2, 3, 3, 4, 5, 14, 5, 7, 7, 4, 4, 5, 4, 6, 5, 4, 5, 5, 3, 3, 4, 5, 6, 8, 5, 4, 5, 5, 15, 6, 7, 8, 9, 6, 5, 6, 5, 8, 54, 5, 5, 5, 5, 6, 6, 11, 4, 7, 3, 3, 3, 4, 5, 5, 4, 4, 10, 3, 3, 10, 5, 6. Total, 62 eggs. Av., 1 per 6 sec.

3d group, Sept. 9, 12 m.—2, 3, 3, 11, 4, 5, 6, 5, 4, 4, 3, 5, 5, 5, 5, 4, 4, 13, 5, 4, 5, 5, 5, 14, 5, 32, 4, 7, 5, 4, 5. Total, 31 eggs. Av., 1 per 6 sec.

4th group, Sept. 9, 12.15—3, 2, 6, 6, 5, 6, 7, 8, 4, 3, 4, 5, 3, 4, 4, 4, 4, 4, 5, 18, 5, 7, 7, 7, 5, 7, 5, 30, 6, 31, 4, 6, 9, 11, 5, 6, 36, 5, 8, 8, 7, 6, 18, 18, 57. Total, 44 eggs. Av., 1 per 9 sec.

5th group Sept. 9, 12.20—4, 9, 13, 7, 7, 5, 5, 5, 5, 5, 6, 6, 5, 5, 5, 5, 5, 5, 5, 6, 10, 3, 7, 10, 9, 13, 8, 6, 13, 3, 10, 25, 19, 11, 4, 25, 3, 7, 4, 6, 27, 20. Total, 42 eggs. Av., 1 per sec. 8.

6th group, Sept. 9, 12.30—3, 4, 23, 26, 11, 10, 11, 14, 14, 4, 27, 4, 5, 32, 6. Total, 15 eggs. Av., 1 per 13 sec.

9th group, Sept. 11, 4 p. m.—6, 15, 22, 15, 4, 4, 11, 4, 5, 5, 9, 4, 5, 26, 5, 7, 8 (intermittent groups not timed), 4, 9, 7, 5, 6, 5, 4, 6, 29, 4, 7, 6, 5, 6, 33, 2, 5, 9, 11, 6, 6, 4, 9, 5, 9, 3, 7, 6, 19, 5, 5, 6, 9, 9, 5, 8, 4, 8, 3, 5, 6, 5, 13, 5. Total, 61 eggs. Av., 1 per sec.

10th group, Sept 11, 4.15 p. m.—4, 13, 14, 7, 55, 57, 31, 44, 51, 16, 4, 7, 28. Total, 13 eggs. Av., 1 per 26 sec.

The percentage of the variability fluctuates, it does not progress from day to day as one might expect if one assumed a gradual decrease of tone in the system from day to day. Such an assumption appears to be unwarranted with reference to the reproductive system. The following fact lends additional evidence to the unwarrantability of this assumption with reference to the ovipositor. After the placing of the full quota of eggs, as in Nos. 1 and 3 in Table IV, stimulation still brings about extension of this organ and normal egg placing movements. In one particular case a moth issued July 10 and produced, after decapitation, and through a series of stimulations, 314 eggs in twelve groups, covering a period of seven days. The last eggs were oviposited July 17. Thereafter until July 22, when the moth died, at each stimulation (stimulation was repeated daily) the ovipositor was extended, remaining so for from twenty to twenty-seven seconds before being withdrawn. This was the rule in stimulated, decapitated moths after the ovariole tubes were known to be empty.

In insects that had been mated previous to decapitation, the eggs were all or nearly all fertile, whether these were oviposited immediately or not for ten or twelve days after decapitation. This was evidenced by the gray appearance assumed a few days after ovipositing—a color characteristic of the monovoltin egg, or egg destined to lie over the winter before issuing. An occasional non-fertile egg occurs. This frequently occurs also in masses of eggs oviposited under normal conditions.

That the full quota of eggs were not procured in every case, as the tables show, was due merely to the fact that the moth was not submitted to a sufficient number of stimulations. In each case where stimulations were continuous, an unexpectedly large number of eggs were placed, for example Table IV, Nos. 1 and 3. In the former (No. 1) frequent stimulations occurred throughout September 6, two days after the moth had issued and twelve days before death ensued. In the latter (No. 2) frequent stimulations occurred throughout September 9, five days after the moth had issued, then two stimulations twenty-four hours apart, and not again for ninety-six hours, twenty-four hours before death ensued, like results following in each case.

These tables, therefore, with the supplementary data, show again that the reproductive mechanism is perfect even for eight or ten days after decapitation, or as long as the moth lives. The sperm also retains vitality for that length of time within the body of the female.

In Series 12, as in Series 9, the moth was first decapitated and either immediately afterward or from one to three days afterward, mated. Mating takes place several days after decapitation with the same ease as before decapitation. In every case, eggs followed a few seconds after stimulation. Table V shows a series of individuals that were protected from external stimulus for several days after decapitation (from one to fourteen) and subsequently mated.

Inspection of the table shows that while eggs are produced as successfully upon the fifteenth day after issuing as upon the first, those produced after the thirteenth day are apt to be unfertilized. Either the vitality of the sperm has ceased, the mechanism for the passage of sperm into vagina has ceased working, or there may be an imperfect action on the part of the micropyle in the fifteen day old eggs. As to whether this was true exclusively in moths mated after decapitation was not sufficiently tested. The cement gland secretion also gives out about this time and eggs are thereafter apt to be non-adhesive.

*Series 12. Moth decapitated, afterward mated and stimulated at various intervals.*

TABLE V.

| No. 1.<br>Issued Sep. 4 a.m.<br>Decap. Sep. 4 a.m.<br>Mated Sep. 5 p.m.<br>Died Sep. 14. | | No. 2.<br>Issued Sep. 4 a.m.<br>Decap. Sep. 4 p.m.<br>Mated Sep. 5 p.m.<br>Died Sep. 15 | | No. 3.<br>Issued Sep. 3 a.m.<br>Decap. Sep. 4 p.m.<br>Mated Sep. 4 p.m.<br>Died Sep. 19. | | No. 4.<br>Issued Sep. 4 a.m.<br>Decap. Sep. 4 p.m.<br>Mated Sep. 5 p.m.<br>Died Sep. 20. | |
|---|---|---|---|---|---|---|---|
| Stimulated. | Eggs. | Stimulated. | Eggs. | Stimulated. | Eggs. | Stimulated. | Eggs. |
| Sep. 12 p.m. 8.30 | 9 | Sep. 12 p.m. 8.45 | 96 | Sep. 12 p.m. 9 | 20 | Sep. 18 a.m. | 18 |
| 12 p.m. 8.45 | 20 | 17 p.m. 8.50 | 3 | 17 p.m. | 3 | (not fertile) | |
| 12 p.m. 8.50 | 52 | 12 p.m. 9 | 25 | 18 p.m. | 10 | | |
| (one not fertile) | | (all fertile) | | (The last ten not fertile) | | | |

TABLE V—*Continued.*

| No. 5.<br>Issued Sep. 4 a.m.<br>Decap. Sep. 5 p.m.<br>Mated Sep. 5 p.m.<br>Died Sep. 18. | | No. 6.<br>Issued Sep. 6 a.m.<br>Decap. Sep. 6 a.m.<br>Mated Sep. 6 p.m.<br>Died Sep. 12. | | No. 7.<br>Issued July 6<br>Decap. July 6 a.m.<br>Mated July 9 a.m.<br>Died July 15. | |
|---|---|---|---|---|---|
| Stimulated. | Eggs. | Stimulated. | Eggs. | Stimulated. | Eggs. |
| Sep. 17 a.m. | 80 | Sep. 7 a.m. | 10 | July 10 p.m. 3 | 16 |
| 17 p.m. | 32 | 10 a.m. | 20 | 10 p.m. 4 | 10 |
| (all fertile) | | 13 a.m. | 3 | 10 p.m. 4.30 | 23 |
| | | 17 a.m. | 15 | 10 p.m. 4.45 | 38 |
| | | 21 a.m. | 6 | 10 p.m. 5.15 | 13 |
| | | (The last 6 not fertile) | | 10 p.m. 5.30 | 5 |
| | | | | 11 a.m. 9.15 | 4 |
| | | | | 11 p.m. 3.10 | 136 |
| | | | | 11 p.m. 3.45 | 14 |
| | | | | 11 p.m. 4.18 | 68 |
| | | | | 12 a.m. 11 | 12 |
| | | | | 12 a.m. 11.20 | 14 |
| | | | | 13 a.m. 11.50 | 0 |
| | | | | Total (all fertile) | 353 |

In No. 7 only was an effort made to induce an ovipositing of the full quota of eggs. A later dissection of this individual (353 eggs having been deposited in twelve groups, covering a period of six days) showed but four eggs left in the body and these were well back in the ovariole.

In Series 13 both head and thorax were removed, either before or after mating. Such an abdomen, carefully protected from external stimulus, produced no eggs, nor is there any extension of the alluring glands. The average length of life, however, is reduced to five days.

With the dethoraxed abdomen, persistent efforts upon the part of the male failed to perfect a mating. The difficulty seemed to be partly at least a mechanical one due to the continuous projection of the ovipositor in egg laying position. The tone of the muscles moving the ovipositor was apparently lost, for no stimulation was sufficient to induce its total withdrawal. No test was applied to determine whether or not the tone of the sphincter muscles surrounding the copulatory pore was also lost.

In Series 14 the thorax was removed from the moth after mating had taken place. In every case, as shown in Table VI, application of stimulus was followed by a group of eggs. The size of the group was as variable as in the normal or decapitated moths, but no more so. The length of life averaged five days, as in the dethoraxed, non-mated moth.

The ovipositor moved from side to side now with the same precision as in the normal or decapitated insect, but was rarely entirely withdrawn beneath the anal plates (frequently partially withdrawn). In the absence of the legs, the body was dragged from side to side simply by the action of the muscles of the abdomen. No attempt was made to obtain the full quota of eggs under this condition, but there was no reason to believe that it might not have been obtained by persistent stimulation.

The factor seeming to control the functioning of the ovipositor was determined with moths in the dethoraxed condition. While the decapitated insect experiences no difficulty in righting itself when placed upon its back, the dethoraxed moth, when so placed, makes absolutely no effort to right itself. This reflex has apparently disappeared with the thorax. In a stimulated abdomen lying in this position (that is, upon its back), the ovipositor is extended for its full length. The sides of the abdomen are slightly drawn in as when an insect is making a forced effort to oviposit. (This movement has been observed in both normal and dethoraxed moths.) The egg is ready to be expelled, but the ovipositor fails

*Series 14. Moth mated, afterward dethoraxed and stimulated at various intervals.*

TABLE VI.

| No. 1.<br>Issued Sep. 12.<br>Mated not.<br>Dethor. Sep. 13.<br>Died Sep. 15. | | No. 2.<br>Issued Sep. 23.<br>Mated Sep. 23.<br>Dethor. Sep. 24.<br>Died Sep. 29. | | No. 3.<br>Issued Sep. 26.<br>Mated Sep. 26.<br>Dethor. Sep. 28.<br>Died Sep. 30. | | No. 4.<br>Issued Sep. 27.<br>Mated Sep. 27.<br>Dethor. Sep. 28.<br>Died Oct 2. | |
|---|---|---|---|---|---|---|---|
| Stimulated. | Eggs. | Stimulated. | Eggs. | Stimulated. | Eggs. | Stimulated. | Eggs. |
| Sep. 13 a.m. 9 | 4 | Sep. 25 a.m. | 42 | Sep. 29 p.m. 2 | 24 | Sep. 28 p.m. 2 | 5 |
| 14 a.m. 9 | 10 | 26 a.m. | 20 | 29 p.m. 2.15 | 44 | 28 p.m. 2.15 | 22 |
| 14 p.m. | 25 | (all fertile) | | 29 p.m. 2.30 | 34 | 28 p.m. 2.30 | 8 |
| (all fertile) | | | | 29 p.m. 3 | 24 | 28 p.m. 2.45 | 16 |
| | | | | (all fertile) | | (all fertile) | |

TABLE VI—*Continued.*

| No. 5.<br>Issued Sep. 28.<br>Mated Sep. 28.<br>Dethor. Sep. 29.<br>Died Oct. 4. | | No. 6.<br>Issued Sep. 28.<br>Mated Sep. 28.<br>Dethor. Sep. 29.<br>Died Oct. 3. | | No. 7.<br>Issued Sep. 23.<br>Mated Sep. 23.<br>Dethor. Sep. 24.<br>Died Sep. 29. | |
|---|---|---|---|---|---|
| Stimulated. | Eggs. | Stimulated. | Eggs. | Stimulated. | Eggs. |
| Sep. 29 p.m. | 94 | Sep. 29 p.m. | 262 | Sep. 24 p m. 2 | 2 |
| 30 p.m. | 20 | 30 p.m. | 20 | 24 p.m. 21.0 | 22 |
| Oct. 1 p.m. | 30 | Oct. 1 p.m. | 25 | 24 p.m. 2.15 | 9 |
| (all fertile) | | (all fertile) | | 24 p.m. 8 | 39 |
| | | | | 24 p.m. 8.30 | 20 |
| | | | | (all fertile) | |

to open, and no egg appears. If, now, the sensory hairs that cover the outer surface of the ovipositor be barely touched with a pencil, or if a fiber of cotton held by a pair of pincers is brought into contact with these hairs, the lips of the ovipositor immediately open and an egg is pushed out. Each such contact brings forth an egg. In an insect in normal position, the sensory surface of the ovipositor is brought into contact with the surface upon which the insect rests. This serves as a stimulus for the action of the lips. Unfortunately, no experiments were tried to determine whether the nature of the material affected the functioning of these lips. It would be interesting to know whether the lips would open if these sensory hairs came in contact, for instance, with another egg. If not, we could understand how it was that one egg is rarely placed, either under normal or experimental condition, upon another. A study of the action of the ovipositor in this regard might also throw light upon the "selections" of various insects of certain plants only for placing their eggs—these plants being the particular food to which the larvæ of their kind is adapted.

Series 15 was a further reduction of the nervous system.

The first abdominal ganglion lies in the second abdominal segment. The commissure connecting it with the second abdominal ganglion lies close to the ventral surface of the body. This commissure can be snipped in two through the ventral wall of the body with but little loss of blood. With the first abdominal ganglion severed from the rest of the nervous system, egg placing followed, as before, upon stimulation, the rate of egg placing not being materially lowered. By snipping through the suture separating the third and fourth abdominal segments, the second abdominal ganglion was severed from the posterior part of the nervous system. Again stimulation resulted in egg placing. Snipping through the suture separating fourth and fifth abdominal segments severed the third abdominal ganglion from the fourth and last abdominal ganglion. As before, egg-placing took place with no more hesitancy than in the intact nervous system. That severance of the commissures in insects thus operated upon had actually taken place was later verified in several cases by dissections.

Upon severance of the nerve connections between the last abdominal ganglion and the ovipositing apparatus, stimulation failed to bring about movements in the ovipositor. That this was not due to loss of blood or disturbance of the respiratory apparatus incident upon the incisions, is evidenced by the fact that the ovipositing apparatus (egg tubes, ovipositor, etc.) with its controlling ganglion may be completely severed from the body, and eggs will yet pass down through the egg tube and out between the lips of the ovipositor, if the parts are kept normally moist.

The following examples give the time rate of egg placing under the several conditions enumerated above of a single representative moth.

Moth issued Sept. 21, decapitated Sept. 23, 11.36 a. m. Stimulated immediately.

Time rate of ovipositing—9, 16, 26, 13, 12, 10, 8, 7, 10, 12, 13, 15, 12, 9, 9. 15 eggs. Av. of 1 per 12 sec.

Dethoraxed Sept. 23, 4.25 p. m. and stimulated immediately.

Time rate of ovipositing—7, 17, 17, 36, 15, 9, 9, 21. 8 eggs. Av. of 1 per 16 sec.

First abdominal ganglion severed 4.30 p. m. and stimulated immediately.

Time rate or ovipositing—7, 6, 8, 8, 9, 19, 17, 7, 22, 9, 17, 21, 22, 24, 20, 21, 24, 20. 18 eggs. Av. of 1 per 15 sec.

Second abdominal ganglion severed, 4.35 p. m. and stimulated immediately.

Time rate of ovipositing—8, 8, 11, 8, 14, 12, 11, 8, 15, 27, 23, 8, 17, 19, 19. 15 eggs. Av. of 1 per 13 sec.

Third abdominal ganglion severed, 4.40 p. m. and stimulated immediately.

Time rate of ovipositing—9, 5, 7, 16, 34, 19, 6, 31, 15, 13, 25, 7, 24. 13 eggs. Av. of 1 per 16 sec.

The coördination of movement in various segments, after each operation, is progressively lost. The ovipositor, throughout, makes the same effort to avoid placing one egg upon another, by moving from side to side. With abdominal ganglia intact, this effort is successful. It becomes, noticeably less and less so as each abdominal ganglion is severed, until when but two remain, muscular coöperation of the segments is so far reduced that the combined efforts of the last three abdominal segments is not sufficient to pull the body around and the eggs (after the first three or four, which are placed side by side) are piled one upon another.

The results from the last series of operations show the high degree of independent activity exhibited by the controlling center of the reproductive apparatus, namely the last abdominal ganglion, and the coördination of the functions of this ganglion with those of the preceding ganglia in the ventral chain.

Hence the general opinion that "each segment of a segmental animal may be regarded as a simple reflex animal" is only a part of the truth. Bethe found that certain reflexes are located in each thoracic ganglion for the corresponding segment, as already cited. Each thoracic and abdominal ganglion in the silkworm is so organized that the reflexes carried on in the last segment of the abdomen are accompanied by a set of reflexes in other segments of a kind altogether different from that of the initial reflex. The functioning of the ovipositor is perfected by the movements in space of the legs, or in the absence of these, of the anterior segments of the abdomen.

*Direct Stimulation of the Commissure.*—In direct stimulation of the ventral commissure with an electric current, which is quite possible in silkworms, the response is not so determinate. Then only an occasional egg follows upon stimulation. The difference in response to direct stimulation and integumental stimulation may be due to the fact that in integumental stimulation only those neurones are affected that are in direct connection with the ovipositing machinery promoting movement, whereas in direct stimulation through the commissure, all the neurones are similarly stimulated, the inhibitory as well as those promoting movement.

## SUMMARY

1. The vitality of the silkworm moth, as measured by length of life and capacity of the reproductive system to function, is not impaired by removal of the head (supra- and sub-œsophageal ganglia).

Length of life is shortened, but functioning of the reproductive system is not impaired by removal of thorax (thoracic ganglia).

2. The mating instinct is dominant in unmated moths and in some way correlated with an inhibition of the ovipositing mechanism. This inhibition is reduced in the mated moth, functioning of the ovipositing mechanism then dominating. The inhibition is reduced in decapitated moths, as evidenced by the early response to stimulation.

3. Effectual mating takes place several days after decapitation of the female. It is impossible with the dethoraxed female.

4. In the presence of the brain or brain and thorax, reaction of the ovipositor to external stimulus is resisted. In the absence of the brain, or brain and thorax, spontaneous movements cease, but reaction of the reproductive mechanism to external stimulus is prompt and efficient.

5. The effectual stimulus is pressure and contact, this being a stimulus to which the normal silkworm moth is constantly subjected under normal conditions.

6. The time duration of the reflexes centered in the last abdom-

inal ganglion is much more limited in the decapitated or dethoraxed insect than in the normal insect. Repetition of stimulation causes repeated responses with no evidence of fatigue or decrease of functional activity until death ensues. There is neither awkwardness nor feebleness exhibited, neither is there evidence of augmentation.

7. Response of the ovipositor is initial and endures after all eggs have been oviposited, therefore entirely independent of the rest of the reproductive apparatus.

8. The posterior abdominal ganglion is the controlling center of the reproductive mechanism and exhibits a high degree of independent activity.

9. The reflexes of movement connected with the three anterior abdominal and the thoracic ganglia are coördinate with the reflexes of the ovipositing apparatus connected with the posterior abdominal ganglion.

In conclusion, it is apparent that while an intact nervous system is necessary for a prompt, efficient and continuous functioning of the reproductive system, in the absence of the head or head and thoracic ganglia, external stimulus brings about prompt, efficient and complete though not continuous reaction. In the absence of head or head and thorax, there is no apparent augmentation of the reflexes. This reaction is efficient if the posterior abdominal ganglion alone is intact. Corresponding ganglia in the anterior abdominal segments are not only reflex centers but centers of correlation as well.

# A STUDY OF THE CHOROID PLEXUS.

BY

WALTER J. MEEK.

(*From the Neurological Laboratory of the University of Chicago.*)

WITH NINE FIGURES.

With the exception of scant references in the standard anatomies, very little literature treating of the choroid plexuses is available to the general student. The literature dealing with the subject directly is not as full as one might wish, and in fact many questions of interest concerning these structures still remain unanswered. The object of the present paper is to review the subject briefly to date, and to present some results of the author's own investigations.

The writer's attention was called to the choroid plexuses by Dr. SHINKISHI HATAI at the University of Chicago. Dr. HATAI had noted that the position of the nucleus in the cells of the fœtal plexus was apical, while in the adult it was central.

The problem as first undertaken was to determine the time of this shifting of the nucleus, but as the work proceeded, it seemed best to prepare a brief study of the entire subject.

## TECHNIQUE AND MATERIAL.

Fixation of tissue is at best an unsatisfactory process, and doubly so when structures as delicate as the choroid plexuses are concerned. Slight differences of osmotic pressure cause shrinkage or swelling of the cell. Mechanical injury must also be avoided. The number of fixing fluids adapted to the plexuses is somewhat limited. The following were used, and the order indicates approxlimately their relative merit.

1. Bouin's fluid.
2. Carnoy's solution.
3. Acetic sublimate.
4. Potassium bichromate-corrosive sublimate solution.
5. Kopsch's fluid.

For small animals the best results were obtained by fixing the entire brain. In the case of larger forms, the lateral ventricles were opened to allow an easy access of the fixative. Often the plexus was left untouched on the floor of the ventricle while the overlying nervous matter was trimmed away. These devices all avoid mechanical injury, and they also preserve the position of the plexus in the ventricle. Only in the largest brains were the plexuses removed and fixed separately.

The period of immersion in the fixative is important. When an entire brain is fixed the average time required by the fixative may be allowed, but if the plexuses are exposed the length of time should be reduced to about one-third. In the case of CARNOY'S solution, about 20 minutes gave by far the best results.

The usual methods of embedding in paraffin and sectioning were employed.

Sections were cut 3 and 4 micra thick. Many different stains were used in the hope of differentiating various structures. The most satisfactory results were obtained with iron hæmatoxylin followed by acid fuchsin. Other stains, copper-chrome hæmatoxylin,[1] toluidin blue, erythrosin, VAN GIESON'S acid fuchsin, and EHRLICH'S triacid stain were used as controls, and for the sake of comparison.

On account of their accessibility and their size, the plexuses of the lateral ventricles were used exclusively. So far as known, the plexuses of the other ventricles are precisely the same in function and structure. Mammalian material was studied from the following forms: albino rat, rabbit, guinea pig, cat, dog, sheep and man.

## GENERAL MORPHOLOGY.

The choroid plexuses of the lateral ventricles are due to an ingrowth of the pia mater pushing the mesial wall of the hemispheres into the ventricles. The arachnoid is not supposed to be present, although the plexus is but a fringe of the velum interpositum, into the structure of which the arachnoid does enter. The neural wall is of course preserved, but consists only of a simple epithelium. The plexuses then are thin laminæ covered with an epithelium, beneath which is a connective tissue stroma containing an extraordinarily rich network of blood vessels.

In many animals, the laminæ are smooth, but in others, they are covered with projecting villi. Between these two extremes

---

[1] The formula for this stain was kindly given by Dr. BENSLEY of the Department of Anatomy, University of Chicago.

are to be found all the intermediate gradations. The guinea pig, mouse and rat possess plexuses that are smooth. Fig. 1 shows the cross section of a lateral plexus of a one day old rat. It will be noted that the surface is not entirely regular. There are projections and prolongations of the folds, but the typical villi are absent. In the rabbit, the laminæ are still more irregularly folded, but they are not villous. Villi are scarce in the chicken, duck and pigeon, but more abundant in the hog, while they reach a considerable development in the horse, ox, and especially among porpoises, crocodiles, and some of the selachians (PETTIT '02–'03). In the sheep, villi are numerous along the free edge of the plexus, but they are thick and short. In man, the villosities are also found but the type is somewhat intermediate. IMMAMURA ('02) states that the human plexus consists of two parts, a villous and a villus-free portion. There seems, however, to be much variation in this respect.

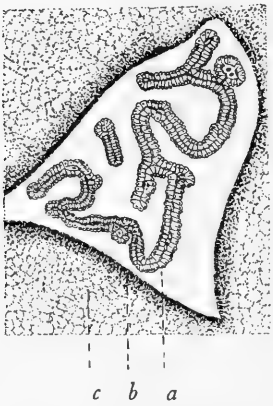


FIG. 1. Cross section through the right ventricle of a one day old rat. Magnification × 150. *a*, Plexus in ventricle; *b*, ependyma; *c*, nervous tissue.

The surface of the plexuses is much greater than one would suppose. FAIVRE ('54) has estimated it for the human plexuses in the lateral ventricles. He considers the average length as 7 centimeters, and the width as 2 centimeters. By estimating 40 villi to each square centimeter, he calculates that the surface would be increased about four times, making a total of 112 square centimeters for the two plexuses. We might add that since the folds hang freely in the ventricles, and are covered on all sides by the same epithelium and villi, that twice this number, or 224 square centimeters, is more nearly the total area of the free surface.

The blood supply of the plexuses in man is well known. Two-thirds is supplied by the anterior choroid branch of the internal carotid which enters the plexus at the anterior end of the descending cornu. The remainder is supplied by the postero-lateral choroid artery, a branch of the posterior cerebral. These arteries break up into arterioles, the largest of which are visible to the naked eye. After passing through the network of capillaries, the blood returns through the choroid vein to the V. cerebri interna which joins its fellow and forms the V. cerebri magna or vein of GALEN.

It is generally believed that the choroid plexuses are largest in the embryonic state, and that their volume diminishes as the brain reaches its full development. LOEPER ('04) states that in the human fœtus the plexuses are largest from the third to the sixth month, after which they decrease in size. Possibly a more accurate statement would be that after the sixth month they are outgrown by the other parts, and the decrease in size is only proportional. The HIS-ZIEGLER model for the three months human fœtus, shows the plexuses as large swollen glandular organs occupying practically all of the space in the lateral ventricles. Along with this presentation, has grown the idea that the plexuses furnish some kind of a fluid food necessary for the growth of the brain during the fœtal period. Accordingly, they have sometimes been called the "cerebral placenta."

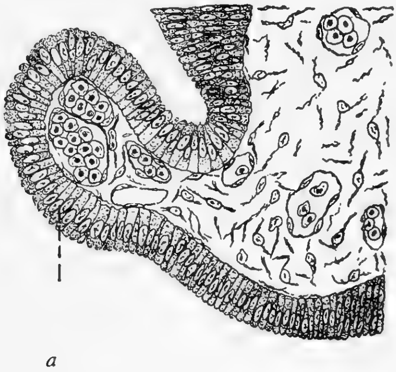


FIG. 2. Cross section through the brain of an embryo rat, showing the origin of the choroid plexus. Magnification × 500.

Whatever the facts may be in man,[2] it seems that the above description does not apply to all forms. Fig. 2 shows the begin-

---

[2] A recent reconstruction of the encephalon of a human embryo (length 22.8 millimeters, age approximately 2 months) by Dr. EWING TAYLOR, of the Universtiy of Pennsylvania, shows the plexuses of the lateral ventricles as much smaller and more folded than they appear in the HIS-ZIEGLER model of three months. A similar difference is shown by the model of the encephalon reconstructed from a slightly larger embryo (length 30 mm., approximate age 55 days) by Dr. G. L. STREETER of the Wistar Institute of Anatomy. In view of these results, the relations exhibited by the HIS-ZIEGLER model can hardly be considered as typical.

ning of the plexus in the albino rat. The exact age of this embryo unfortunately is not known, but the neural walls are thick and the ventricles large. In a two centimeter embryo rat, which has about the same brain development as a three months human fœtus, the plexus has elongated somewhat more than in Fig. 2, but it is not essentially different. From this time to birth, there seems to be a steady growth of the plexus, until the structure assumes the appearance of Fig. 1. At no time is there any evidence that the organ is enlarged or distended, or that it fills anything like all of the ventricular space.

## MICROSCOPIC HISTOLOGY.

I. *Examination of Living Tissue.*—From a freshly killed adult albino rat, the plexuses may be removed and examined in cerebrospinal fluid, or in normal salt solution. Often under these conditions the blood will continue to flow through the capillaries for several minutes. This circulation is due to a gradual shrinkage of the tissues and the weight of the cover slip, both of which aid in forcing the blood out of the ruptured capillaries. In case the arterioles are not clogged, this circulation may be in a reverse direction, since resistance would be less toward the open arterioles. Not a great amount of detail can be obtained in this way, still it serves as a control for the sections subjected to reagents.

Under low power, the plexuses of the rat appear as a thin, semitransparent membrane, which is threaded by an immense number of capillaries. The edges are somewhat sinuous, and these curves are closely followed by the blood vessels, so that the appearance is not unlike the scalloped edge possessed by many leaves. Under a high power, it is readily seen that the lamina consists of an upper and a lower layer of epithelial cells, with the blood vessels embedded between. Details are plainest at the edges. The cells are cuboidal, and can best be located by their nuclei, which appear as shadowy discs. The cell boundaries can be made out only with much difficulty. Occasionally on a flat surface, the ordinary mosaic appearance of the cell walls may be brought into focus. The apical plate or marginal zone of the cell is visible as a thin refractive line. The apical end of the cell is curved with the convexity outward. At times, the lateral cell walls may be detected, but not usually. The cytoplasm appears finely granular throughout. Very small refractive globules may be seen within it. No pigment has been noted in the rat's plexuses. The most careful examination has failed to show the presence of cilia *in the adult.* These are present in younger forms but it seems reasonably certain that cilia are not present in the adult. At the same time, cilia are often noticed in the adult on the ependyma, which has been torn from the ventricular walls. The ependyma, in certain portions, is ciliated at all ages.

The microscopic appearance of the plexuses of other forms is similar to that of the albino rat. In most forms, particularly the guinea pig, dog and rabbit, the marginal or apical zone of the epithelial cells seems more specialized. The rabbit's plexus is remarkable in being studded with clear drop-like spaces within the cells. These will be discussed more at length in the next section.

II. *Examination of Stained Material.* Under the influence of fixatives and stains, many other details of the cells are brought out. At best, there must be some distortion, but judging from the appearance of the fresh tissues it is believed that the most successful preparations are a fair representation of the structures in the fresh condition.

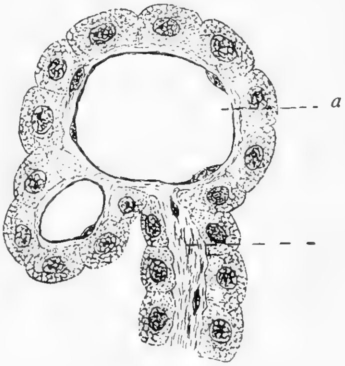


FIG. 3. Cross section of a portion of an adult rat's plexus. Magnification × 1500. *a*, Capillary; *b*, connective tissue.

Fig. 3 shows the cross section of a small loop of an adult rat's plexus. The two capillaries represented, show about the two extremes in size, the smaller being about 12 micra in diameter. The capillaries consist of a delicate endothelial intima, with elongated nuclei. This intima is strengthened by connective tissue cells and fibrils. FINDLAY ('99) considers this as an adventitial coat. Between this adventitial and the epithelium are more connective tissue cells and their processes. In young animals, lymphocytes are occasionally noticed.

The epithelium covering the plexus of the rat is composed of cubical cells, which in cross section average about 10–12 micra in width, and 8–10 micra in height. The basal wall is rather poorly defined. Often it is difficult to seperate the cell wall from the connective tissue beneath. The lateral walls of the cells are also obscure, but they may usually be identified by a hazy line. Under a low power, the cytoplasm appears finely granular and homogeneous, but with higher magnification, it is easily seen that it is finely reticular. In the meshes are deeply staining granules, which are often collected into small irregular masses. For the most part the reticulation is more pronounced near the periphery. Neither vacuoles, clear spaces of any kind, nor pigment granules have been found in the plexuses of the rat. The nuclei of the epithelial cells are oval or circular in outline, and centrally located in the adult. They average about 6 micra in diameter. Nucleoli are frequently present. The free edge of the cell is slightly convex. It consists of a thin apical plate or cuticle, which is not very apparent.

Embryologically the epithelial cells of the plexuses are derived from the inner layer of the neural tube which also produces the ependymal cells, and which is called the ependymal zone. The ependymal cells and the epithelial cells of the plexuses are therefore parts of the same layer. This may be plainly seen by tracing the plexus back to where its epithelial covering joins the ependyma lining the ventricle. Here the two types of cells pass into each other by an easy gradation. Fig. 2 illustrates this for the embryo, and the condition is not essentially different in the adult. It is generally conceded that the epithelium of the plexus has lost all vestiges of the neuroglia, which normally underlies the ependyma. CATOLA ('02), however, reports that he has found glia fibers by the WEIGERT method. So far as known, his observations have not been confirmed. The epithelial cells have also lost all projections from the base, a characteristic of so many ependymal cells.

There has been some discussion as to whether or not the epithelium of the plexuses consists of a single layer. HAECKEL ('60), HELDT ('74), DEJERINE ('95) and KÖLLIKER ('96) describe only a single layer. LUSCHKA ('55), however, recognizes several layers with transitional forms. HAECKEL admits that in pathological cases the cells may greatly increase in number. FINDLAY ('99) reports that there may be from one to four, or even more layers, and that the cells change in character as they pass from the basal layers toward the surface. He finds this condition in the sheep, calf, ox and man, and believes it occurs too frequently to be explained as pathological.

The writer's own results are decidedly in favor of there being but a single layer of the epithelial cells. In about 100 plexuses examined, there has never been the slightest suggestion of stratification. This refers, of course, to normal tissue. Pathological proliferation would be both likely and possible. No such cases, however, were noted. It may be that observers have been misled by oblique sections of some of the villi. It is not possible to have all of the tissue when it is covered with villosities, at right angles to the plane of section. In such a case, an oblique section might lead one to believe that the tissue had several layers of cells.

Intercellular spaces have been found in ependymal tissue by OBERSTEINER ('01), RENAUT ('99) and STUDNICKA ('00). RENAUT's idea is that the spaces are filled with a delicate cement substance, while STUDNICKA holds that they are true lymph spaces. STUDNICKA has found similar spaces between the epithelial cells of the choroid plexuses in the case of the shark, Notidanus cinereus. MILIAN ('04) and PETTIT and GIRARD ('02–'03), on the contrary, believe that normally the cells are closely appressed. They have noticed that such spaces increase in number as the result of poor fixation and post-mortem changes. They therefore regard them as due to changes in the cytoplasm, occasioned by faulty fixation, or post-mortem alterations. We have observed intercellular spaces in but a single specimen, that of a sheep's plexus, which had been fixed with the brain in formalin, the ventricles not having been opened. In freshly fixed tissue, there was not even a suggestion of spaces between the cells. There is no reason for doubting that the observations on the ependymal cells

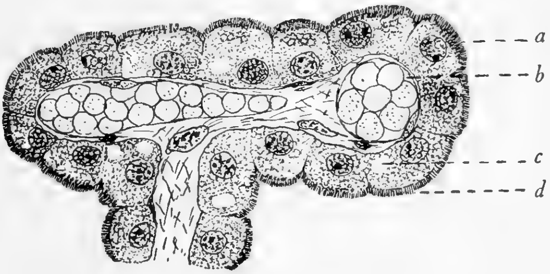


FIG. 4. Cross section of a portion of an adult rabbit's plexus. Magnification × 1500. *a*, Microsomes simulating basal bodies; *b*, capillary with blood corpuscles; *c*, clear space (fat droplet); *d*, marginal zone.

are correct, but the intercellular spaces do not occur between the epithelial cells of the plexuses, at least in the forms here studied.

Gold preparations show that nerves are present in the plexuses in the vicinity of the large blood vessels. BENEDIKT ('73 and '74) described nerves in the plexuses of the fourth ventricle, and thought he traced them into the vagus. FINDLAY ('99) found nerve fibers in the plexuses of man and the calf, by using a modification of HELLER's method. These fibers are probably vasomotor fibers to the blood vessels.

Fig. 4 shows the cross section of a small irregularity in the plexus of the adult rabbit. In regard to capillaries, connective tissue, and endothelium, it exhibits no particular difference from the plexus of the rat. The cytoplasm is somewhat more plainly reticular. Nucleoli are more evident, and often there is more than one present. The rabbit's plexus is especially characterized by the presence of circular or oval clear spaces. They are from 2–6 micra in diameter, and really much more numerous and noticeable than Fig. 4 could indicate. The contents are dissolved out by alcohol and xylol. In the ordinary stained sections they show as clear round or oval areas. The contents are of a fatty nature, for they readily stain with osmic acid or Sudan III. Fig. 5 is a cross section of a rabbit's plexus treated with osmic acid. It gives a fair idea of the number of the droplets and their position in the epithelial cells. The basal droplets are the smallest. Toward the apex of the cell, they gradually increase in size. Sometimes one may be seen lying half within, half without the cell. This shows that they are expelled through the top wall. During this process, the nucleus remains entirely unchanged, but rarely it is pressed to one side by the droplet. There is no evidence, however, that the discharge of the droplet is attended by the death of the cell. These fatty droplets have not been found in the normal plexuses of any other form studied. LOEPER ('04) speaks of small globules in the plexus of the guinea pig that stain with

FIG. 5. Section through an adult rabbit's plexus after staining in osmic acid. The protoplasm is faintly granular, and the droplets are stained black. Magnification × 500.

osmic acid, but he does not intimate that they are anything like the large droplets found in the rabbit. As before noted, these clear spaces can be seen in the fresh tissues even before the blood has ceased circulating. For this reason, it is not believed that they can be due to any error in technique or to post-mortem processes. Vacuoles have been mentioned in a general way as occurring in the typical cells of the plexuses, but to our knowledge, nothing similar to these clear areas has been described. It is not believed that they represent the chief secretion of the cells, since they have not been found in the other forms examined, and it is therefore best to consider them as of secondary importance.

A second feature in the rabbit's plexus is the development of the modified structures at the apex of the epithelial cells. In the rat, the marginal zone is at best but a double contoured line. In the rabbit, however, it is wider, and composed of filaments placed perpendicularly to the surface of the cell, and embedded in some kind of a matrix. This gives the cells the appearance of ciliation, but this cannot be confirmed by ciliary movements in the fresh tissue. The structure is what VIGNON ('01) describes as the "bordure de brosse" or filamentous plateau. At the base of the filaments are cytoplasmic microsomes, which take up the stain and simulate basal bodies. Terminal bars may be seen in cross section at the corner of the cells.

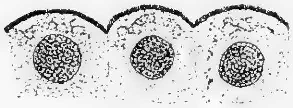


FIG. 6. Three cells from a dog's plexus. The animal was killed with illuminating gas, and the cells are in a resting state. Magnification × 1800.

Fig. 6 shows the epithelium of a dog's plexus. The stain is rather diffuse, and the reticulations show poorly, but it differs from the rabbit's in no particular way, except by the absence of the clear spaces or droplets. The epithelial cells of the guinea pig's plexus are somewhat peculiar in having a great many nucleoli. There are usually two or three, and often four or five. In other respects, the plexus is similar to that of the dog, as shown in Fig. 6.

The preceding description has referred entirely to the adult plexuses of the rat, sheep, rabbit and dog. If a late fœtal or a new-born specimen be examined, striking differences will be noticed. Fig. 7 is a section from a one day old rat. The epithelial cells differ from those of the adult in three particulars: Shape, staining power and location of the nucleus. A comparison with Fig. 3 from the mature rat, shows that in the one day form the cells are narrower and deeper. The long diameter is perpendicular to the base of the cell, while in the adult it is parallel with it. Many measurements give the following averages. Cells from the one day old plexus are 13 micra in height, and 8 micra in width. Cells from the adult are 9 micra in height, and 11.6 micra in width. This would indicate that the young cells were a trifle the smaller.

An interesting question here is: How does growth take place? The extent of the plexus is greater at maturity than it is at birth, and it is therefore necessary to account for the extension of the epithelial layer to cover the larger area of the adult plexus. A partial answer is contained in the fact shown above, that the adult epithelial cells are about one-third wider than those of the fœtal type and so cover about twice the area. This is possibly sufficient to account for growth from the fœtus to the adult. Growth might, however, take place in another way by a regular mitotic division of the epithelial cells. So far as known this has not been observed in epithelial cells of the plexus in late stages of growth, but it has been reported as occurring in the ependyma.

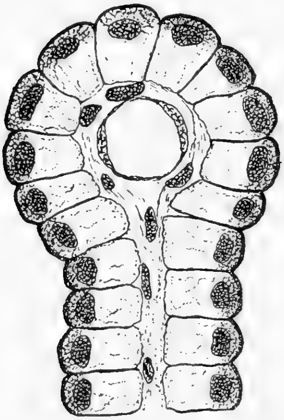


FIG. 7. Loop of a plexus from a one day old rat. The cells are high and narrow, and the nucleus is peripheral, and most of the protoplasm fails to stain. Magnification × 1500.

The location of the nucleus in the one day form is apical, while in the adult it is central or basal. In the former the nucleus is removed from the base of the cell by three-fourths the vertical diameter of the cell; in the latter, it is removed by one-half the vertical diameter.

The contents of the cell in the one day plexus are well nigh unstainable, at least by ordinary methods. The basal part of the cell shows a few radiating lines of microsomes, but it is for the most part clear. The nucleus stains deeply and so diffusely, that in only a few cells is its structure visible. Under favorable conditions of staining, reticulations are visible. Between the nucleus and the apex of the cell, the cytoplasm stains somewhat diffusely, but a reticulation with granules in the meshes can be made out.

The free margin of the cell shows double contoured lines. As the rat grows older, the cells gradually assume the adult type. Plexuses four days old show the nuclei removed by two-thirds the diameter of the cell from the base, and by the seventh day the position of the nucleus is similar to that in the adult. A change in the staining reactions of the cells occurs at the same time.

The primitive columnar condition of the epithelial cells is therefore retained until extra-uterine life is well begun. Whether this means that the cells do not function until this time cannot be said. It would certainly indicate that their work could not be the same as in the adult. This rapid change in the epithelium after birth seems to occur in the plexuses of other forms than the white rat. We have observed it in the rabbit and cat, and judging from STUDNICKA ('00, Plates XXXII, XXXIII), it occurs in man also.

## SECRETORY PHENOMENA.

Thus far we have studied the plexus in what might be termed its resting stage. Careful examination shows that in any adult plexus there are always some cells that have the appearance of secretory activity. It is to this phenomenon and its relation to the production of the cerebro-spinal fluid that we would now direct attention.

For many years there has been a suspicion that the choroid plexuses secreted, or at least aided in the secretion of the cerebro-spinal fluid, but the idea, until recently, remained without much supporting evidence. Even as late as 1901, CHARPY ('01) stated that the origin of the cerebro-spinal fluid was unknown.

Although the possibility had been mentioned the century before, it was E. FAIVRE ('54) who first definitely stated that the plexuses were probably concerned in the production of the fluid. LUSCHKA ('55) published an important monograph in which he produced evidence to show that the cerebro-spinal fluid could not be a transudate, and that it must be considered as a secretion produced by the membranes of the brain.

For many years no further evidence appeared. In 1897 PAUL CLAISSE and CHARLES LEVI ('97) reported a case of internal hydrocephalus, in which there was hypertrophy of the plexuses. There was a great amount of granulation, and the veins were dilated and gorged with blood. KINGSBURY ('97), while working on ganoid fishes, came to the conclusion that the columnar cells of the membraneous portions of the brain must be of use in the elaboration of the cœliolymph. He was led to this opinion by the many evidences of secretion shown by the cells. FINDLAY ('99), GALEOTTI ('97) and STUDNICKA ('00) all believed the plexuses secretory in function, and based their conclusions on the presence of secretory globules which will be discussed later. CAVAZZANI ('93) advanced negative evidence, by showing that lymphogogues did not affect the flow of the cerebro-spinal fluid. He therefore concluded that it was a secretory product of the epithelial cells.

To secure cerebro-spinal fluid, CAVAZZANI ('99) made use of a cerebro-spinal fistula between the first cervical vertebra and the occipital bone. CAPPELLETI ('01) used this fistula to study the effect of certain drugs on the flow of the fluid. He found that ethyl-ether and pilocarpin increase the flow, while atropin and hyoscyamin retard the flow, sometimes even to the point of suspending it. Of course these substances all have a vasomotor action, but pilocarpin and atropin are supposed to affect secretory cells directly. PETTIT and GIRARD ('02–'03) went a step farther by administering drugs, such as pilocarpin, muscarin and ether to animals, and then removing the plexuses to find whether there was any evidence of secretion. Their results have amounted almost to a demonstration of the origin of the cerebro-spinal fluid.

The writer has made experiments along the same line as CAPPELLETI and PETTIT and GIRARD. No claim is made for originality, but it is hoped that a brief description of the results may be of interest both as corroborative testimony and also because some of the forms used had not been studied by the investigators just mentioned.

The canula described by CAVAZZANI for his cerebro-spinal fistula is a rather complicated instrument. In practice it was found that with care a simple glass canula with a short rubber tube was satisfactory, at least for demonstrating the action of drugs. The musculature is cleaned away and the dura mater over the space between the atlas and the occipital bone laid bare. A small puncture is made and the canula inserted. The elasticity of the dura is enough to press the tissue against the tube, and thus avoid loss of fluid or entrance of blood. In etherized dogs, the insertion of the canula is followed by a rush of fluid. This is due to a secretion under the influence of the ether, and an accumulation of the fluid. A flow of about two drops per minute develops. If 1 per cent pilocarpin now be injected through the femoral vein the secretion becomes more marked, and may more than double in amount. An injection of atropin will abolish the secretion entirely.

It is realized that the account just given does not contain sufficient data. Many experiments should be made before definite statements are submitted, regarding the rate or amount of flow, or the time in which it develops. It is hoped that these omissions may be supplied in some succeeding paper. The important fact, however, seems perfectly clear, and that is, that the secretion of the cerebro-spinal fluid is accelerated by pilocarpin and retarded or abolished by atropin.

Microscopic examination has been made of the plexuses of dogs and rabbits that had been under the influence of ether for 20 minutes, and also of rabbits, guinea pigs, and rats injected with muscarin. The latter drug was most useful when diluted to 1–500. Two injections were made from 15–20 minutes apart, and 15 minutes later the animal was killed, and the plexuses removed. The injections were made with a hypodermic syringe, and no anæsthetic was given.

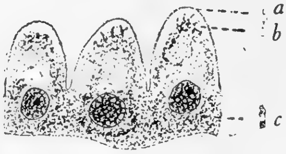


Fig. 8. Three cells from an adult rabbit's plexus after injection of muscarin. Magnification × 1500. *a*, Marginal zone which has become a thin granular line; *b*, clear spaces toward the apex; *c*, basal granular zone.

In the rat, muscarin did not give decisive results, but in the case of rabbits and guinea pigs the results were definite. Often as many as two-thirds of the cells showed evidences of secretion. Fig. 8 shows cells from a rabbit's plexus after treatment with muscarin. Normally, the epithelial cells in the rabbit are about 6 micra high (see Fig. 4) but here the height has increased to 12 micra. A differentiation into two zones, a basal granular, and an outer clear, is suggested, but it is not quite so well marked as in the figures of Pettit and Girard. The granulations, however, are always heavier and more compact toward the base of the cell. Clear spaces begin to appear toward the top, and rarely does the stainable cytoplasm extend to the upper cell wall. Masses of larger granules are common in the upper part of the cell where the lines forming the reticulations cross. The nucleus remains globular with a clear outline, in fact is not distinguishable from that of the resting cell. The two things most striking about these modified cells are their great increase in height, and the appearance of so much clear space at the distal side of the nucleus.

The apical structures of epithelial cells according to VIGNON ('01) take no part in the functional activity of the cell. In case of the extrusion of droplets, they may be pierced, but there is no change in their structure during the process. In the case of the rabbit, where there are fatty droplets, which we consider a secretion of secondary importance, we can find no evidence of any change in the marginal zone of the cell. The globules evidently pass out without anything more than rupturing the plateau, and this soon reunites. In the case of the typical secretion, however, the evidence seems to be that the marginal zone of the cell is modified. A comparison of Fig. 4 with Fig. 8, both from the rabbit, will show that the marginal zone of the resting cell has been transformed into a simple, thin, granular wall. We do not believe that the apical wall of the cell disappears during the secretion, but it is evidently considerably modified.

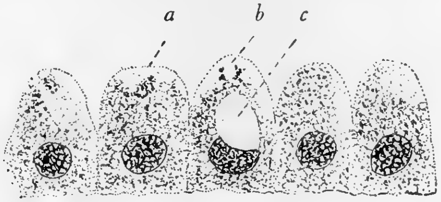


FIG. 9. Cells from a dog's plexus after ether anæsthesia. Secretory changes are to be noted Magnification × 1800. *a*, Marginal zone; *b* clear areas toward apex; *c*, fat droplet.

Fig. 9 shows secreting cells from a dog subjected to ether anæsthesia for 30 minutes. Fatty droplets have not been found in the normal epithelium of the dog's plexus, but it is seen that they appear after use of ether. The third cell from the left shows a large droplet which has compressed the nucleus. As in the preceding case, the cells are twice as high, the outer part of the cell contains many clear areas, and the marginal zone has been transformed into a simple granular line.

The mechanism of secretion, not only in the choroid plexus, but in general, has been a much discussed subject. In this connection, we may quote some observations on the vesicular theory. LUSCHKA ('55), FINDLAY ('99), STUDNICKA ('00) and GALEOTTI ('97) have all observed small globules within the epithelial cells of the plexus, and on the free surface of the plexus itself. These they have taken as evidence of the vesicular secretion by the epithelial cells. PETTIT and GIRARD ('02–'03) call attention to the fact that these globules increase in number with the time the tissue remains unfixed, and also with the slowness of fixation. These globules are analogous to the sarcode globules which are known to be due to post-mortem changes. These globules have been reported for fresh tissue, but they must have been due to mechanical injury. If any one will crush a fresh plexus under the microscope, he can see these structures form before his eyes. It would seem that in the choroid plexuses fatty droplets may be extruded in a way prescribed by the vesicular theory, but the normal secretion passes through the marginal zone in another way, possibly by some kind of canaliculi.

The chemical composition of the cerebro-spinal fluid has often been advanced as a proof of its being a secretion and not a transudate. HALLIBURTON ('89) has shown that it is peculiar and different from the lymph and blood serum in its proteids and in the presence of a reducing substance. The proteids are a globulin coagulating at 75° C. and albumoses and peptones. The reducing substance HALLIBURTON identified as pyrocatechin, but this identification does not seem to have been confirmed, later investigators reporting the presence of glucose. In the amount of sodium and potassium salts, there is but little difference from the blood serum.

The function of the cerebro-spinal fluid and its circulation are of interest, but related only indirectly to our subject, so we shall discuss them very briefly. The general idea has always been that the fluid is a nutritive solution to nourish the nerve cells with which it may come in contact. SPINA ('01) has shown that absorption of the cerebro-spinal fluid may take place, since fuchsin injected into the subdural spaces appears in the jugular vein. He concludes that the absorption is proportional to the pressure exerted on the fluid. The plexuses themselves, however, can scarcely be resorptive organs, for the blood pressure in the capillaries is too great to admit of it. Still it is not inconsistent to believe that the cerebro-spinal fluid may be absorbed to some extent by the walls of the ventricles, and thus reach the true nervous tissues. LEWANDOWSKY ('01) finds that an amount of strychnine so small that when injected into the blood there is no result, causes violent spasms if injected into the subdural spaces. From this he argues that the fluid bathes the nervous tissue and carries the poison directly to the nerve cells. There can be no doubt that the fluid is in intimate relation to the nervous tissues, nor that small amounts of poison might reach the nerve cells more surely by way of the subdural channels, than by the systemic blood stream, still the fluid can scarcely be distinctively nutritive. It is too poor in proteid. One function that it undoubtedly has is the purely mechanical one of supporting the nervous walls, preventing friction, and serving as a water bed for the brain and cord. This is probably its main function. PETTIT and GIRARD have suggested that it may also serve as some kind of an internal secretion, but for this suggestion no evidence has been presented.

Having been secreted, the cerebro-spinal fluid accumulates in the ventricles and their continuations, and in all the spaces beneath the dura. The connection between the ventricular cavities and the subdural spaces has been thought to be by means of the foramen of MAGENDIE and the two lateral foramina of the fourth ventricle. According to MILIAN ('04), some doubt seems to have been thrown on the presence of these foramina by the recent work of CANNIEU and GENTES. They consider the above mentioned foramina due to post-mortem changes, and in a number of cases the foramina could not be demonstrated. It is possible, then, that the manner of communication between the ventricles and the subarachnoid spaces is not yet definitely known. MILIAN ('04) and CATHELIN ('03) hold that the fluid reaches the lymphatic system from the subarachnoid spaces by means of the arachnoid sheaths around the nerves, the Pacchionian bodies and the perivascular lymphatic sheaths.

## SUMMARY.

The animals used in this study were the albino rat, guinea pig, cat, dog, sheep and man. The best microscopic preparations were made from material fixed in BOUIN'S or CARNOY'S solution, and then stained in iron hæmatoxylin and fuchsin. As a control, examination was made of fresh material either in cerebro-spinal fluid or in physiological salt solution.

The choroid plexuses are due to the invagination of the neural wall by the pia mater. They are thin laminæ with an epithelial covering, derived from the neural wall, a connective tissue stroma, and a rich supply of blood vessels. *Villi are absent in the rat,*[3] guinea pig, and mouse, but they are present in man, horse and ox. Villi are poorly developed in most birds, but they are especially well developed in the selachians and the crocodile.

In area, the plexuses have a greater free surface than would be supposed. This free surface is quite large enough to account for the secretion of the cerebro-spinal fluid.

*In the case of the albino rat, the plexuses increase in size gradually, from their first appearance, until they reach their maximum growth, and at no time do they seem to be relatively enlarged, or to fill all of the ventricular space.*

Microscopic examination of the fresh plexuses show that they are semi-transparent membranes, covered with ill defined cubical cells. The cytoplasm is finely granular. Cell walls and nuclei are dimly visible.

Stained material shows that the capillaries have an endothelial intima, which is strengthened by connective tissue. *The epithelial cells in the albino rat are 8–10 micra high, and 10–12 micra wide. The nuclei are oval or circular and after birth located basally or centrally. The cytoplasm is reticular with granules in the meshes. The free or apical edge of the cell is convex, and consists of a cuticle which is little developed in the rat,* but is more highly differentiated in the rabbit and dog, where it appears as a filamentous plateau. *In no case have cilia been found on these cells after birth.*

The epithelial cells of the plexuses have lost all basal projections which are characteristic of the ependymal cells from which they were derived.

*The epithelium consists of a single layer, and the cells are closely appressed without intervening intercellular spaces. In the case of the rabbit, many of the epithelial cells contain droplets of fat. These increase in size as they approach the apex of the cells, and appear to be extruded without causing a destruction of the cell from which they come.* Vasomotor nerves to the blood vessels have been reported by BENEDIKT ('73) and FINDLAY ('99).

*The epithelial cells of embryonic and young forms, differ from*

---

[3] Italics are used to indicate the results which are new, or to which the author believes he may have made some contribution.

*those of the adult, in being more columnar in shape, less easily stained, and in having the nuclei located nearer the cell apex. Soon after birth the cells rather rapidly assume the adult form. In the rat this is accomplished by the seventh day.*

Only recently has definite proof been offered that the plexuses are concerned in the secretion of the cerebro-spinal fluid. This proof rests on the following facts:

*The administration of ether, pilocarpin or muscarin, increases the flow of the fluid. Atropin or hyoscyamin retards the flow. After the administration of muscarin or ether, if the plexuses be removed, the epithelial cells will be found very much modified.*

*The apical portion has increased in height, and become clear, while the basal portion has remained granular.* In other words, they show changes characteristic of typical secreting cells. The fact that the flow of cerebro-spinal fluid is increased by injection of drugs that usually stimulate secretion in the epithelial cells, and that the cells themselves show secretory changes, justifies the conclusion that the fluid is secreted by the choroid plexuses. The ependymal cells may have their part in the production of the cerebro-spinal fluid, but it is certainly a minor one compared to that of the choroid plexuses.

Additional evidence that strengthens this conclusion is the occurrence of hypertrophy of the plexuses in certain cases of hydrocephalus. The fact that the fluid differs from the serum or lymph is also in favor of the view that it is a secretion.

## BIBLIOGRAPHY.

BENEDIKT.

'73. Ueber die Innervation des Plexus choroideus inferior. *Canstatt's Archives.*

CAPPELLETI, E.

'01. L'ecoulement du liquide cérébrospinal par la fistule céphalorachidienne en conditions normales et sous l'influence de quelques médicaments. *Archiv. Ital. de Biol.*, Vol. 36, pp. 299–302.

CAVAZZANI, A.

'93. Sur la circulation du liquide cérébro-spinal. *Archiv. Ital. de Biol.*, Vol. 18, p. 475.

CAVAZZANI, E.

'99. Die Cerebrospinalfistel. *Centralblatt für Physiologie*, Vol. 13, p. 345.

CATOLA, G.

02. Sulla presenza di neuroglia nella struttura du plessi coroidei. *Riv. di Patol. Nerv. e Ment.*, No. 9.

CHARPY.

'01. Traité d'anatomie de Poirier et Charpy. t. iii, p. 147.

CATHELIN.
'03. *Presse Médicale,* No. 90.
DEJERINE.
'95. Anatomie des Centres Nerveaux.
FAIVRE, E.
'54. Recherches sur la structure du conarium et des plexus choroideus chez l'homme et chez les animaux. *Comptes Rendus de l'Acad. Sciences,* Vol. 39, pp. 424–427.
FINDLAY, J. W.
'99. The choroid plexuses of the lateral ventricles of the brain. *Brain,* Vol. 22, pp. 161–202.
GALEOTTI, G.
'97. Studio morfologico e citologico della volta del diencefalo in alcuni vertebrata. *Riv. di Pat. Nerv. e Ment.* Vol. 12, pp. 480–517.
HAECKEL.
'60. Zur normalen und pathologischen Anatomie des Plexus choroideus. *Schmidt's Jahrbücher.*
HELDT.
'74. Ueber die Kalkoncretionen in den Plexus choroideus des menschlichen Gehirns. *Thesis.*
HALLIBURTON, W. D.
'89. Cerebro-spinal fluid. *Journ. Phys.,* Vol. 10, pp. 232–258.
IMMAMURA, S.
'02. Beiträge zur Histologie den Plexus choroideus des Menschen. *Arbeit aus dem neurologischen Institute an der Weiner Universität. Herausgegeben von Professor* H. OBERSTEINER, Fasc. 7, pp. 272–280.
KÖLLIKER.
'96. Handbuch der Geweblehre des Menschen.
KINGSBURY.
'97. The encephalic evaginations in ganoids. *Journ. Comp. Neurology,* Vol. 7, pp. 37–44.
LOEPER, MAURICE
'04. Sur quelque points de l'Histologie Normale et Pathologique des Plexus Choroides de l'homme. *Archiv. de Méd. Expérimentale,* Vol. 16, p. 473.
LUSCHKA.
'55. Die Adergeflechte des menschlichen Gehirns.
LEWANDOSKY.
'01. Zur Lehre von der Cerebrospinal-flüssigkeit. *Neurol. Centralblatt,* p. 497.
MILIAN.
'04. Le Liquide Céphalo-rachidien. *Paris.* 1904.
OBERSTEINER, H.
'01. Anleitung beim Studium des Baues der Nervosen Centralorgane im gesunden und kranken Zustande.
PETTIT A. ET J. GIRARD.
'02–'03. Sur la Fonction Secretoire et la Morphologie des Plexus Choroides. *Archiv. d'Anat. Mic.,* Vol. 5, pp. 213–264.
RENAUT, J.
'99. Traité d'Histologique pratique. t. ii, pp. 339 et 719.
STUDNICKA, A. K.
'00. Untersuchungen über den Bau des Ependyms der Nervösen Centralorgane. *Anat. Heft.,* Vol. 15, pp. 303–429.

SPINA, A.

'01. Untersuchungen über die Resorption des Liquors bei normalen und erhöhtem intercraniellem Druck. *Neurol. Centralblatt*, Vol. 20, p. 224.

VIGNON.

'01. Réchérches de Cytologie générale sur les Epitheliums. *Archiv. de Zool. Ex. et Gén.*, Vol. 9, p. 371.

The Journal of
Comparative Neurology and Psychology

Volume XVII JULY, 1907 Number 4

# THE TACTILE CENTERS IN THE SPINAL CORD AND BRAIN OF THE SEA ROBIN, PRIONOTUS CAROLINUS L.

BY

C. JUDSON HERRICK.

(*Studies from the Neurological Laboratory of Denison University, No. XXI.*)

With Fifteen Figures.

The nervous system of the gurnards (notably the European genus Trigla) has long been recognized as exhibiting points of special interest from the standpoint of functional differentiation. The brains of these fishes differ but little externally from the usual teleostean type, but the cephalic end of the spinal cord exhibits a series of segmentally arranged dorsal enlargements ("accessory lobes," Ussow) which receive huge nerve roots from the specially modified free rays of the pectoral fins. Since the demonstration by Morrill ('95) that in the allied American genus, Prionotus, the function of the free rays and their specially modified nerves is purely tactile and that neither gustatory sensation nor specially modified end-buds of any description are found upon them, the neurological interest of these fishes is enhanced. For it now appears that these lobes are simply enlargements of the dorsal cornua of the spinal cord and their associated fiber tracts and that they therefore exhibit an extraordinary development of the unspecialized somatic sensory system uncomplicated by any other modifications.

Through the kindness of Professor I. A. Field of Western Maryland College I have received a number of brains, with a portion of the spinal cord attached, of Prionotus carolinus from which serial sections were cut for me in the transverse and horizontal planes and stained by the method of Weigert by my former pupil Mr. P. S. McKibben, to whom I am also greatly indebted for assistance in other ways.

Morrill has figured an excellent dissection of the organs here under consideration in Prionotus carolinus, and also the histological details of the peripheral terminations of these modified spinal nerves; but the central connections of these nerves have not been analyzed microscopically so far as I know.

In Fig. 1 is given a sketch of the external form of one of my alcoholic specimens as seen from the left side. The spinal cord caudad of the so-called accessory lobes is considerably larger than is usual among the teleosts, the enlargement being confined chiefly to the dorsal and lateral parts (Fig. 2). The ventral funiculi and ventral commissure are as usual. The tractus spino-tectalis (fasciculus lateralis, Mayser, the tract which is continuous cephalad with the lemniscus of my nomenclature in former papers) is well-defined, but not greatly enlarged, immediately behind the accessory lobes; farther caudad it can with difficulty be distinguished from the adjacent fasciculi proprii. The latter region is enlarged and filled with fine medullated longitudinal tracts (fundamental lateral tracts). Farther laterally the ventro-lateral and dorso-lateral fasciculi are still more greatly enlarged, the fibers being larger and with denser sheaths, especially dorsally. The dorsal cornu and dorsal funiculus, which are very small in most telecosts, here comprise nearly one-half the total cross-section of the spinal cord. This region is made up of small bundles of medulated fibers separated by dense masses of unmedullated fibers or neuropil. Strong tracts pass obliquely laterally and ventrally between these masses and the dorso-lateral fasciculus and more diffuse fibers, chiefly unmedullated, to the fasciculi proprii (formatio reticularis) and dorsal commissure. At intervals, also, bundles of medullated fibers pass along the extreme external surface between the dorsal and ventral funiculi. These are uncrossed.

The longitudinal tracts in the dorsal funiculi are mostly short paths. Individual bundles as a rule do not long remain distinct, and medullated tracts leave them at frequent intervals to enter the fasciculus dorso-lateralis, where they appear to turn caudad, for the latter fasciculus increases in size and compactness for a time as it passes backward. Ultimately, however, it blends with the adjacent fasciculus ventro-lateralis and fasciculus proprius, as in teleosts generally. The tracts which I here term dorsal funiculi are apparently chiefly descending secondary fibers from the accessory lobes. It is doubtful whether either here or in the region of the accessory lobes there is any considerable true funiculus dorsalis as that term is used in higher vertebrates, though the scattered bundles of root fibers and secondary tracts which permeate the dorsal cornu and, farther cephalad, the accessory lobes in a general way correspond with the dorsal funiculi.

As the sections are followed toward the head, at the level of the fourth spinal nerve the grey matter of the dorsal cornu becomes still more greatly enlarged, the sensory root of this nerve terminating in the center of this dense mass of neuropil. Headward of the fourth nerve the dorsal cornu becomes more compact with bundles of well medullated fibers scattered within the neuropil, the whole complex occupying the dorsal third of the cross-section of the spinal cord. Large, medullated tracts of descending fibers run from the dorsal cornu into the dorso-lateral fasciculus and fasciculus proprius of the same and opposite side, the latter crossing in the dorsal commissure. Both dorsal and ventral commissures are very small in this region, the latter especially being no larger than usual in fishes with spinal cords of the usual form. As we approach the last (sixth) accessory lobe the medullated fiber tracts in the dorsal cornu increase in number, many of these fibers crossing in the dorsal commissure, which increases in size, and the grey matter accumulates chiefly at the dorso-lateral border, where it is overlapped by the accessory lobe, with which it becomes continuous a little further cephalad.

Meanwhile the dorso-lateral fasciculus has retained its original form and position, as have all of the more ventral structures; but the tract occupying the position of the dorsal funiculus is represented by a small area of compact medullated fibers bounded laterally by the dorsal cornu and accessory lobe, with both of which it is connected by transverse medullated fibers. A short distance farther headward the dorsal cornu fuses with the lateral border of the accessory lobe, the median portion of the lobe being free from the underlying tissue.

The accessory lobes vary somewhat in appearance in different specimens. Morrill follows Ussow ('82) and enumerates six of these lobes. Their number in Prionotus might be counted as one or two more or less depending upon whether account is taken of some of the shallower furrows. That they are really enlargements of the dorsal cornu and not adventitious structures is shown by their continuity caudad with these cornua, and by their relations with the dorsal roots which supply tactile sensibility to the free pectoral fin rays, and also by their secondary connections.

These outgrowths evidently arose from the dorso-lateral border of the spinal cord and then from broad pedicles at this point spread in mushroom form both mesially and laterally (Fig. 3). The enormous dorsal root of the third spinal nerve enters the lateral border of the fourth, fifth and sixth lobes and terminates within them.

Secondary tracts in large heavily medullated bundles pass from these accessory lobes ventro-laterally to descend in the fasciculus dorso-lateralis. The greater part of this tract caudad of this point is apparently derived from the sixth lobe, only a small proportion of the descending fibers of this tract coming from the spinal cord farther toward the head. Very large tracts of medullated fibers pass in the fasciculus dorso-lateralis between the fifth and sixth lobes, which are separated by a wide and deep furrow (Fig. 4). The dorsal commissure contains massive bundles of medullated decussating fibers in the inter-lobar spaces as well as in the regions of the lobes. These fibers run between the lobes and the opposite dorsal and dorso-lateral tracts.

As we pass cephalad under the fourth and fifth accessory lobes, the relations of the funiculus ventralis are little modified; the dorsal and ventro-lateral fascicles are somewhat enlarged; and the dorso-lateral very greatly so. This enlargement is due partly to fibers which run between the fifth and sixth lobes and also to large bundles of root fibers, which pass toward the head to end in the fourth and fifth lobes. These lobes, like the others, send tracts of medullated fibers downward to the ventral cornua and ventro-lateral fasciculi of the same side.

Between the fourth and third lobes (Fig. 5) the dorso-lateral funiculus shrinks to small dimensions—scarcely larger than in some other fishes, like Ameiurus. The tract which I have termed the funiculus dorsalis, however, maintains its large size. From these relations of the dorso-lateral fasciculus, which is evidently the chief path of communication between these tactile centers of the spinal cord, it appears that the fourth, fifth and sixth lobes, which receive the dorsal root of the third spinal nerve, constitute a functional unit, being more closely related with each other than with any structures above or below them. Within the third lobe the fasciculus dorso-lateralis rapidly increases again in size and a lateral protrusion of this lobe receives the dorsal root of the second spinal nerve (Fig. 6).

Between the second and third lobes the dorsal root of the second spinal nerve enters and distributes to both of these lobes. Between them the dorso-lateral fasciculus also increases to its maximum size, composed largely of dorsal root fibers of the second spinal nerve, some of whose fibers extend forward to the first lobe.

The first and second lobes are somewhat smaller than the others and are but indistinctly separated by a wide shallow groove. At a point near the cephalic end of the second lobe the grey mass of the lobe (dorsal cornu), which behind this point is separated like the other lobes from the lobe of the opposite side by a deep dorsal fissure, fuses across the median line (Fig. 7). This fusion, which at first involves only the second lobe, a little farther forward becomes overlapped by a similar fusion of the first lobe, the second lobe being thrust far forward embedded under the first (Fig. 8). In this way there are formed two commissural grey masses, a dorsal connected with the first lobe, and a ventral connected with the second lobe, both lying dorsally to the ventricle and both containing cells and medullated and unmedullated commissural fibers. These median grey masses constitute the somatic commissural nucleus and the fibers which decussate associated with them the somatic element of the commissura infima Halleri. The commissure is continuous caudad with the dorsal inter-lobar commissure already described. It is considerably enlarged at its cephalic end just behind the membranous roof of the fourth ventricle (Fig. 11). The somatic commissural nuclei in WEIGERT preparations resemble closely in structure the accessory lobes with which they are directly connected.

The first accessory lobe functions also as the nucleus of the spinal V tract. It is related with the fasciculus dorso-lateralis and with the scattered tracts which I have designated funiculus dorsalis and so may be regarded as sharing some of the functions of the nucleus funiculi, though the latter structure is separately represented in a well defined nucleus associated with the fasciculus dorso-lateralis.

The dorsal root of the first spinal nerve is small, entering the caudal end of the first accessory lobe. From the cephalic end of the second lobe a short and broad tract of medullated fibers passes ventrally into the formatio reticularis and dorso-lateral fasciculus (Fig. 9). Here most of the fibers seem to end in the large fasciculi proprii which fill this region and pursue only a short course headward or tailward. This tract is merely a concentration of a similar connection found in all of the lobes. The formatio reticularis, which under the other lobes is composed mostly of alba, here becomes somewhat more loosely aggregated, with large fasciculi proprii scattered through a grey field. The grey matter is nowhere extensive.

As the first accessory lobe merges with the medulla oblongata it shrinks in size and becomes enveloped dorsally by the fibers of the very large spinal V tract. Meanwhile the number of fibers in the dorso-lateral fasciculus diminishes, some passing into the formatio reticularis and others disappearing into a mass of grey which occupies the whole of the median part of the fasciculus (Fig. 10). This mass is the *nucleus funiculi.* From this nucleus a strong tract of heavily medullated internal arcuate fibers passes ventro-mesially, decussating in the ventral commissure, to reach the ventral funiculus and the ventral cornu of the opposite side at the level of the origin of the first ventral root of the first spinal nerve.

As we pass forward into the oblongata, just before the level of the vagal lobe is reached, the last vestige of the first accessory lobe disappears and the somatic commissural nucleus shows no longer any distinction between its dorsal and ventral portions. Massive medullated commissural tracts pass between the funicular nuclei of the opposite sides, greatly augmenting the most cephalic part of the commissura infima. There are also broad connections between these nuclei and the formatio reticularis of the same side and the ventral funiculi of the opposite side via the ventral commissure.

As we reach the level of the vagal lobe, more than half of the fasciculus dorso-lateralis has terminated in the funicular nucleus and this nucleus itself is rapidly replaced by the vagal lobe (Figs. 11 and 12). A considerable portion of the dorso-lateral fasciculus continues cephalad into the oblongata, apparently without interruption in the funicular nucleus region. These are probably ascending correlation fibers of the tactile system, since this tract is larger in this fish than in any other which I have examined and there is no enlarged structure in the oblongata from which its fibers may arise. There are also added to the ventral side of the ventro-lateral fasciculus large heavily medullated tracts which arise from the funicular nucleus and pass cephalad into the oblongata. These are believed to be in the main ascending correlation tracts for the same reason as those last mentioned. Some of these tracts enter the dorso-lateral fasciculus by way of the adjacent formatio reticularis.

Probably there are important descending secondary tracts from the funicular nucleus in the lateral and dorso-lateral fasciculi, but they are not separately distinguishable. Contrary to my expectations, neither the funicular nucleus nor any of the accessory lobes send large secondary tracts to the ventral funiculi. The very large internal arcuate tracts from the funicular nucleus nearly all terminate in the ventral cornu immediately adjacent. Nor do any large numbers of these secondary fibers ascend in the fasciculus lateralis (of MAYSER, "lemniscus," HERRICK), as was to have been expected by analogy with other fishes. In short, the enlargements represented in the accessory lobes represent a sensori-motor mechanism for the free rays of the pectoral fins, and these modifications do not extend far beyond the limits of the segments of the spinal cord directly involved in the innervation of these fins. The modifications of the spinal cord behind the "lobes" is more evident than that of the medulla oblongata in front of them. This doubtless is correlated with the fact that the sensory stimulation of the free rays is more apt to call forth swimming movements of the trunk and tail musculature than any cephalic reaction. The specialized apparatus of these free rays, then, is adapted for reflexes of only the simplest order.

A study of the series of excellent figures of Lophius given by KAPPERS ('06) reveals in the funicular nucleus region an arrangement very similar to that of Prionotus. The somatic sensory centers are much enlarged and are designated nucleus Rolandi and, farther caudad, lobus sensib. Probably these masses of grey include both my funicular nuclei and the spinal V nucleus. The commissura infima is no doubt chiefly somatic, the visceral centers being small in this fish.

The accessory lobes, as we have already seen, are enlarged dorsal cornua. The dorsal root of the first spinal nerve, which terminates in the first lobe, is, however, not greatly enlarged. The prime motive, then, for the development of this lobe is not the modification of the pectoral fin, but, rather to serve as the terminal nucleus of the spinal V tract, which is of very great size in Prionotus. In this fish the spinal V nucleus is a direct derivative of the dorsal cornu. The funicular nucleus is not closely related to the dorsal cornu (the grey matter of the "lobes"), but rather with the adjacent formatio reticularis. In both of these respects Prionotus agrees very closely with the morphological relations in Ameiurus (HERRICK '06), although the structural details are very different. The spinal V tract, as in other fishes, can be separately followed by reason of the heavier medullation of its fibers, into the spinal cord beyond the first spinal nerve, a remnant of it being recognized in Fig. 9.

As we pass forward into the oblongata from the funicular nucleus region, the first accessory lobe (dorsal cornu + nucleus of spinal V tract) disappears before the funicular nucleus, and the latter is enveloped dorsally by the spinal V tract, laterally by the dorso-lateral fasciculus and ventrally by the latter tract and massive bundles of the formatio reticularis alba, which farther forward become incorporated into the dorso-lateral fasciculus (Fig. 11). When the level of the vagal lobe is reached the funicular nucleus has entirely disappeared, its place being occupied by a very small substantia gelatinosa Rolandi. Here the spinal V tract receives a strong accession of descending fibers from the general cutaneous root of the vagus (Fig. 12), and there is added to the dorso-lateral fiber complex on its ventral side the ascending secondary gustatory tract from the vagal lobe. Whether there is a descending secondary gusatory tract from the vagal lobe represented in the fasciculus lateralis my preparations do not enable me to state. I find no clear evidence of it. Secondary vagus fibers clearly pass in large numbers to the formatio reticularis of the same side and others cross as internal arcuate fibers in the ventral commissure (Fig. 12). These are of fine caliber, like the other secondary vagus fibers, and can therefore be distinguished from the other and coarser fibers of this commissure which are derived from the substantia gelatinosa and tuberculum acusticum and belong to the secondary somatic sensory system. They arise from the whole extent of the vagal lobe, which is not obviously differentiated into various functional regions. They pass into the opposite formatio reticularis for the most part, apparently to effect connection with the dendrites of the nucleus ambiguus. Unlike the somatic commissural fibers, they do not appear to enter either the funiculus ventralis or the fasciculus lateralis. In this they differ from the secondary fibers which enter the ventral commissure from the lateral division of the vagal lobe in Gadus. In the latter species I have found ('07) that the cutaneous taste buds are innervated from a different part of the vagal lobe from those taste buds which lie in the mucous membranes of the mouth and pharynx, the secondary connections of the cutaneous, or "somatic," gustatory center passing through the ventral commissure to the opposite somatic motor centers by way of the funiculus ventralis. Prionotus, however, is not known to possess taste buds in the outer skin, nor does it react to gustatory stimuli applied to the skin (cf. HERRICK '04, p. 264), and since the secondary gustatory path from the vagal lobe to the opposite funiculus ventralis in Gadus is a special adaptation called forth by the cutaneous taste buds, we are not surprised to find that the commissural secondary gustatory tract terminates differently in Prionotus. The primary gustatory centers of Prionotus are not large, though their peripheral and central connections are of the typical form. The crossed secondary connection in the ventral commissure, though present in other fishes, is relatively larger in this species, a peculiarity which I am not able to explain.

The vagal lobes are extended caudad into the visceral commissural nucleus under the commissura infima Halleri in the typical teleostean way, though this nucleus is small and not clearly separated from the much larger somatic commissural nucleus (Fig. 11). The visceral commissural nucleus receives sensory root fibers from the vagus and sends a broad unmedullated secondary tract to the formatio reticularis. The visceral part of the commissura infima is diffuse and chiefly unmedullated.

The tubercula acustica are very large, but I find no indication of the commissural fibers which pass between them in the commissura infima, such as appear in Conger.

The general composition of the fasciculus dorso-lateralis proximally of the funicular nucleus has already been indicated. This tract, as I here define it, includes the whole dorso-lateral fiber complex and therefore more than is comprised in the "dorso-lateraler

Stränge" of GORONOWITSCH ('88, '96). The "System $\gamma$" of this author's descriptions comprises chiefly the ascending and descending secondary gustatory tracts. The descending fibers of the spinal V and spinal (general cutaneous) vagus roots occupy the most dorsal part of the cross-section of the dorso-lateral fasciculus. This tract is very large and more heavily medullated than the other fibers of this complex, so that its course can easily be separately followed to its terminus in the first accessory lobe of the spinal cord. The more ventral bundles of this fasciculus in the oblongata comprise tracts (probably mainly ascending) which pass between the first accessory lobe and the adjacent formatio reticularis alba and the funicular nucleus on the one hand and the formatio reticularis of the oblongata farther proximally, on the other hand. There are other tracts in this fasciculus which pass between the oblongata and lower regions of the spinal cord, but they are so confused with the shorter tracts that it is not possible to follow them separately for their entire length.

As the dorso-lateral fasciculus passes under the vagal lobe, it receives on its ventral side the fine fibered ascending secondary vagus tract in the way characteristic of teleosts in general (Fig. 12). Farther forward, at the level of the origin of the sensory IX root (Fig. 13), the fasciculus becomes very compact and deeply embedded in the substance of the oblongata under the massive tuberculum acusticum. Here the three chief elements mentioned attain about equal proportions in the area of the cross-section of the fasciculus, viz: the spinal V tract dorsally, the ascending secondary gustatory tract ventrally and between them fibers of the fasciculus lateralis of mixed character, probably mainly of the fasciculus proprius type, putting the accessory lobes of the spinal cord and the funicular nucleus into relation with the medulla oblongata. The greater part of the latter fibers break up in the formatio reticularis under the tuberculum acusticum.

*Tractus Cerebello-spinalis.*—There is, however, one important tract in the complex last mentioned, whose relations are more clearly brought out in these sections than in those of any other fish which I have examined. Its fibers are heavily medullated and on the average of greater diameter than those of the spinal V tract, with which they are closely associated. There is no possibility of confusing them with the latter fibers, nor with any others of the fasciculus lateralis complex, all of the remainder of these being smaller and more lightly stained in WEIGERT preparations. This tract can be clearly followed between the granular layer of the body of the cerebellum dorsally of the superior secondary gustatory nucleus (Fig. 15) and the spinal cord in the funicular nucleus region. It retains its individuality perfectly as far back as the vagal lobe (Figs. 13 and 14); but in this region its outlines become somewhat confused with those of the spinal V tract and other elements of the dorso-lateral fasciculus. It can, however, be separately distinguished, though its outlines are not clearly defined, as far as the funicular nucleus (Figs. 11 and 12). I have no doubt that it extends far back in the spinal cord in the fasciculus dorso-lateralis below the accessory lobes, as figured by EDINGER ('96, p. 61, Fig. 30) for Trigla, though I am not able to follow its fibers separately. Whether the direction of conduction is ascending or descending, I am not able to state. In other fishes where I have found a spinal cerebellar tract it lies farther laterally and ventrally in the oblongata. Except in Ameiurus, where I have described it ('06, p. 413) under the name tr. spino-cerebellaris. I am unable to account for its association with the spinal V tract in Prionotus, nor even to assert positively its homology with the more lateral tract of other fishes.

## CONCLUSION.

The six "accessory lobes" or dorsal swellings of the cephalic end of the spinal cord of Prionotus are simple enlargements of the dorsal cornu evoked by the highly differentiated tactile organs on the free finger-like rays of the pectoral fins. The first spinal nerve is but little enlarged, but the dorsal roots of the second and third are greatly so and give rise to the second to sixth accessory lobes.

The first lobe receives the first spinal nerve, very large spinal V and spinal X tactile roots and secondary fibers of the fasciculus proprius type from the accessory lobes farther caudad. The second spinal nerve terminates in the second and third lobes, which are broadly connected by short secondary tracts in the fasciculus lateralis. The third spinal nerve terminates in the fourth, fifth and sixth lobes, which are closely bound together by massive short secondary tracts, as are the second and third. But between the third and fourth lobes these short tracts (fasciculi proprii) are relatively very feebly developed. From the sixth lobe massive tracts run caudad in the spinal cord, which is much larger than usual among teleosts, though the remaining nerves are not greatly enlarged. This enlargement is seen in the dorsal, dorso-lateral and ventro-lateral tracts, including the funiculi proprii, but does not involve the ventral funiculi. This would imply that reflex movements of the trunk musculature habitually follow tactile stimulation of the free pectoral fin rays, an inference which is substantiated by observations made on the living fish. But as we pass toward the head from the first accessory lobe, there is evident very little modification of the central nervous system due to the enlargements of the spinal cord. These facts show that the reflexes connected with the free pectoral fin rays are of the simplest type, not involving extensively the higher cranial centers.

The relations described in the preceding paragraph seem to be merely a special case under the general rule formulated by SHERRINGTON ('06), where he says (p. 58), "Broadly speaking, the degree of reflex spinal intimacy between afferent and efferent spinal roots varies directly as their segmental proximity. * * * The spread of short spinal reflexes in many instances seems to be rather easier tailward than headward. * * * Taken generally for each afferent root there exists in immediate proximity to its own place of entrance in the cord (*e. g.*, in its own segment) a reflex motor path of as low a threshold and of as high potency as any open to it anywhere." It is possible, too, that if an analogous relation holds in the spinal cords of higher vertebrates, it may have some bearing on the further fact brought out by SHERRINGTON (p. 241), that "spinal shock appears to take effect in the aboral direction only."

Associated with the first and second accessory lobes are the large somatic commissural nucleus and commissura infima. A short distance headward from this lobe there is a very highly developed median funicular nucleus, the lateral nucleus not being differentiated. This nucleus sends massive medullated tracts into the commissura infima.

The secondary connections of these extensive somatic sensory centers at the lower end of the oblongata are mainly with the adjacent formatio reticularis, ventral cornua and dorso-lateral fasciculus. No unusually large numbers of long tracts descend in the ventral funiculi or ascend in the crossed fasciculus lateralis (tractus spino-tectalis or "lemniscus"). This again illustrates the essentially local character of the chief reflex paths associated with the tactile system. There is a cerebellar connection of the funicular nucleus region which is stronger than in any other teleost which I have examined.

The visceral sensory centers of Prionotus are rather poorly developed, though the visceral commissura infima and commissural nucleus have the typical teleostean relations.

## LITERATURE CITED.

EDINGER, L.

Vorlesungen über den Bau der nervösen Centralorgane des Menschen und der Thiere. 5 Ed. *Leipzig.* 1896.

GORONOWITSCH, N.

Das Gehirn und die Cranialnerven von Acipenser ruthenus. *Morph. Jahrb.*, vol. 13. 1888.

Der Trigeminofacialis-Complex von Lota vulgaris. *Festchr. f. Gegenbaur*, vol. 3. 1896.

HERRICK, C. JUDSON.

The organ and sense of taste in fishes. *Bul. U. S. Fish Commission for 1902.* 1904.

The central gustatory paths in the brains of bony fishes. *Journ. Comp. Neurol. and Psych.*, vol. 15, no. 5. 1905.

On the centers for taste and touch in the medulla oblongata of fishes *Journ. Comp. Neurol. and Psych.*, vol. 16, no. 6. 1906.

A study of the vagal lobes and funicular nuclei of the brain of the cod-fish. *Journ. Comp. Neurol. and Psych.*, vol. 17, no. 1. 1907.

KAPPERS, C. U. A.

The structure of the teleostean and selachian brain. *Journ. Comp. Neurol. and Psych.*, vol. 16, no. 1. 1906.

MORRILL, A. D.

The pectoral appendages of Prionotus and their innervation. *Journ. Morph.*, vol. 11, no. 1. 1895.

SHERRINGTON, C. S.

The integrative action of the nervous system. *New York.* 1906.

USSOW.

De la structure des lobes accessoires de la moelle épinière de quelques poissons osseux. *Arch. de biol.*, tom. 3. 1885.

Fig. 1. The central nervous system of Prionotus carolinus seen from the left side. Drawn from an alcoholic specimen which had been fixed in potassium bichromate and designed to illustrate the relations of the spinal nerve roots to the six "accessory lobes" of the spinal cord (*lob. 1* to *lob. 6*). The cranial nerve roots are indicated with Roman numerals; *t. ac.*, tuberculum acusticum. × 3.

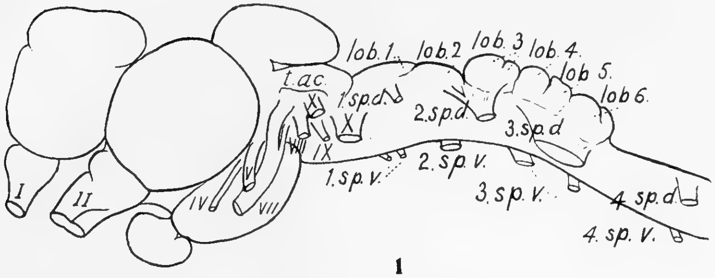
Figs. 2 to 15. A series of transections through the spinal cord and medulla oblongata of an adult Prionotus carolinus, from sections stained by the method of Weigert. All are drawn to the same scale. × 12.

Fig. 2. Section between the fourth and fifth spinal nerves. Areas of unmedullated fibers and neuropil are stippled. The enlarged dorsal cornu fills nearly the whole of the dorsal part of the spinal cord.

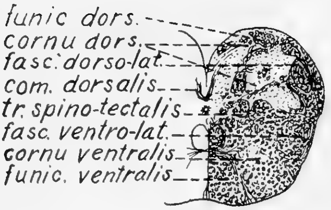
Fig. 3. Section through the middle of the sixth accessory lobe (dorsal cornu), showing the entrance of fibers of the dorsal root of the third spinal nerve. The fibers marked *desc. sec. tracts* are secondary tactile tracts which descend from the sixth lobe and enter the funiculus dorsalis and fasciculus dorsolateralis farther caudad. The more medial of the tracts thus designated extends backward to become continuous with "*funic. dors.*" of Fig. 2.

Fig. 4. Section taken between the fifth and sixth accessory lobes, including the most cephalic tip of the sixth lobe. This also disappears, a few sections farther forward, leaving the dorsal cornu practically unrepresented in the section. The dorso-lateral fasciculus is very large, containing, in addition to root fibers of the third spinal nerve, massive medullated tracts between the fifth and sixth lobes.

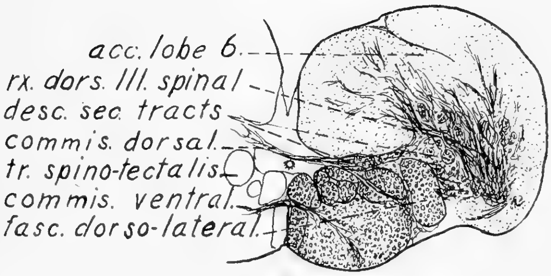
Fig. 5. Section taken between the third and fourth accessory lobes. In comparison with Fig. 4, taken between the fifth and sixth lobes, note the great reduction of the dorso-lateral fasciculus. The large size of this fasciculus between the fifth and sixth and fourth and fifth lobes is due to the facts that the third spinal root passes by way of this tract into each of these three lobes and that very large secondary tactile tracts pass between them. No root fibers pass between the third and fourth lobes and relatively few secondary fibers. This indicates that each spinal root supplying the free fin rays is an independent reflex mechanism within the spinal cord.


lob.1.
lob.2
lob.3
lob.4.
lob 5.
lob 6.
t.ac.
X
1.sp.d.
X
2.sp.d.
3.sp.d
VII
IX
V
1.sp.v.
2.sp.v.
3.sp.v.
4.sp.d.
4.sp.v.
I
II
IV
VII

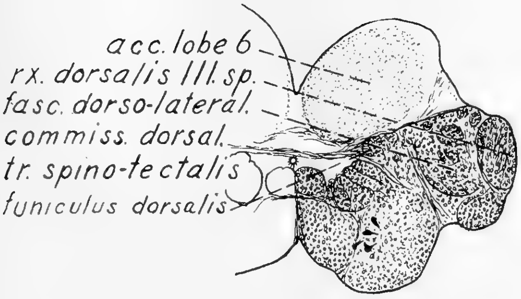
1


funic dors.
cornu dors.
fasc. dorso-lat.
com. dorsalis
tr. spino-tectalis
fasc. ventro-lat.
cornu ventralis
funic. ventralis

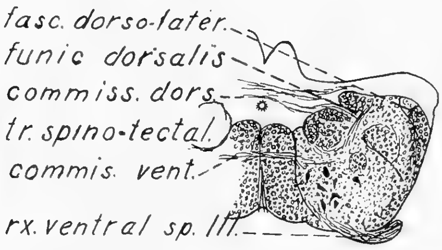
2


acc. lobe 6.
rx. dors. III. spinal
desc. sec. tracts
commis. dorsal.
tr. spino-tectalis
commis. ventral.
fasc. dorso-lateral.

3


acc. lobe 6
rx. dorsalis III. sp.
fasc. dorso-lateral.
commiss. dorsal.
tr. spino-tectalis
funiculus dorsalis

4


fasc. dorso-later.
funic dorsalis
commiss. dors.
tr. spino-tectal.
commis. vent.
rx. ventral sp. III.

5

FIG. 6. Section taken through the caudal end of the second lobe, including a portion of the dorsal and ventral roots of the second spinal nerve. The dorso-lateral fasciculus at this level is composed partly of root fibers and partly of massive secondary tactile tracts between the second and third lobes. Secondary tactile tracts pass from the grey matter of the lobe to this fasciculus and to the ventral cornu and fasciculi proprii adjacent.

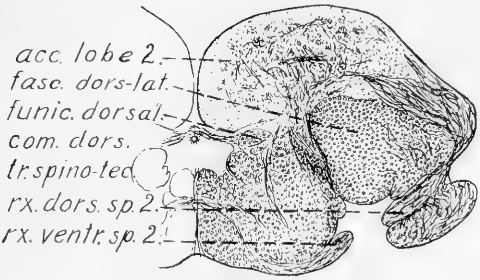
FIG. 7. Section through the cephalic end of the second lobe, showing overlapping first lobe and the caudal end of the somatic commissural nucleus (*comm. nuc.*) and contained dorsal commissure, which from this point toward the head may be termed the somatic commissura infima.

FIG. 8. Section .225 mm. farther toward the head through the somatic commissural nucleus (*comm. nuc.*). This nucleus is divided into dorsal and ventral parts, each with a fascicle of medullated commissural fibers. A vestige of the second accessory lobe surrounded by medullated secondary tactile fibers (cf. Fig. 9) is embedded in the substance of the first lobe.

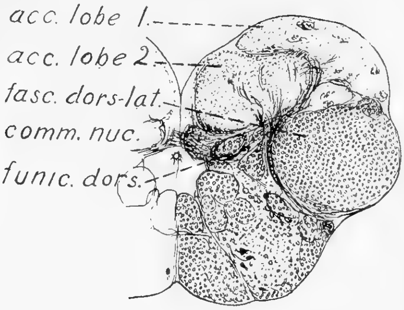
FIG. 9. Section .225 mm. farther toward the head, showing dorsal and ventral portions of the somatic commissural nucleus and their commissures (designated *com. inf. d.* and *com. inf. v.*, respectively). The more dorsal fibers, designated *sec. t. tr.*, are secondary tactile tracts from the cephalic end of the second accessory lobe (cf. Fig. 8); the more ventral ones are short tracts of similar character passing between the first and second lobes (fasciculi proprii).

FIG. 10. Section through the cephalic end of the first lobe and somatic commissural nucleus, the latter still showing the division into dorsal and ventral portions. The spinal V tract occupies the dorsal part of the section and is sending terminal filaments into the first lobe, which thus serves as nucleus spinal V as well as dorsal cornu for the first spinal nerve (cf. Fig. 9). The nucleus funiculi appears at this level and receives terminals of the dorso-lateral fasciculus, embedded within whose fibers it lies. Large secondary tactile tracts spring from the funicular nucleus and cross in the ventral commissure (*sec. t. tr. cruc.*), terminating mainly in the adjacent ventral cornu. Some turn caudad in the ventral funiculi, and probably a smaller number join the tractus spino-tectalis (*tr. sp. tect.*) to form the fasciculus lateralis, or lemniscus, though the latter are not numerous. Uncrossed secondary tactile tracts (*sec. t. tr. rect.*) of the fasciculus proprius type enter the formatio reticularis from both the spinal V nucleus and the funicular nucleus. The nucleus ambiguus (*nuc. amb.*) appears at this level and the canalis centralis begins to dilate into the fourth ventricle.

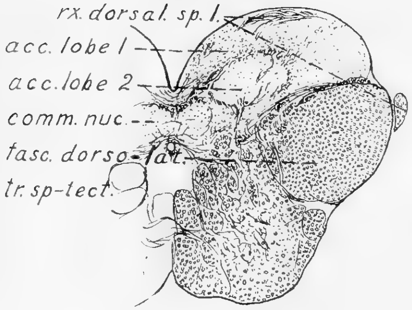
FIG. 11. Section through the visceral commissural nucleus and nucleus funiculi. The first accessory lobe and spina V nucleus lie farther caudad and the fasciculus dorso-lateralis is terminating in the nucleus funiculi. The most cephalic part of the somatic commissura infima (*com inf.*) is shown passing between the funicular nuclei. Ventrally of it is the visceral commissural nucleus which contains no medullated commissural fibers, though diffuse unmedullated tracts cross the median line. At this level this nucleus receives the most caudal sensory vagus root (*rx. sens. vagi.*) The motor vagus root arises from the nucleus ambiguus farther ventrally. Medullated secondary tactile tracts arising in the nucleus funiculi cross in the ventral commissure (*sec. t. tr. cruc.*) to reach the ventral cornu and ventral funiculi. From this level forward the tractus cerebello-spinalis (*tr. cereb. sp.*) can be distinguished from the spinal V and adjacent tracts.


acc. lobe 2.
fasc. dors-lat.
funic. dorsal.
com. dors.
tr. spino-tec.
rx. dors. sp. 2.
rx. ventr. sp. 2.

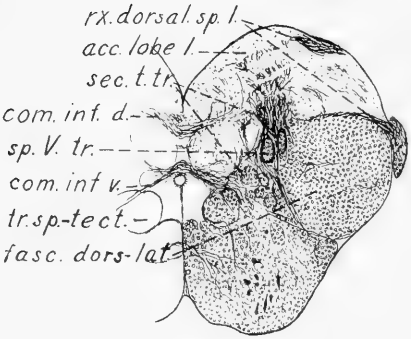
6


acc. lobe 1.
acc. lobe 2.
fasc. dors-lat.
comm. nuc.
funic. dors.

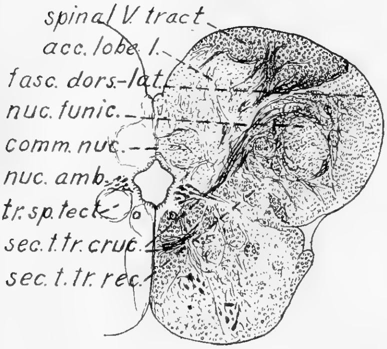
7


rx. dorsal. sp. 1.
acc. lobe 1
acc. lobe 2
comm. nuc.
fasc. dorso-lat.
tr. sp-tect.

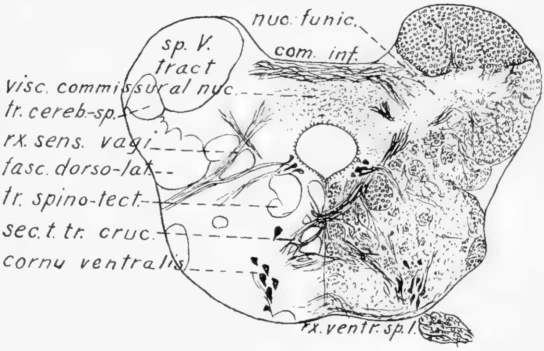
8


rx. dorsal. sp. 1.
acc. lobe 1.
sec. t. tr.
com. inf. d.
sp. V. tr.
com. inf v.
tr. sp-tect.
fasc. dors-lat.

9


spinal V. tract.
acc. lobe 1.
fasc. dors-lat.
nuc. funic.
comm. nuc.
nuc. amb.
tr. sp. tect.
sec. t. tr. cruc.
sec. t. tr. rec.

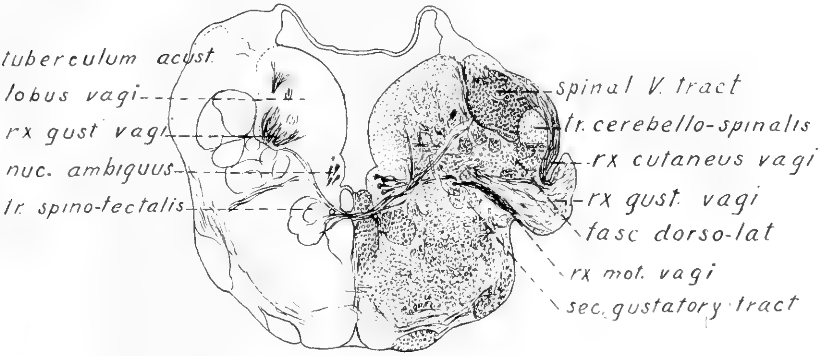
10


nuc. funic.
com. inf.
sp. V. tract
visc. commissural nuc.
tr. cereb-sp.
rx. sens. vagi
fasc. dorso-lat.
tr. spino-tect.
sec. t. tr. cruc.
cornu ventralis
rx. ventr. sp. 1.

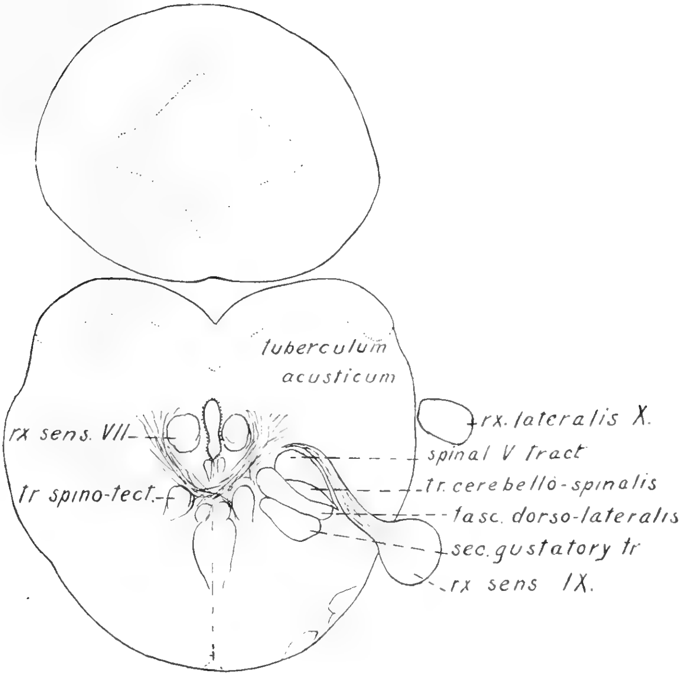
11

Fig. 12. Section through the vagal lobes. The section is slightly inclined, the left side being farther toward the head and including the extreme caudal tip of the tuberculum acusticum. On the right side the general cutaneous root of the vagus is seen entering the spinal V tract dorsally of the gustatory vagus root for the vagal lobe. The small amount of grey among the fibers of the dorso-lateral fasciculus is an extension from the funicular nucleus (cf. Fig. 11).

Fig. 13. Section through the tuberculum acusticum to illustrate the composition of the fasciculus dorso-lateralis at the level of the origin of the IX nerve. Dorsally are the spinal V tract and the tractus cerebello-spinalis; ventrally is the ascending secondary gustatory tract. The fibers between, designated *fasc. dorso-lateralis*, are fasicuclus lateralis fibers of mixed character, between the oblongata and the spinal cord.


tuberculum acust.
lobus vagi
rx gust vagi
nuc. ambiguus
tr. spino-tectalis
spinal V. tract
tr. cerebello-spinalis
rx cutaneus vagi
rx gust. vagi
fasc dorso-lat
rx mot. vagi
sec. gustatory tract

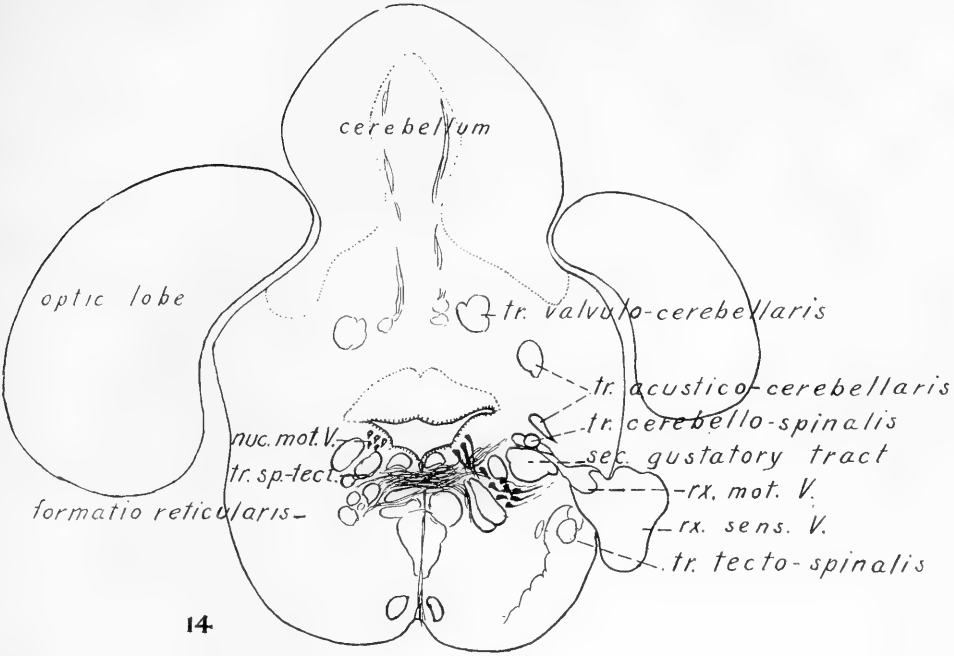
12


tuberculum acusticum
rx sens. VII
tr spino-tect.
rx. lateralis X.
spinal V tract
tr. cerebello-spinalis
fasc. dorso-lateralis
sec. gustatory tr
rx sens IX.

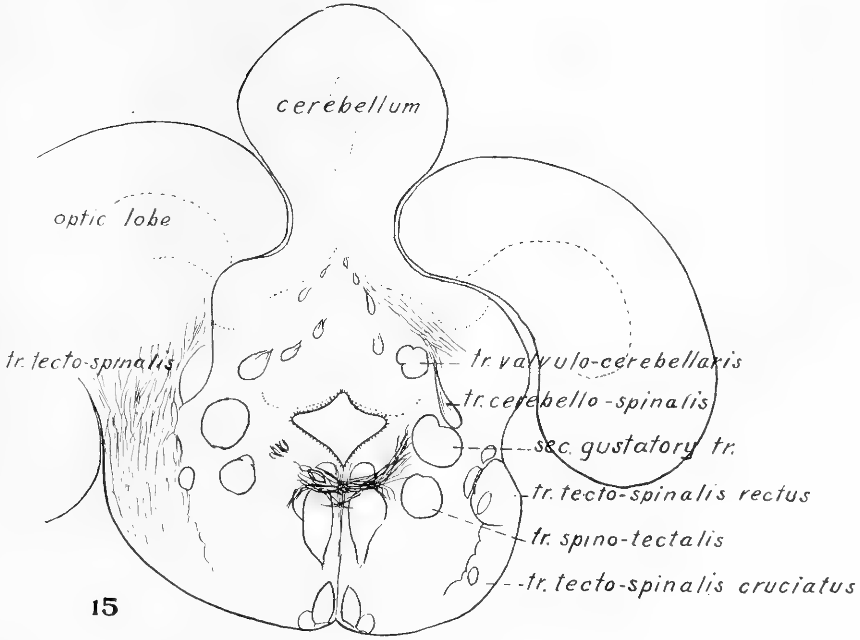
13

FIG. 14. Section at the level of the origin of the trigeminus. The elements of the dorso-lateral fasciculus as shown in Fig. 13, have disappeared in the oblongata farther caudad, for the most part, except the tr. cerebello-spinalis and the secondary gustatory tract from the vagal lobe.

FIG. 15. Section through the body of the cerebellum, illustrating the relations of the tractus cerebello-spinalis in the granular layer.


cerebellum
optic lobe
tr. valvulo-cerebellaris
tr. acustico-cerebellaris
tr. cerebello-spinalis
sec. gustatory tract
nuc. mot. V.
tr. sp.-tect.
rx. mot. V.
rx. sens. V.
formatio reticularis
tr. tecto-spinalis

14


cerebellum
optic lobe
tr. tecto-spinalis
tr. valvulo-cerebellaris
tr. cerebello-spinalis
sec. gustatory tr.
tr. tecto-spinalis rectus
tr. spino-tectalis
tr. tecto-spinalis cruciatus

15

# AN EXPERIMENTAL STUDY OF AN UNUSUAL TYPE OF REACTION IN A DOG.

BY

G. VAN T. HAMILTON, M.D.
(*McLean Hospital, Waverley, Mass.*)

WITH TWO FIGURES.

These experiments were undertaken in the interests of a problem suggested by such instances of animal behavior as are with difficulty, or not at all, interpretable in terms of instinct or of associative memory, and which may be ascribed to accident or not, according to the sympathies and viewpoint of the observer.

The practical difficulties in the way of limiting, regulating and repeating the stimuli that seem to produce unusual adjustments render the always objectionable apparatus necessary to a sufficiently critical investigation of such a problem; but negative conclusions drawn from results obtained by apparatus experiments cannot properly include a denial of the possibility that such animals as habitually solve their problems by the "trial and error" method of reaction (where instinct does not serve) may, under exceptional circumstances, display a type of reaction which stands higher in the scale of modifiability of behavior. Simplicity of an experimental situation calls for like simplicity of reaction to it on the part of the animal; and any artificial complication of an already artificial situation is apt not to be in line with his general reactive tendencies.

It is to be regretted that, owing to the requirements of my method, I was unable to use more than one animal throughout the 600 experiments; but the efficiency of this method, and the suggestiveness of the results obtained by its use will justify, I hope, the report that is to follow. The subject, a bull terrier of mixed breed, was about four months old when he came into my possession. At that time he knew no tricks whatsoever, had never been trained, and was not used to people and houses. Since then he has had no tuition except what has been necessary to overcome certain objectionable habits. Although he has done the usual number of things that are ascribed to "reason" by the uncritically sympathetic, his everyday life has afforded no behavior that instinct, associative memory or accident will not explain.

Early in his career he was familiarized with a simple apparatus which was equipped with four suspended blocks of wood, one of which, if clawed, would release a door which led to food. These blocks were placed in various positions in the cage, alternately attached to the door-release, and labeled in some manner. Thus, colored cards were scattered about the cage, and a white one was always placed on the block that was attached to the door-release. This was merely for the purpose of making experimental situations a part of his daily life; and especially, to insure that later they would not excite fear or aversion. To a playful, well fed puppy all this meant a good time, food, objects to be chewed up, and the presence of his master after an all day absence, whether he succeeded or not in getting out of the cage. If he did succeed many added and unusual pleasures awaited him, and no suggestion of penalty for failure entered into the game.

This preparatory work extended over several months, and in the end afforded me a subject so well fitted for the formal experiments that the reaction-value of the experimental situations was far greater, I think, than is usually obtainable by ordinary experimental methods.

*Description of apparatus.*—(1) A wooden frame, 4 feet wide, 5 feet long, 2¼ feet high was covered with coarse wire netting, as was also the lid. (See Fig. 1.) (2) A door (*A*), 1 foot high, 26 inches wide, fitted with a spring to pull it open when the button (*B*) which held it closed was turned. (3) Four wooden pedals (*D*) which were passed through slots in the rear baseboard, and hinged to a floor railing 11 inches to the rear of this. These pedals were held in a slanting position (anterior ends directed upwards) by means of wire springs. Very slight pressure upon their anterior ends was sufficient to move them toward the floor. (4) Four strings, each of which was attached to a pedal at the point of its emergence from the cage; from there the individual string was carried upward to the series of horizontal rings that carried all four strings to a trigger (*C*) at the left side of the cage. The trigger itself, when sprung, released a spring, which in turn pulled the button aside, thus releasing the door.

By hooking a given string to the trigger the pedal from which it came was thus attached to the door-release. (5) Four "pedal cards" (*F*), which were simply heavy wooden boards, 4 inches wide by 11 inches high; they were furnished with two legs each, which fitted into slanting holes in the pedals in such a manner as to give them an upright position when in place. Each pedal card had a different colored paper pasted upon its anterior surface, viz: black, red, green and yellow. (6) Four pairs of odor cards (*G*); these were small wooden paddles with cotton tacked to their anterior surfaces. Each of these was kept saturated with a drug having a distinctive odor, viz: asafœtida, lupulin, castor oil and beef extract. (7) Four wooden sign boards (*E*), 11 inches wide, 3 feet long. Their anterior surfaces were covered with papers matching in color those of the cards. (8) One white sign board and pedal card, and three plain pedal cards.

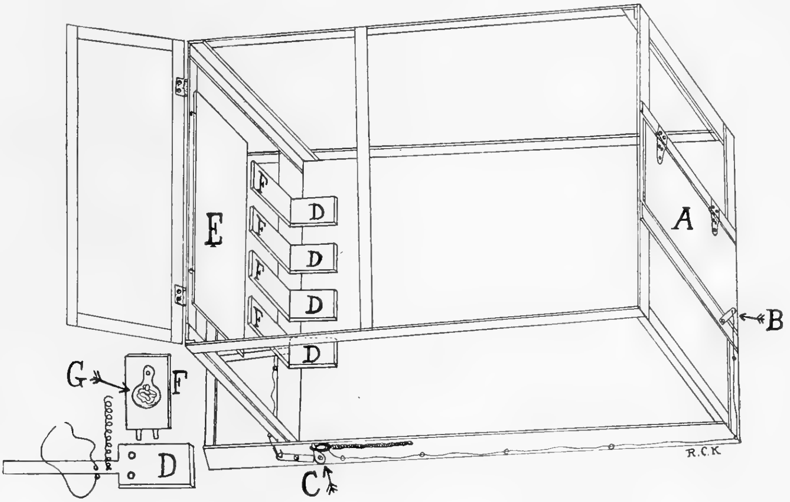


Fig. 1. Diagram of the experiment cage; *A*, spring door; *B*, button with trigger string attached; *C*, trigger with one pedal string attached; *DDDD*, pedals, one of which is shown separately with string and suspension spring; *E*, sign board; *FFFF*, pedal cards, one of which is shown separately, with legs to fit into the holes in the pedals, and with odor card (*G*) suspended from its anterior surface.

*Experiments with the white sign board and white pedal card.*—In this series of experiments the different pedals were attached, one at a time, and in varying order, to the trigger, the attached pedal always bearing the white pedal card, and the unattached pedals bearing plain pedal cards. The white sign board was kept suspended above the row of pedals throughout this series of experiments. The animal was given 160 trials, 20 a day. In calculating results an error was recorded for each attempt to escape by striking an unattached pedal. If the animal struck the attached pedal first during a given trial a "correct first choice" was recorded for that trial (see table). Time measurements proved to be of absoultely no value, since the animal sought the pedals as his means of escape from the start, and was so dexterous in passing from one pedal to another that there was no essential difference between the time of escape when there were no errors, and when there were several. Besides, as there was no pressing desire to escape, conditions external to the interests of our problem determined the length of his stay in the cage. He always came out directly the shock of the discharged trigger was felt, but often he wandered about the cage contentedly before attempting to escape. As a rule he was fed before experiments were begun; the only incentives for escape which the experimenter supplied were a few much gnawed bones and a commending caress. It has been my experience that a well fed, contented dog, if undistracted by other sense-impressions than those of the experimental situation, is apt to inspect his immediate environment quite thoroughly, and to act with more appearance of caution than has been reported by previous experimenters with these animals When put into the cage for his first trial the dog went directly to the attached pedal, struck it, and came out. Of course his previous experience easily accounts for his having struck at the first projecting object that came his way, and I do not doubt that his immediate success in getting at the attached pedal was accidental. When he was put in for the second trial he went at once to the pedal that had just let him out and struck it, then started for the door; the white pedal card was now on another pedal, and that pedal alone was attached. But the animal did not seem to take the directing pedal card into account, for he returned to the unattached pedal again and again, striking it more forcibly each time, and always running to the door after each attempt. After ten such attempts he sat down by the door and began to whine. He was spoken to reassuringly, after which he returned to the pedals and inspected them. After some hesitation he struck the attached pedal, thus releasing himself. His behavior during the remainder of the 160 trials showed nothing of particular interest beyond a progressive decrease of errors, and an increase of correct first choices. The experiments were discontinued after sufficient data had been obtained for purposes of comparison with those to be obtained from the more complicated experiments about to be described.

*Experiments with colors, colors and odors, and odors alone.*—At the 161st experiment the white sign board and white pedal card were discarded. The green sign board was hung in position, the green pedal card was placed in p 1 (the first pedal to the left), the black pedal card in p 2, the yellow pedal card in p 3, and the red pedal card in p 4. There were sixteen different combinations of this sort, so arranged that each color was represented upon each "pedal attached" once in sixteen times, and upon each "pedal unattached" three times in every sixteen. Each of the four pedals was attached four times in a series of sixteen experiments. An irregular order of attaching pedals and placing pedal cards was followed in order to prevent the animal from learning a sequence; but care was taken that no one pedal should be attached twice in succession, that no one color should occur as the sign of "pedal attached" twice in succession, and that every pedal card should be shifted to a different pedal after each experiment.

At the 481st experiment the colors were reinforced by odors: red by lupulin, black by asafœtida, green by castor oil, and yellow by beef extract. Thus, if the yellow pedal card (now reinforced by the beef extract odor card, suspended from its anterior surface) were on the attached pedal, the yellow sign board was hung out with a beef extract odor card attached to it. At the 581st experiment the colors were abandoned, and only odor cards and odor sign boards were used. These were attached to plain sign boards and pedal cards, identical in form with those that bore the colors.

It can be seen from the above that an adequate reaction to the situation required the animal first to seek the sign board, then to inspect it, and finally, to strike the pedal bearing the only card that would afford him the same odor or visual stimuli that he got from the sign board. In this connection it may be said that it was impossible to determine positively whether or not he was ever guided by the colors as such, or even by their differences in light intensity, although the latter increased rapidly in the order from black to yellow. It is probable that the colored papers had each a distinctive odor, since the animal not only looked at them, but sniffed them carefully before reacting. It is to be remembered that so long as distinctive stimuli were afforded, and so long as the sign boards gave the same stimuli as their appropriate pedal cards, the principle remains the same. Color discrimination as such is not a part of our problem, and colors were used only for the sake of a possible reinforcing value.

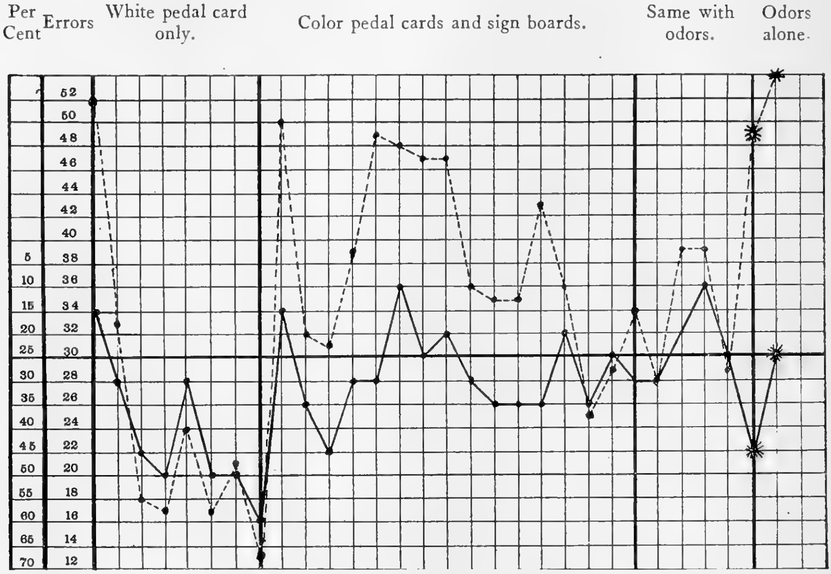


Fig. 2. *Explanation of Table of Curves.* Each of the dots connected by the closed lines represents the percentage of correct first choices in 20 trials; each of the dots connected by the broken lines represents the total number of errors in 20 trials.

Where stars (**) are used in place of dots, sets of experiments in which electricity was used are indicated.

The heavily shaded horizontal line upon which the figures "25" and "30" stand, is the average chance line mentioned in the text.

Our results demand two general analyses: (1) An analysis of errors, *i. e.*, of the number of times that unattached pedals were struck, and of the factors determinative of these inadequate reactions; (2) an analysis of the correct and incorrect first choices. It may be well to remind the reader that the pedal which the animal struck first during a given trial is recorded as his first choice for that trial.

*Analysis of errors.*—This scarcely need be given in detail, since a large number of errors during a given trial seemed to be due variously to, (1) mere playfulness and inattention, (2) a persistent effort to escape by returning (during the same trial) many times to the pedal or pedal card that had proved successful at the immediately preceding trial, or (3), when electricity was finally introduced, to fear and a wild desire to escape.

*Analysis of correct and incorrect first choices of pedal.*—There was such a varying degree of attention to the sign boards and pedal cards, and the formation of so many misleading associations occurred, that a large number of factors determinative of the first choice of pedal is disclosed by the analysis of results. While it seems an almost hopeless task to attempt a complete and adequate classification of these factors, the following will serve, I think, to throw some light upon our problem.

(1) As factor "1" I wish to refer to several closely related factors which can be conveniently grouped together. After the animal had been successful with a certain pedal he was apt to return to it and strike it first for many successive trials. At times this seemed to become a kind of habit with him; he would go to his favorite pedal at once on entering the cage, strike it, and then, failing to get out, inspect the apparatus in a very leisurely manner, and make his second choice.

A preference for p 3 and p 4 was undoubtedly due to the fact that he is "right handed." In clawing things from a table, and in all other acts that call for the use of a single forepaw he almost invariably uses the right forepaw. This is due neither to tuition nor to any injury or discoverable deformity, and has been amply demonstrated by appropriate experiments.[1]

The following table, supplemented by the analysis that follows, will indicate to what extent the complex factor "1" accounts for the dog's first choices:

| | | | | |
|---|---|---|---|---|
| First choice of the same pedal for 2 successive trials......... | p 1 = 7 | p 2 = 11 | p 3 = 18 | p 4 = 11 |
| First choice of the same pedal for 3 successive trials......... | p 1 = 1 | p 2 = 7 | p 3 = 11 | p 4 = 7 |
| First choice of the same pedal for 4 successive trials......... | | p 2 = 2 | p 3 = 2 | p 4 = 1 |
| First choice of the same pedal for 5 successive trials......... | p 1 = 1 | p 2 = 1 | p 3 = 1 | p 4 = 2 |
| First choice of the same pedal for 6 successive trials......... | | | p 3 = 1 | |
| First choice of the same pedal for 7 successive trials......... | p 1 = 1 | p 2 = 1 | | |
| First choice of the same pedal for 13 successive trials......... | | | | p 4 = 1 |
| First choice of the same pedal for 16 successive trials......... | | | | p 4 = 1 |

---

[1] See BALDWIN, Mental Development, Methods and Processes. Second edition, p. 67. 1903. Also ERNST WEBER, Ursachen und Folgen der Rechtshändigkeit. pp 10–13. 1905. It is possible that my dog is exceptional in this respect.

Obviously, factor "1" does not account for all the 266 first choices given in this table. From this total we must subtract (*a*) the 88 first choices that started the 88 series; (*b*) the 49 correct first choices that occurred in the course of the series (although it is a fair inference that factor "1" accounts for many of this latter group, such an inference cannot be drawn with certainty, since the animal often terminated a series by choosing the attached pedal, only to return to the favorite pedal of the series thus interrupted at the next trial); (*c*) the 42 first choices that occurred as the second member of a series when the initial first choice of that series was successful (such reactions are tabulated under factor "2"); and (*d*) the 25 times when the animal might have been following up a successful color or odor in making his second successive first choice of a given pedal.

To summarize: (1) there are left $266-88-49-42-25 = 62$ first choices that cannot be accounted for on the assumption of a transiently formed association between the desired result and an immediately preceding successful pedal, color, or odor, or to the influence of the directing sign board. These 62 first choices—all of them incorrect—may be ascribed to factor "1."

(2) In 101 trials the animal made (incorrect) first choice of the pedal that had just let him out.

(3) In 102 trials he made (incorrect) first choice of the pedal bearing the color or odor of the immediately preceding attached pedal. This occurred in 83 (25.9 per cent) of the 320 experiments with colors alone; in 15 (15 per cent) of the 100 experiments with colors reinforced by odors; and in 4 (20 per cent) of the 20 experiments with odors alone.

(4) Out of the total 440 experiments in which colors, colors and odors, and odors alone were used, he made correct first choice of the attached pedal 122 times (27.7 per cent). It is here that we must look for any light that the experiments may have thrown upon our problem. The question at issue is, "Did the presence of the directing sign board increase the adequacy of the animal's reactions to the situations in which it entered?" Inferences drawn from a mere numerical tabulation of results must, of course, be qualified by the character of these 122 objectively correct first choices. A great deal depends on whether his choice of the attached pedal appeared to be haphazard, "hit-or-miss," or to be attended by such preliminary activities as would have made for

greater adequacy of reaction. But the relatively slight influence of the experimenter's personal equation on tabulations of results, and its inevitably distorting influence on any report of the animal's apparent intention, must, so far as one kind of certainty is concerned, give precedence to mathematically derived inferences.

First of all, then, we must take into account the fact that had the animal been uninfluenced by any associations, mere chance would have enabled him to make correct first choices in approximately 25 per cent of the total number of trials. Or, had he always struck the same pedal first, or the pedal bearing the same color or odor, he would have made 25 per cent correct first choices. Now, the 53 incorrect first choices unaccounted for by any of the above-mentioned factors, and the 62 incorrect first choices ascribed to factor "1" (the latter, since they often came in series of more than four each) can most conservatively be considered to be due to nothing that impaired the animal's chances to make the average chance 25 per cent correct first choices.

The case is quite different with the 101 incorrect first choices ascribed to factor "2," where the animal chose the pedal that had just released him; of necessity any choice due to the influence of such an association would be an incorrect one, thus materially lowering his chance of attaining the average 25 per cent correct first choices. But mere chance would have enabled him to strike first the pedal that was last attached in 110 of the trials. This would be a fatal objection to any attempt to demonstrate that the animal was misled by such associations were it not for the fact that the choose-first-the-last-successful-pedal reactions came, not at irregular intervals, but in definite and prolonged series. Thus, if p 3 had just released him, he would strike it on reëntering the cage, and p 1 proving to be the successful pedal, the next time he would make an unsuccessful attempt to escape by striking p 1, and so on, until some new determinative of first choice became effective. The same is true of the 102 incorrect first choices ascribed to factor "3."

It now becomes clear, I think, that to have made 122 correct first choices the animal must have been influenced by the sign boards; otherwise, the effects of the misleading experience-determinants to first choice would have been reflected in a considerably lower than the average chance per cent (25 per cent) of correct first choices.

Passing now to a consideration of the character of the adequate reactions, it should be said that so far as observation of the individual trials was concerned, the majority of correct first choices might have been due to mere chance. But I was able to record 23 incidents like the following. The animal inspected the sign board, pedal cards, and pedals, turned his head to look at me, wagging his tail (my position was at a point 20 feet directly in front of the door), and then, confining his attention exclusively to the sign board, devoted some time to sniffing its surface. Following this he went up and down the row of pedals, sniffing their cards; then pausing at an unattached pedal, he raised his paw as if to strike, but desisted, withdrawing the uplifted paw slowly, without having struck the pedal. Again he returned to the sign board and sniffed its surface, following which he passed down the line of pedals, sniffing their cards as he went, until he came to the attached pedal (*i. e.*, the one affording him the same stimuli as the sign board); this he struck and was released. There was not a single failure when he behaved in this manner.

An examination of the correct first choice curve will show that there was but little, if any, improvement at the end of the 440 experiments with sign boards. This agrees with the fact that the kind of behavior just described never became a fixed mode of reaction. Usually, after he had once reacted so adequately, he quickly chose the previously successful color or odor, thus falling into error.

It is interesting that the odor reinforcement was of so little value to him. That particular series of experiments would have been continued much longer had it not been for the fact that the animal finally learned a very effective and easy manner of finding the attached pedal. Starting at the third or fourth pedal to the right, he would pass to the left, striking the pedals in succession until the shock of the discharged trigger sent him scurrying to the door. If he started at p 3, and p 4 was attached, he would go down the line to p 1 in the usual manner, then walk directly to p 4 and strike it. Reference to the curves shows that in the third from the last set of 20 experiments he made 29 errors, and struck the attached pedal first in 5 of the 20 trials. That he made only 29 instead of the "average chance" 30 errors, is due to the fact that in switching from the method of starting at p 4 (a method which he pursued for 13 successive trials), to the method of starting at p 3, he avoided making one error. It was to break up this habit that electricity was introduced as a penalty for errors. It seemed to be effective during the first 20 trials of its use, but after that all previously acquired fondness for the experiments was replaced by fear, and I found myself working with an animal that reacted like THORNDIKE's hungry cats and dogs.[2]

LLOYD MORGAN defines a psychological process as "the middle term between results of complex stimuli from the environment on the one hand, and the results of complex reactions to that environment on the other hand."[3] Instead of stating our problems in the interests of hypothetical interrelations of these "middle term" processes, and instead of making our experimental and clinical observations subservient to problems so stated, it seems desirable to pursue a method of studying animal behavior which will keep us more closely in contact with the facts accessible to us. Such a method is realized, I believe, in the clinical[4] and experimental study of reaction-types.

It is true that partially objective methods have been followed in this field so far as the higher vertebrates are conerned, but the divorcement from middle term speculative demands has been more apparent than real. Otherwise, there would be no appeal to "criteria of conciousness;"[5] no catering to hypothetical modes of mental elaboration of sense-data; and, in short, no need of psychological inferences, in our interpretations of animal behavior.

Animal behavior affords data for the solution of a great and comprehensive problem: Starting with the assumption that from the lowest forms of life to human life, there is an ever increasing adequacy of adjustment to complex environments, and that the adequacy (in the sense of complexity) of adjustment implies a corresponding complexity of effective inner elaboration intervening between reception of stimuli and reaction to them, the general

---

[2] THORNDIKE, E. L., Animal Intelligence. *Psychological Review Monograph supplement,* vol. 2, no. 4, pp. 30–32. 1898.

[3] LLOYD MORGAN. Comparative and Genetic Psychology. *Psychological Review,* vol. 12, p. 79. 1905.

[4] For the lack of a better term "clinical" is used here to indicate the kind of observation that is employed by the psychiatrist in his studies of insane patients. It is generally recognized by clinical psychiatrists that the academically trained psychologist (if he lack adequate clinical knowledge of insanity) is greatly hampered in his experimentation with patients by his lack of clinical checks upon his work. The case is quite analogous where experimental work with animals is not supplemented by prolonged and extensive observation of the subjects dealt with.

[5] See YERKES, Animal Psychology and the Criteria of the Psychic. *Journal of Philosophy, Psychology and Scientific Methods,* vol. 2, pp. 141–150, 1905, for a viewpoint which recognizes the value of psychological inferences.

problem becomes far simpler, and loses none of its importance if it have to deal only with the possibility of establishing the presence or absence of a continuity of the third terms of the formulæ, stimuli—inner elaboration—reaction. Attempts to conduct experiments for the sake of gaining knowledge of the intimate workings of the "inner elaboration" seem only to retard and unnecessarily to complicate the problem. If the complexity of a given situation be definitely known, and if there be only one "most adequate" reaction possible to that situation, these, and not inferred psychic processes will enable us to give the reaction its continuity-position. Of course, other objectively determined factors must enter into consideration, such as the relative influence of instinctive equipment and of experience.

Returning to an interpretation of the results obtained from the experiments just reported, it is required of us, then, to isolate such reaction-types as appeared there. Of these, two stand out more or less distinctly. (1) During the first 160 experiments, when only the white pedal card was used, the animal showed an increasing adequacy of reaction. Here, amongst several constant factors, the most important experience-determinant (the white pedal card), was the only one that made one situation different from another; but in spite of its changing pedal relations, the white card, in its direct sense-value to nose and eyes, was a simple, concrete, persistently recurring experience-determinant. Innumerable observations, both in the laboratory and in everyday life, have shown that dogs' experience-determined reactions are usually thus conditioned, and that final unfailing and perfect adequacy of reaction to such factors requires their frequent recurrence in situations in which the animal is placed. (2) In the last 440 experiments, where the directing sign board was used, the important experience-determinant was constant in principle, but not in direct sense-value. A perfectly adequate reaction to the situation required that, as the result of previous experience with a concretely dissimilar situation, the dog be so influenced by the stimuli derived from the sign board as to strike first and only the pedal bearing a card which afforded him the same kinds of stimuli. A given situation was repeated only once in sixteen times, and no simple associations could be of any positive assistance to him in guiding him to the attached pedal; on the contrary, they only served to mislead him.

Although such behavior cannot, if my analysis be correct, fall under the head of accidental happenings, and therefore stands out as an actual reaction-type, it did not tend to increase in frequency. Whether the capacity for occasional adjustments of this degree of complexity is a necessary part of the canine endowment, or merely an individual trait, it strongly suggests the possibility of there being still higher reaction-types higher in the phylogenetic scale.

The reader will be better oriented as to the nature of the views and problems just expressed if a brief reference be made to the fact that they are due, in part, to certain investigations in the field of psychiatry. From the extremely inadequate reaction-types observed in certain psychoses, to the relatively adequate reaction-types of relatively normal individuals, there is unbroken continuity. KRAEPELIN,[6] with his keen insight into abnormal reactions, establishes this continuity by means of transitional clinical pictures, which lead us from the abnormal to the normal. And in spite of his objections to the radical degeneracy doctrines of LOMBROSO and the Italian school of positivists, he makes frequent references to the fact that many of the reactions occurring in the "degenerative psychoses" strongly suggest the reactions of primitive peoples. On the assumption of degenerative reversion in certain psychoses, there at once arises the possibility that the apparent gap between human and animal adequacy of adjustment may be bridged by means of studies of reaction-types of the highest of the animals below man on the one hand, and of studies of reaction-types in savages and the degenerative insane on the other hand.

The writer wishes to acknowledge the obligations under which he has been placed by his colleague, Dr. R. C. KELL, who rendered much valuable assistance in the construction of apparatus, the drawing of figures, and the actual carrying out of experimental work.

KRAEPELIN, Psychiatrie, II Band, siebente Auflage. 1904.

# THE NORMAL ACTIVITY OF THE WHITE RAT AT DIFFERENT AGES.

BY

JAMES ROLLIN SLONAKER.
(*Stanford University, California.*)

WITH EIGHT FIGURES.

While observing Dr. WATSON'S experiments to test the ability of white rats at different ages to learn new tricks,[1] it occurred to me that possibly their greater susceptibility to education at a certain age might be due, to some extent at least, to the fact that they were more active at that age than at any other, and that they were thus able to try more avenues of approach to their food in a given time. With this thought in mind, I planned to test their voluntary activity at different ages to ascertain how the age of greatest activity compared with that at which they were the most capable of education.

Three preliminary experiments were performed in the Neurological laboratory of the University of Chicago, and other experiments are now being carried on in the Physiological laboratories of Stanford University. In this connection I wish to thank Dr. HENRY H. DONALDSON for his ready coöperation and assistance in providing necessary materials for the apparatus and Dr. WATSON for his aid in constructing the apparatus.

The apparatus employed was very similar to that used by Dr. C. C. STEWART[2] in his experiments on different animals. Several improvements have been made which will be described in a later paper.

The apparatus consists of two essential parts: first, the revolving

---

[1] WATSON, J. B., Animal Education; An Experimental Study on the Psychical Development of the White Rat, Correlated with the Growth of its Nervous System. *The University of Chicago Press.* 1903.

[2] STEWART, C. C., Variations in Daily Activity Produced by Alcohol and by Changes in Barometric Pressure and Diet, with a description of Recording Methods. *Am. Journ. Physiol.*, vol. 1, pp. 40–56. 1898.

cage and its accessory parts for obtaining and transmitting a certain kind of action; second, the recording apparatus composed of a clock which accurately records the number of revolutions made, and the writing lever and kymograph which graphically show the distribution of the activity during the day and night. As each rat is in a separate cage and each cage has its own recording clock and writing lever these records may be directly compared at any time.

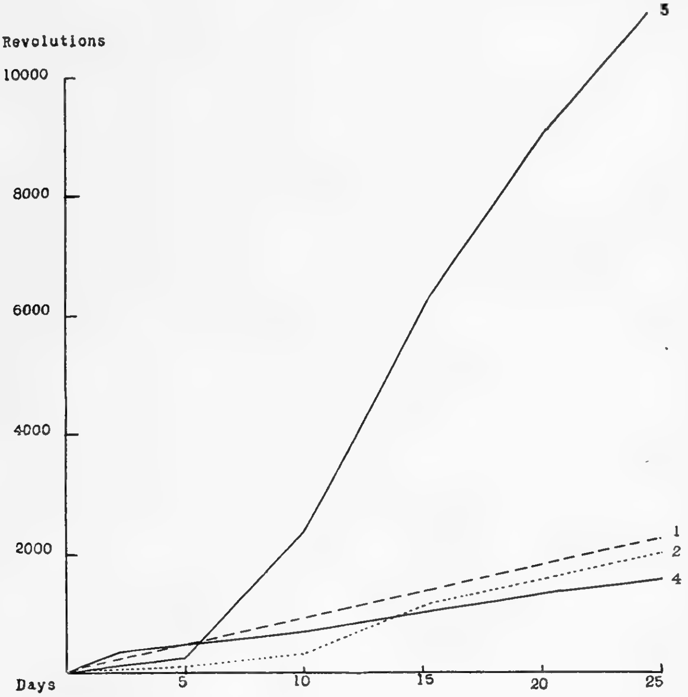


FIG. 1. Curves representing the total activity of each rat as indicated by the number of revolutions recorded by the clocks.

All the experiments were carried on in a large basement room facing the north and west. Frosted windows furnished a subdued and almost uniform light during the daytime. At night street lights cast in a very dim light, but this was not sufficient to enable a person to avoid coming in contact with obstacles when entering the room. The temperature was fairly constant during the day and varied between 60° and 70° F. At night it was much cooler but never lower than 40°, even in extreme cold weather.

The rats were fed and watered about 8 a.m. each day. At this time the clocks recording the number of revolutions were read. They were also read late in the afternoon between 5 and 6 o'clock. In this manner the activity for daytime and night time was easily ascertained. Further details will be described in the discussion of the different experiments.

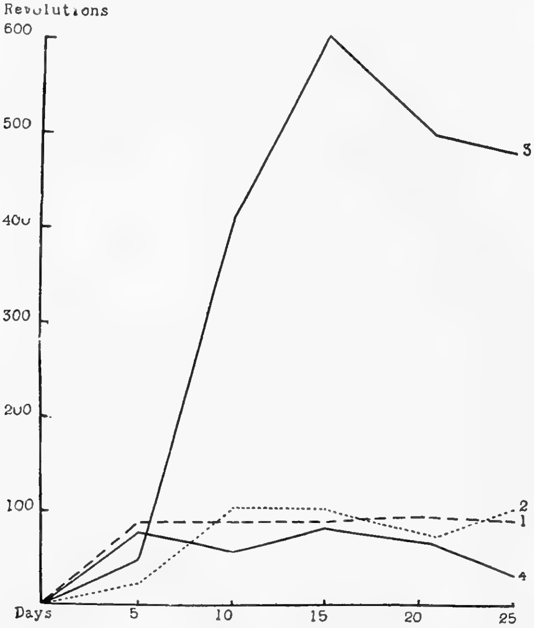


Fig. 2. Curves of the average number of revolutions of each rat per day based on the data in Table I.

### EXPERIMENT I.

For Experiment I four healthy rats of different ages were selected. Their ages at the beginning of the experiment were as follows: No. 1, 30 days; No. 2, 60 days; No. 3, 71 days; No. 4, 266 days. Rats of different ages were taken in order to ascertain at once whether there was any marked difference in activity due to a discrepancy in age. The experiment lasted 25 days, beginning February 1 and ending February 25.

The curves of Figs. 1 and 2 and the tabulations in Tables I and II show the condensed results of the experiment. While these show a great difference, they cannot be wholly relied upon as being characteristic for the age which they represent. Individual variation plays an important rôle, as will be seen later on. The results, however, can in general be considered as fairly typical for the different ages, as later experiments will show.

The curves in Fig. 1 indicate the total activity of each rat as represented by the number of revolutions recorded by the clocks. The curves pass through ordinates erected on the base line at points corresponding to the fifth, tenth, sixteenth, twenty-first and the twenty-fifth days of the experiment. As can be readily seen the curves of No. 1, No. 2, and No. 4 run fairly close together, while that of No. 3 is very different. The total amount of activity as represented by the number of revolutions is: No. 1, 2224; No. 2, 2040; No. 3, 10,740; No. 4, 1640.

TABLE I.

Average number of revolutions for a period of 24 hours at different ages.

| RAT. | Age in Days | Number of Revolutions. Average of 5 days | Age in Days | Number of Revolutions. Average of 5 days | Age in Days | Number of Revolutions. Average of 6 days | Age in Days | Number of Revolutions. Average of 5 days | Age in Days | Number of Revolutions. Average of 4 days |
|---|---|---|---|---|---|---|---|---|---|---|
| I | 35 | 86 | 40 | 87 | 46 | 86 | 51 | 95 | 55 | 92 |
| II | 65 | 20 | 70 | 105 | 76 | 104 | 81 | 75 | 85 | 103 |
| III | 76 | 50 | 81 | 417 | 87 | 609 | 92 | 503 | 96 | 484 |
| IV | 271 | 80 | 276 | 55 | 282 | 84 | 287 | 67 | 291 | 28 |

From this it is not safe to infer that No. 3 represents the age of greatest activity. If this were true, No. 2 would have been a close second, as it was only eleven days younger. It only shows the great individual variation which occurs and must be considered.

Table I is a tabulation of the average number of revolutions per day on the same days of the experiment as Fig. 1. These tabulations are plotted as curves in Fig. 2. From these it would appear that No. 3 reached its greatest average daily activity on the sixteenth day of the experiment. It was then 87 days old. After that age the number of daily revolutions steadily decreased. Nos. 1 and 2 increased slightly. No. 4 shows a gradual decrease from an average of 80 revolutions on the fifth day to 28 on the twenty-fifth day of the experiment. One should not infer that the curves would continue to rise or decline as the case may be had the experiment continued.

TABLE II.

Representing four single days activity at the ages indicated.

| RAT. | Age in Days. | Number Revolutions daily. | Total Number Revolutions. | Number Periods daily activity. | Longest Period of Activity in minutes. | Shortest Period of Activity in minutes. | Longest Period of Rest in minutes. | Shortest Period of Rest in minutes. |
|---|---|---|---|---|---|---|---|---|
| I | 31 | 72 | 130 | 9 | 12 | .5 | 180 | 10 |
| II | 61 | 8 | 24 | 10 | 120 | 1. | 300 | 10 |
| III | 72 | 28 | 48 | 8 | 20 | .2 | 390 | 20 |
| IV | 267 | 236 | 256 | 10 | 12 | 1. | 300 | 20 |
| I | 36 | 132 | 660 | 6 | 20 | .1 | 300 | 70 |
| II | 66 | 150 | 250 | 8 | 40 | .1 | 305 | 15 |
| III | 77 | 364 | 612 | 13 | 20 | .1 | 240 | 30 |
| IV | 272 | 104 | 516 | 14 | 10 | .1 | 130 | 30 |
| I | 48 | 114 | 1494 | 5 | 50 | 10. | 480 | 120 |
| II | 78 | 82 | 1334 | 8 | 70 | .1 | 300 | 15 |
| III | 89 | 538 | 6830 | 13 | 70 | 2. | 340 | 15 |
| IV | 284 | 52 | 1244 | 7 | 60 | 2. | 300 | 90 |
| I | 56 | 40 | 2224 | 4 | 15 | 2. | 700 | 180 |
| II | 86 | 110 | 2040 | 7 | 20 | 5. | 360 | 60 |
| III | 97 | 294 | 10740 | 11 | 100 | 1. | 300 | 30 |
| IV | 292 | 16 | 1640 | 10 | 55 | 1. | 190 | 80 |

The tabulation in Table II is intended to show the work, the number of periods of rest and activity, etc., during four of the days of the experiment. The table is self-explanatory and needs no further comment. From this it is observed that the rats become more regular in their activity toward the end of the experiment. The daily records show this much more prominently than is seen in this tabulation. The reason for this is no doubt due to their becoming accustomed to the environment.

This experiment shows that the very young rat is more active than the old one and that somewhere between these two extremes the period of greatest activity is to be found. According to these results the period of greatest activity for No. 3 was at the age of 87 days. The period of greatest activity for Nos. 1 and 2 had not yet been reached. No. 4 was decidedly on the decline from the very beginning of the experiment. The marked discrepancy between No. 2 and No. 3, which are so nearly the same age, is certainly due to individual variation.

## EXPERIMENT II.

On the twenty-fifth of February the rats of Experiment I were replaced in stationary cages where they remained for fifteen days, At the end of this time their ages were 70, 100, 111 and 306 days, respectively. They were then returned to the revolving cages from which they were taken. This was done primarily to give a different series of ages from those of Experiment I and incidentally to test their memory. In the former experiment each rat had learned a way peculiar to itself of reaching the food box, of getting down to the wheel and of entering the nest box.

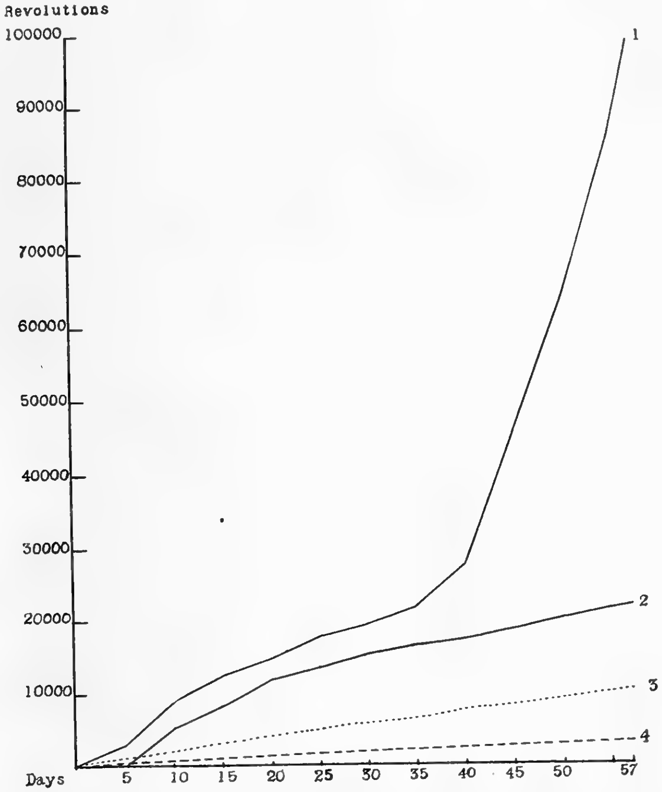


FIG. 3. Curves of total activity of each rat at different ages as represented by the recording clocks for a period of 57 days. The age of each rat at the end of this time was: No. 1, 127 days; No. 2, 157 days; No. 3, 168 days; and No. 4, 363 days.

After an interval of fifteen days it was interesting to note that when they were first returned to the revolving cages they appeared completely at home and within two minutes each had sought the entrance to the nest box in the same manner as in Experiment I. In going to and from the food box each showed its peculiar tricks. This showed conclusively that the duration of memory for these rats was at least fifteen days. Since the experiment was not intended to follow along this line no further tests were made.

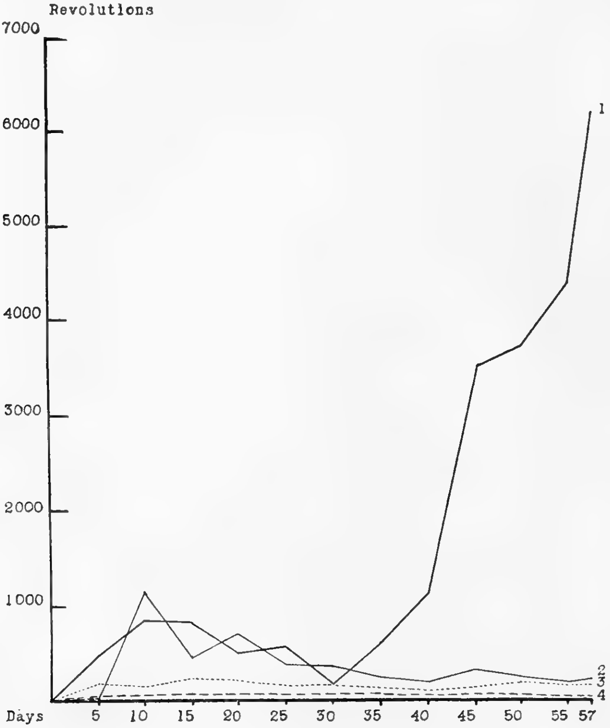


FIG. 4. Curves of daily activity of each rat for the same period as in Fig. 3. For simplicity the average of each five days is taken.

In regard to their activity there was a very noticeable change. No. 1 was exceedingly active, while No. 4 was very slow and showed decidedly the effects of advanced age. No. 2 and No. 3 showed a degree of activity approaching that of No. 4.

The marked differences in activity are best seen in the curves of Figs. 3 and 4. Fig. 3 represents the curves of total activity from the beginning of this experiment, March 13, to the end, May 9, a period of 57 days. Fig. 4 represents the curves of daily activity. For simplicity the curves pass through the ordinates erected on each fifth day of the experiment, each representing the average of the number of revolutions for the preceding five days.

By comparing the curves of Fig. 3 and those of Fig. 1 a marked difference is noticed. No. 3 was the most active in Experiment I, but now it occupies third place. No. 1, whose position was second in the former experiment, now far surpasses all the others.

When we compare the ages of these individuals at which they were the most active we find that No. 3 did the most work when it was between 85 and 95 days old, No. 1 (Fig. 4) at the age of 110 to 127 days, No. 2 somewhere between 100 and 120 days, while No. 4 never seemed to show much change from day to day. In other words, No. 4 had passed the age of greatest activity before the beginning of Experiment I. Individual variation no doubt accounts for these differences in the age of greatest activity. If the average were taken it would bring the most active period as indicated by greatest number of revolutions, at about the age of 105 days.

Taking the data we now have, a hypothetical curve representing the curve of activity from birth to death from old age could be constructed. Such a curve would show a gradual increase in activity to about the age of 100 days after which it would begin to fall and would finally reach the base line at death.[3] But owing to the individual variation manifested in these experiments, such a curve could not be relied upon as being correct. In order to construct such a curve Experiment III was begun.

## EXPERIMENT III.

The foregoing experiments show the need of a curve representing the average of a number of individuals subjected to the same conditions. That this might prove successful the rats should be the same age, as closely related as possible, and all subjected to the same food and environment. Accordingly, a litter of eight rats was selected. At the age of 25 days they were practically

---

[3] The age which rats living in the above conditions would attain has not yet been ascertained.

uniform as to size and general appearance. Their weights, however, varied somewhat as can be seen by consulting Table III.

Owing to the fact that the young cannot very successfully be weaned before 25 days, the early activity could not be definitely ascertained. But from observation of the young previous to this age one perceives that they move very little except when they begin to crawl out of the nest between the fifteenth and the twentieth day. The amount of activity therefore previous to the beginning of this experiment is very little.

At the age of 25 days these eight rats were placed in eight separate cages. Four of the cages were the revolving ones used in the former experiments. The other four cages were of the ordinary stationary type in which rats are usually reared for laboratory purposes. This arrangement was made in order to see what effect, if any, the voluntary exercise of those in the revolving cages might have on the rate of growth and the longevity.

TABLE III.

Weights of rats from the same litter at different ages, showing sex and gain of weight of each. The averages of those in the stationary cages are for the two females only.

| | RAT. | SEX. | Weight in grams Age 25 days. | Weight in grams. Age 45 days. | Gain in 20 days. | Weight in grams. Age 56 days. | Gain in 11 days. | Weight in grams Age 61 days. | Gain in 5 days. | Weight in grams. Age 73 days. | Gain in 12 days. | Weight in grams Age 85 days. | Gain in 12 days. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Revolving Cages. | I | Female | 24.1 | 58 | 33.9 | 86 | 28 | 93 | 7 | 123 | 30 | 146 | 13 |
| | II | Female | 23.5 | 56.5 | 33 | 84 | 27.5 | 93 | 9 | 113 | 20 | 132 | 19 |
| | III | Female | 25.5 | 64.5 | 39 | 85 | 20.5 | 104 | 19 | 121 | 17 | 146 | 25 |
| | IV | Female | 22.3 | 55.8 | 33.5 | 86 | 30. | 90 | 4 | 113 | 23 | 138 | 25 |
| *Average* | | | 23.8 | 58.9 | 34.8 | 85.2 | 26.5 | 95 | 9.7 | 117.5 | 22.5 | 140.5 | 20.5 |
| Stationary Cages. | V | Male | 26.3 | 76.3 | 50 | 114 | 37.7 | 127 | 13 | 163 | 36 | 191 | 28 |
| | VI | Female | 22 | 58 | 36 | 85 | 27 | 95 | 10 | 112 | 17 | 124 | 12 |
| | VII | Male | 23.8 | 73 | 49.2 | 105 | 32 | 118 | 13 | 161 | 43 | 188 | 27 |
| | VIII | Female | 24.7 | 71 | 46.3 | 93 | 22 | 105 | 12 | 123 | 18 | 138 | 15 |
| *Average* | | | 23.2 | 64.5 | 41.1 | 89 | 24.5 | 100 | 11 | 117.5 | 15.5 | 131 | 13.5 |

For convenience these rats were numbered from one to eight. Nos. 1, 2, 3 and 4 were placed in the revolving cages and 5, 6, 7 and 8 in the stationary cages. The experiment was started May 9 and stopped July 8, extending over a period of 60 days.[4]

The rats were all fed the same kind and approximately the same amount of food each day. The food given to each was not weighed but was measured in a fairly accurate manner. Any slight variation in amount would have no effect because more food was given than they could eat during the time elapsing before they were fed again. They were fed about 8 o'clock each morning. This consisted in washing the drinking cups, filling with clean water, removing scraps of food not eaten and putting in fresh. An abundance of cracked corn was always provided so that food was always at hand.

In order to determine the rate of growth each rat was weighed at certain intervals during the experiment. Table III indicates the sex, the weights at different ages and the gains. It is readily seen that No. 5 and No. 7 soon surpass the others in weight. It is also noticed that No. 5 is the heavier of the two at the first weighing and that this relationship obtains throughout the experiment. These two were males, the other six being females. The females run fairly close in their weights. But here again it is seen that those that were the heaviest at 25 days of age are among the heaviest when the final weights were taken at the age of 85 days. It thus appears that the start which they get while nursing is maintained.

Since the males soon surpass the females in weight, they were not taken into consideration in computing the averages. The average of those in the stationary cages is therefore an average of only two. In the revolving cages it is an average of four.

Table III shows some very interesting results. In the first place, the average weight of those in the revolving cages is greater than the average of the females in the stationary cages both at the beginning and at the end of the experiment. However, at the ages of 45, 56 and 61 days those in the stationary cages surpass the others. At the age of 73 days they are the same. Just what this means one can not say. It is probable, however, that the averages of those in the stationary cages are based on too few individuals and for that reason can not be relied upon. The

---

[4] It was the intention that this experiment should continue throughout the normal life of the rats, but owing to my change of residence to California it had to be terminated prematurely.

differences are so slight that no conclusions regarding the advantage or disadvantage in growth can be reached. Experiments now in progress will be able to determine this question.

Owing to the early termination of the experiment, nothing can be said regarding the effect on their longevity.

When these rats were first weaned and placed in revolving cages their graphic records showed that their activity was more or less distributed over the entire 24 hours of each day. With the exception of the feeding time, when all were active, there was no regularity in their activity. This is easily perceived by consulting the graphic record in Fig. 5 which represents 24 hours' activity at the age of 36 days. The interrupted line below indicates the hours as marked by the electric clock. The line representing the activity of each rat is indicated by the appropriate number at the left. Where the record is a straight line the cage was stationary and the rat was to all appearances resting. Occasionally the interval between revolutions was so great that the individual turns can be made out in the records. But since the kymograph paper moved very slowly—about four inches per hour—the records more often appear as a solid band with occasional interruptions of rest. This record shows the irregularity in the periods of activity. It also shows that the rat is resting much more of the time than it is active.

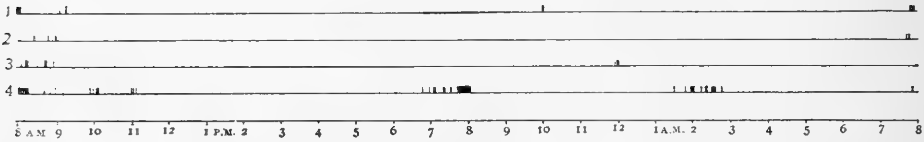


Fig. 5. The graphic record of the activity of each rat at the age of 36 days for a period of 24 hours as recorded on the kymograph paper. The broken lines indicate periods of activity, the straight lines periods of rest.

In using the term resting I do not wish to be interpreted as meaning that the rat was asleep. As a matter of fact immediately after feeding they begin at once to carry their food into the nest boxes. This accounts for the regular and general activity at 8 a.m. They no doubt eat this food as they desire during the day. Since the water cannot be carried inside, they are forced to come out to the water boxes. This I think accounts for the occasional short runs of often only a few revolutions of the cage.

As the rats grow older, they become more and more like their wild gray relatives in that they are almost wholly nocturnal in their habits. They also become much more regular in their periods of activity and rest. With the exception of a short period of activity at the feeding time (8 a.m.) and an occasional short run at other times during the day, they spend the entire day time within their nest boxes. They are presumably asleep during the greater part of this interval.

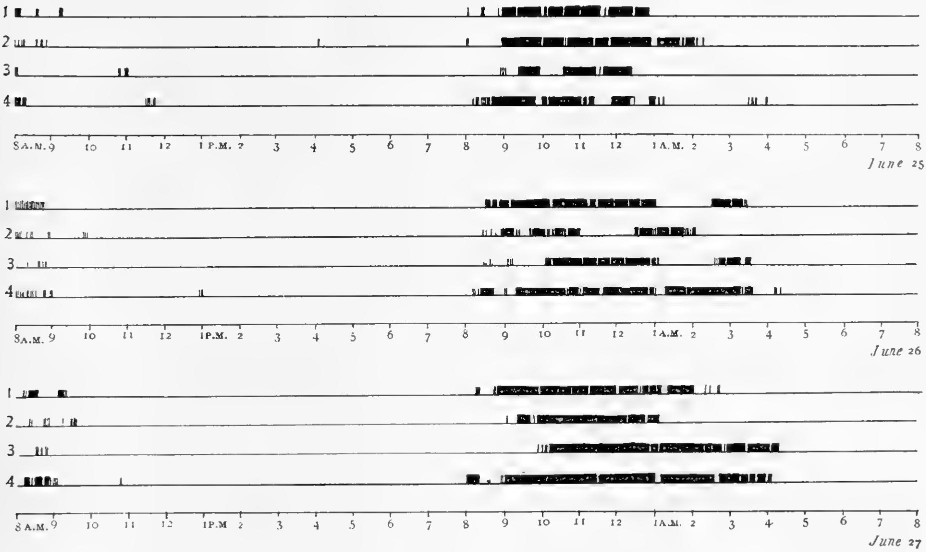


FIG. 6. The graphic records representing the activity of each rat at the ages of 70, 71 and 72 days as traced on the kymograph paper. The broken lines indicate periods of activity, the straight lines periods of rest.

The time in which they did the great bulk of their work varies somewhat. In the winter time when the days were short they began their running at an earlier hour. As the seasons changed and the days became longer the time when they began their activity gradually shifted to a later hour. In every case this time appeared to coincide, in a general way, with the first deep shadows of night. Earlier darkness caused by a storm or cloudy sky did not seem to cause any marked advance in the time of beginning their activity. In other words, the periods of activity seem quite regular and are not materially affected by incidental circumstances.

In this experiment the period of activity extended between the hours of 8 p.m. and 4 a.m.—a period of eight hours. The remainder of the 24 hours, with the exceptions noted above, was devoted to rest. This is beautifully shown in Fig. 6 which represents the graphic records for three successive days, extending from 8 a. m., June 24, to 8 a. m., June 27. The ages of the rats during this interval were 70, 71 and 72 days. By comparing these records with those of Fig. 5 one is impressed with the marked regularity of activity at this later age. They began their work with a noticeable degree of punctuality. Rat No. 4 was especially prompt and usually began within a few minutes of 8 o'clock each evening.

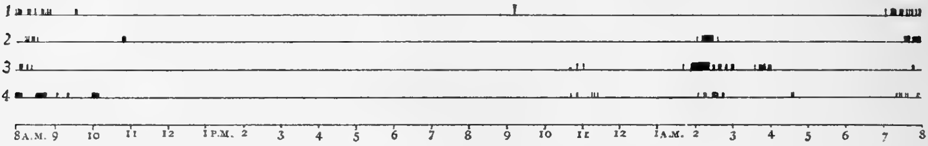


Fig. 7. The graphic records of the activity of each rat for a period of 24 hours at the age of 77 days, showing the effect of continuous light. The electric lights were left burning during the entire night.

To what is this nocturnal activity due? Is it due to the absence of light or to some other cause? In order to see if light had any effect on their activity the electric lights were left burning during the night of July 3. The graphic record for that period is shown in Fig. 7. A great difference is observed between this record and those of Fig. 6. The lack of regularity and the great reduction in the amount of activity are very noticeable. The marked difference in activity is also seen in Table IV, which illustrates the average number of revolutions for day and night. On the nights of July 3 and July 6 the lights were left burning and the readings the next morning at 8 o'clock are indicated. I can give only two suggestions for the difference between these two nights' work. From midnight on during the night of July 3–4 there was an almost continual roar and racket from the explosion of giant firecrackers, cannon, etc., in celebrating independence day. This may have had some effect in retarding their activity. Or on the second night the rats may have become somewhat accustomed to the light from their former experience and were reasonably active in spite of it.

From this only one conclusion can be drawn; that is, light does seem to have an influence on the time of the rat's activity. The wild gray rat has by natural selection become accustomed to seek its food at night to escape its enemies. Its various organs have been modified to fit it for this nocturnal habit. The most prominent organ that has been changed is the eye. The very large pupil and the great predominance of rods in the retina fit it especially for perceiving objects in dim and diffuse light. Bright light would not only be blinding but very probably painful. In the white rat, owing to the absence of pigment in the eye, this effect of light would be more marked. This I think is the most instrumental cause for the nocturnal activity in the white rat.

TABLE IV.

Representing the number of revolutions of the revolving cages during the night time and the day time of a number of days. The lights were left burning during the entire night on July 4 and 7 to determine what effect light would have on the activity.

| DATE. | Average Number of Revolutions during night, 6 p.m. to 8 a.m. | Average Number of Revolutions during day, 8 a.m. to 6 p.m. |
|---|---|---|
| June 25 | 2383 | 42 |
| 26 | 4233 | 60 |
| 27 | 5870 | 94 |
| 28 | 4085 | (?) |
| 29 | 4175 | 57 |
| 30 | 4753 | 135 |
| July 1 | 8214 | 20 |
| 2 | 5313 | 405 |
| 3 | 7182 | 51 |
| 4 | 464 | 909 |
| 5 | 6512 | 332 |
| 6 | 9430 | 105 |
| 7 | 2013 | 133 |

In order to show more clearly the actual difference in activity between day and night work Table IV has been constructed.

These figures are the averages of the four rats. Slight fluctuations in the averages occur. I can not give the cause of this difference. It certainly cannot be due to their food, for they were fed the same during the time represented in this table. The fluctuations might be due to changes in barometric pressure. I have not as yet demonstrated this. The cause, therefore, cannot at present be given.

It is very noticeable that in general when there is a great reduction in the average amount of work during the night the following day shows a marked increase. In other words, they seem to prefer to do about so much work each 24 hours and if this amount is not done during the night they are more active the following day.

A better idea of the amount of work may be gotten if the number of revolutions is converted into distance. A little less than 1175 revolutions of each cage are equal to one mile. From this we see that the average nightly run at the age of 70 days is about five miles. The average number of revolutions during the day time at the same age is only about one-tenth of a mile. Many individual cases far surpass this average amount of work. The greatest run which I have observed for a single night (14 hours and 45 minutes) was 16,516 revolutions, or a distance of fourteen and one-tenth miles. Such a run is usually followed by a noticeable reduction in activity the following day.

By close and quiet observation one could see that activity was apparently performed from the mere love of it. The rats would frisk about, jump and play, then start the wheel going and run it for a number of turns without a stop. After a few seconds, or minutes' rest they would start it again with renewed vigor. This playful attitude was especially noticeable at the age of 50 days. As they grow older this activity which was displayed in frolicking and investigation gradually assumed the form of turning the wheel. So that by the time the rat reached the age of 80 days most of its spontaneous activity was manifested in revolutions of the cage. I have seen them run as many as 100 revolutions in a minute without a single stop. This is equivalent to a twelfth of a mile The records in Fig. 6 show that in many cases if periods of rest occurred they were extremely short. In one case (No. 4, last record) there appears to be continuous activity for two and a half hours before a rest. This appearance, I think, is due to the slow movement of the paper. I have never yet seen a rat run continuously but a few minutes. They may be active, however, for hours with only very short periods of rest.

The curves of the total activity are seen in Fig. 8. For the first twenty days after the experiment started there was little or no variation in the curves and they coincided with the average curve. From this time on individual variation appears. A marked difference is thus seen in the total number of revolutions. It is also noticed that each curve very closely resembles in general appearance the average curve. Whether these curves would finally have approached each other or would have diverged more had the experiment continued can not be predicted.

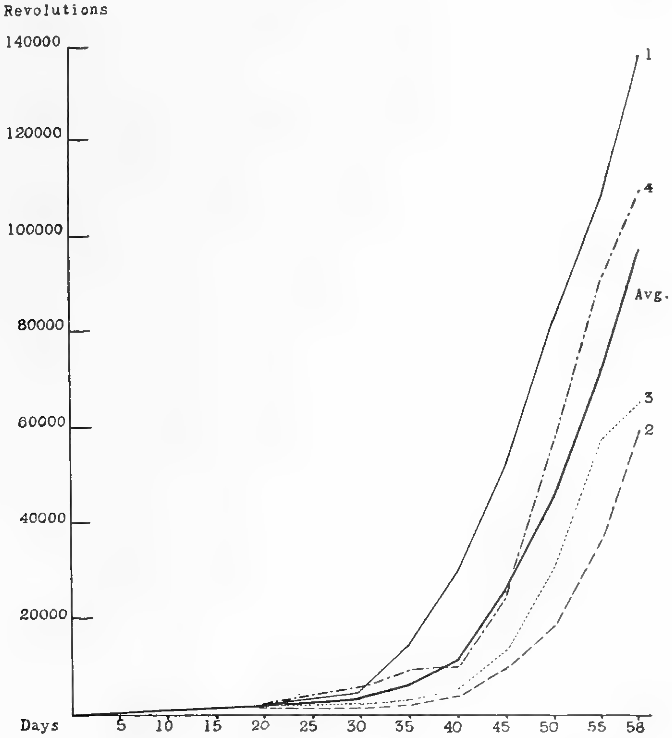


FIG. 8. Curves representing the total activity of rats from the same litter as indicated by the number of revolutions of the revolving cages. The average curve is shown in heavy line.

The following table (Table V) gives the average daily activity throughout the experiment. The average is computed for each fifth day and is based on the records of the preceding five days. Some very interesting things are brought out in this table. At first the environment was new to the rats and everything was strange. No attempt was made to show them the way to the food nor to the nest box. As a result they did much more work at first than later when they had become accustomed to their surroundings. This accounts for the apparent decrease in activity from an average of 121 revolutions on the fifth day to 26 on the fifteenth day. From this time on there is an almost constant increase in the daily activity. It is especially noticeable toward the termination of the experiment.

TABLE V.

Average number of daily revolutions.

| DATE. | May 15. | May 20. | May 25. | May 30. | June 4. | June 9. | June 14. | June 19. | June 24. | June 29. | July 4. | July 8. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Age in Days | 30 | 35 | 40 | 45 | 50 | 55 | 60 | 65 | 70 | 75 | 80 | 84 |
| Average Number Daily Revolutions | 121 | 58 | 26 | 62 | 52 | 242 | 886 | 1065 | 2111 | 4239 | 5313 | 5917 |

This experiment coincides so far as it goes with the results obtained in the former experiments. It shows that the period of greatest activity, as measured by the number of revolutions, for these four rats has not been reached at the age of 84 days. Whether the average age of greatest activity would be greater or less than that determined by Experiments I and II can not be determined from these results. It could only have been ascertained by continuing the experiment. The experiment now under way should make this clear.

## CONCLUSIONS.

1. White rats of different ages show a marked difference in in their activity.
2. The very young rat and the old rat are each noticeably

inactive. Somewhere between these two extremes we find the age of greatest activity.

3. These experiments indicate that the age of greatest activity, as represented by the number of revolutions of the revolving cages, ranges between 87 and 120 days.

4. Owing to the marked individuality exhibited, a correct curve of activity from birth to death cannot be constructed from the results of one rat or of several individuals of different ages.

5. A curve representing the normal activity from birth to death due to senility must be based on the records of a number of individuals of the same age and subjected to the same conditions.

6. The white rat is affected by light. This, I think, is mainly due to the structure of the eye and to certain tendencies which they inherited from their wild ancestors.

7. From these preliminary experiments no correlation can be made between the age at which they are most active and the age at which they learn most rapidly.

# EDITORIAL.

## CONCILIUM BIBLIOGRAPHICUM.

The revision of the Anatomical Bibliography of the Concilium Bibliographicum at Zurich, as announced in their latest publication, is a matter of importance to anatomists in general and to neurologists in particular. Very few anatomists in America are so situated as to be able to search out the literature even within their own specialties; fewer still are fond of such work even when facilities for it are amply provided. And yet failure to study the literature of his subject, especially the current literature, from the whole world is fatal to thoroughly broad work in any field of morphology.

The path of the neurologist is peculiarly difficult, for his subject is not only the most intricately complex of all of the morphological specialties, but any detail of an inquiry may develop the most unexpected relations with remote parts of the field and even with far distant departments of inquiry. While, therefore, the neurologist is more in need of bibliographic assistance than are other morphologists, the problem of producing a servicable bibliography is immensely more difficult.

In the past the writer has found the anatomical bibliography of the Concilium Bibliographicum of great service in spite of its conspicuous defects. The Concilium, though founded and maintained by a morphologist, has hitherto been compelled by the exigencies of its organization to devote its first energies to other departments and anatomy has remained frankly neglected. The zoölogical, physiological and other bibliographies have now so far progressed that the Concilium is able to take up the anatomical bibliography in earnest. The revised Anatomical Conspectus has been elaborated after nearly ten years of practical experience with the scheme on a more modest scale, and in our opinion this document should receive the careful attention of every working anatomist.

We have used the Concilium Bibliographicum scheme of classification, not only for bibliographies, but also for many other kinds of cataloguing (such as microscopic slides, etc.) and find it as simple and easy of application as any practicable scheme could be expected to be. Some of the details of the classification are in our opinion unfortunate, but the principle on which it is based is sound and is the only practicable principle for a card bibliography. And the card bibliography is the practicable one for a working anatomist.

This does not imply that it will run itself. Any scheme of anatomical classification which is comprehensive enough to have more than local usefulness must be complicated. At least this is true of the neurological sections, where unless a minute subdivision of topics is employed the vast number of diverse entries will very soon become a useless mass of inaccessible material. The complication is inherent in the subject matter. This means that intelligent and continuous attention must be given to the bibliography from the start or it will break down in use, no matter how perfect may be the system. If only each investigator could take the time to elaborate his own bibliography the problem would be much simpler, but each system so devised is likely to be useful to its inventor alone. If in the course of the further division of labor in scientific work a *general* bibliographic scheme is to be adopted, the individual must subordinate his own point of view somewhat. In spite of its defects, this bibliography is practicable. Moreover it is sufficiently flexible to enable each individual to adapt it to his own needs and still have the enormous advantage of the prompt issue of titles already printed on cards, with the privilege of subscription to such topics only as interest him. It enables one for a nominal sum to purchase information which every investigator needs, but will not and usually cannot procure for himself, and to *keep it in available form.* Inquiry usually develops the fact that those who find the system impracticable have never spent half an hour in serious study of the theory and detail of its organization.

The writer has kept his neurological bibliography on library cards catalogued by the Dewey numbers for about a decade. After subscribing to the neurological series from the Concilium (the cost of which has been trifling) these cards have been slipped into their places as they arrived and now completely overshadow the original list, into which they were incorporated without disturbance of the arrangement. And my complete bibliographic list on any subject is together, so that if I wish to assemble all of my available titles on, say the facial nerve, instead of searching through many volumes of periodically published lists, I simply pick out the cards between two guides and the whole list is before me. The same series of cards may also be used as a catalogue of one's own library without disturbing their position in the file. By marking one of the upper corners of every card which bears a title which is represented in the library with a colored wafer or a rubber stamp, inspection of the card instantly tells whether the article is in the library and the shelf number may be added, if necessary.

The Concilium, as is well known, is not a commercial enterprise; nor is it necessarily a rival of the various other bibliographies now serving the scientific public. The monthly and annual lists are valuable in their way, but in our opinion cannot replace the card catalogue. And now that the anatomical bibliography of the Concilium has been thoroughly established and enlarged, we bespeak for it the hearty support of anatomical laboratories and libraries and remind our readers that standing orders for all cards on individual topics can be placed. For instance, the neurological cards alone will be sent independently of the rest of the bibliography. But the cost of the whole anatomical bibliography is at present (author and subject catalogue) only about nine dollars per year.

This revision differs from the original anatomical classification chiefly by the addition of more subdivisions of the leading topics, thus in no way disturbing the placing of the old cards. There are only two places where the old numbers are changed. The first is a transposition to secure a more logical position of the general introductory divisions. In this case the original numbers occupied by these subjects are left vacant, so that confusion is not likely to occur. The second change involves the substitution in the neurological bibliography for two relatively unimportant entries of a division for Tectonics (including the course of fibers and gray substance) and a division for Localizations. But few old cards are involved in this change and these the Concilium has decided to reprint. The change strengthens the weakest point in the old classification, a point where it quite broke down in actual practice, and, with the very great amplification of details throughout the neurological bibliography, has made a great improvement in these sections. In the preparation of the neurological bibliography the Concilium has had the active and very valuable coöperation of Professor v. MONAKOW.

C. J. H.

# LITERARY NOTICES.

**Edinger L.** Ueber das Gehirn von Myxine glutinosa. Aus dem Anhang zu den *Abhandlungen der Königl. Preuss. Akad. der Wissenschaften* vom Jahre 1906. Berlin. 1906. 36 pp., 3 plates.

The results are based largely upon the new fiber method of BIELSCHOWSKY, which however, EDINGER finds it necessary to modify for Myxine by leaving the heads to be studied much longer in the silver solution—as long as 30 days. The method gives a histological picture which is more like that of certain invertebrates than of other vertebrates, differing even from Petromyzon and Amphioxus. Especially in the forebrain and thalamus, there is a much smaller number of cells and fibers and the fibers are finer than in any other vertebrate. The tissue between these cellular elements appears in these preparations as a very fine fibrous reticulum.

In the discussion of the morphology of the forebrain EDINGER distinguishes two divisions of the cerebral hemispheres, (1) a ventral, the hyposphærium, which receives the olfactory nerves and contains internally the striatum and nucleus of origin of the tænia thalami; and (2) a dorsal, the episphærium, containing the pallium. On the basis of his more recent work (and also that of KAPPERS which was published in January, 1906, in this *Journal*), he has receded from his former position on the morphology of the pallium in fishes and adopted the view of C. L. HERRICK and STUDNICKA that the fish brain does not consist exclusively of hyposphærium but contains at least the beginnings of an episphærium, though in an abnormal position. The obscurity regarding the ventricles of the forebrain of Myxine is at last satisfactorily cleared up by the discovery of actual cavities or definite epithelial vestiges in all of the places where other vertebrates possess forebrain ventricles.

The cerebellum is said to be totally absent, a statement which suggests an interesting field for inquiry in the exact relations of cells and fibers in the somatic sensory centers of the oblongata from which the cerebellum of other vertebrates has quite certainly been derived phylogenetically.

The plates include an excellent series of cross-sections through the medulla oblongata, but the author has been able to unravel but few of the fiber complexes and to identify few of the structures, remarking, "to cumber the literature with a new description whose basis is no better established than that of earlier authors would be to no purpose. . . . Doubtless it will be possible later, when the fish oblongata is better known, to study more closely and to identify the relations of the fiber tracts shown for the first time in these very accurately drawn figures." This illustrates very clearly the opinion long held by the reviewer, that the fundamental plan of structure of the nervous system can best be discovered by an exhaustive comparative study of a large number of types in which the systems in question are very diversely developed rather than by exclusive attention to primitive or generalized species. Having discovered the fundamental vertebrate plan of each functional system, by the comparison of forms where it attains maximal and minimal development, then this schema can be read back with ease into the primitive and unspecialized types, which before were incapable of analysis. In other words, the phylogeny should be read backward as well as forward. Only in this way can the study of generalized types yield its best fruits.

C. J. H.

**Van Gehuchten, A.** La loi de Waller. *Le Névraxe*, vol. 7, fasc. 2. 1905.

In this lecture, delivered at the University of Utrecht, Professor VAN GEHUCHTEN has summarized the recent experimental work on WALLER's law, and sketched the history of the conflict which has waged about the question of so-called retrograde degeneration. As is well known, he has studied exhaustively the phenomena of central degeneration, which he finds sometimes to occur, though more tardily than the degeneration of the peripheral portion of the nerve. This is not, however, a cellulipetal process; it is initiated in the cell body. VAN GEHUCHTEN would reformulate the law of WALLER thus: When a central or peripheral nerve tract is severed, the peripheral portion always degenerates. The behavior of the central portion depends upon the intensity of the reaction of the cells of origin to the lesion. If the lesion is not so severe as to cause the death of these cells, the fibers of the central portion remain intact. Otherwise the atrophy of the cells of origin induces the secondary degeneration of the central portion of the nerve.

VAN GEHUCHTEN criticises the current conception of nervous degeneration. It is not a process signalizing the death of the nerve. Quite the contrary, it is a process of reorganization, a regulatory phenomenon. Even the destruction of the axis cylinder and the fragmentation of the myelin take place only in an evnironment of living tissue, and the proliferation of the nuclei of the sheath of SCHWANN is distinctly a step in regeneration, which may or may not come to anything, depending on the other conditions of the tissue.

C. J. H.

**Maxwell, S. S.** Chemical Stimulation of the Motor Areas of the Cerebral Hemispheres. *Journal Biol. Chem.*, vol. 2, no. 3. 1906.

We quote the author's summary: (1) Substances applied to the surface of the cortex either give no indication of stimulation, or do so after so long an interval that they would have time to act osmotically or by diffusion upon the underlying white matter. (2) The white matter of the motor areas can be stimulated chemically by the calcium precipitates and by barium chloride in solutions isosmotic with the blood serum. The response to such stimulation is very prompt, occurring within a few seconds at most, after application of the solution. The same substances when applied in the same concentration to the cortex give no result at all or only after an interval of some minutes. (3) Solutions of high concentration can stimulate the white matter by osmotic action very promptly and effectively. (4) When solutions are injected into the gray matter but not so deeply as to reach the white matter no evidence of stimulation is seen. The gray matter is apparently devoid of irritability to chemical and osmotic stimulation as well as to mechanical and electrical stimulation.

**Grasset, J.** Demifous et demiresponsables. *Paris, F. Alcan.* Pp. 297. 1907.

In this work the author takes up the consideration of those individuals who are not insane or mentally deficient in the ordinary sense of these terms. An attempt is made to show that individuals cannot be classed solely as responsible and irresponsible, but that there is a class that has degrees, one may say, of responsibility. The individuals making up this class are mentally ill, and may sooner or later become insane; and they, like the insane, may be cured. The demifous is one characterized by an enfeeblement of the higher mental faculties and an uncontrolled functional hyperactivity of the lower psyche (p. 130). In opposition to this generalization it is pointed out that these individuals are often mentally brilliant and have contributed much to literature, science and art, as well as taking a considerable part in politics, etc. The treatment and the legal standing of the individuals must be considered individually.

S. I. F.

## BOOKS AND PAMPHLETS RECEIVED.

**Wallenberg, Adolf.** Die secundäre Acusticusbahn der Taube. Reprinted from *Anatom. Anzeiger*, Bd. 14, no. 14. 1898.

**Wallenberg, Adolf.** Der Ursprung des Tractus isthmo-striatus (oder bulbo-striatus) der Taube. Reprinted from *Neurol. Centralbl.*, no. 3. 1903.

**Wallenberg, Adolf.** Neue Untersuchungen über den Hirnstamm der Taube. Reprinted from *Anatom. Anzeiger*, Bd. 24, nos. 5, 6, 13, 14. 1903-1904.

**Wallenberg, Adolf.** Die basalen Aeste des Scheidelwandbündels der Vögel (Rami basales tractus septo-mesencephalici). Reprinted from *Anat. Anzeiger*, Bd. 28, nos. 15 and 16. 1906.

**Dodds, Gideon S.** On the brain of one of the salamanders (Plethodon glutinosus). Reprinted from *Univ. of Col. Studies*, vol. 4, no. 2. 1907.

**Dahlgren, Ulric and Sylvester, C. F.** The electric organ of the stargazer, Astroscopus (Brevoort). A new form of electric apparatus in an American teleost. Preliminary paper. *Anat. Anz.*, Bd. 29, no. 15. 1906.

**Hrdlicka, A.** Measurements of the cranial fossæ. Reprinted from the *Proc. U. S. Natl. Museum*, vol. 32, pp. 177-232. Washington. 1907.

**Eycleshymer, Albert C.** The habits of Necturus maculosus. Reprinted from *Am. Naturalist*, vol. 40, no. 470. 1906.

**Parker, G. H.** The influence of light and heat on the movement of the melanophore pigment, especially in lizards. Reprinted from the *Journ. Exp. Zoöl.*, vol. 3, no. 3. 1906.

**Parker, G. H. and Metcalf, C. R.** The reactions of earthworms to salts: A study in protoplasmic stimulation as a basis of interpreting the sense of taste. Reprinted from *Am. Journ. of Physiol.*, vol. 17, no. 1. 1906.

**Driesch, Hans.** Analytische und kritische Ergänzungen zur Lehre von der Autonomie des Lebens. Reprinted from *Biol. Centralblatt*, Bd. 27, nos. 2 and 3. 1907.

**Cole, Leon J.** An experimental study of the image-forming powers of various types of eyes. Reprinted from *Proc. Am. Acad. Arts and Sci.*, vol. 42, no. 16. 1907.

**Herms, Wm B.** An ecological and experimental study of Sarcophagidæ with relation to lake beach débris. Reprinted from *Journ. Exp. Zoöl.*, vol. 4, no. 1. 1907.

**Herms, Wm B.** Notes on a Sandusky Bay shrimp, Palæmonetes exilipes Stimson. Reprinted from *Ohio Naturalist*, vol. 7, no. 4. 1907.

**Pearl, Raymond.** Variation and differentiation in Ceratophyllum. *Publ. of the Carnegie Institution of Washington*, no. 58. 1907.

**Mettler, L. Harrison.** Clinical physiopathology. The need of a new classification of diseases of the nervous system. Reprinted from *Journ. Am. Med. Assoc.*, vol. 48, pp. 664-669. 1907.

Neurographs. A series of Neurological Studies, Cases and Notes. Edited by William Browning, M. D. Vol. 1, no. 1. *Brooklyn, N. Y.* 1907.

The Journal of
Comparative Neurology and Psychology

Volume XVII SEPTEMBER, 1907 Number 5

# THE HOMING OF ANTS: AN EXPERIMENTAL STUDY OF ANT BEHAVIOR.

BY

C. H TURNER.

With Plates ii–iv, and One Figure in the Text.

CONTENTS.

Introduction.

## INTRODUCTION.

*Technique.*—In the following experiments on ants the attempt has been made to have the conditions so simple that disturbance of the normal activities is reduced to a minimum, and yet to present in each experiment a definite problem which the ants must solve. Excepting where it is otherwise stated, each experiment recorded represents one of several similar experiments.

The apparatus used consisted chiefly of stages, inclined planes and dark chambers. All of these were constructed of cardboard. Occasionally a Lubbock or a Fielde nest was used, but for most experiments I used a modification of the Janet nest. These nests were 39 x 15 x 2.5 to 3 cm. Each contained a well 10 x 5 x 1.5 cm., two living chambers, each 10 x 7 cm. and from a few mm. to a cm. or more in depth and a food-chamber of the same dimensions as the living chambers. The edges of the top of the nest, as far back as the beginning of the well, and the partitions between the chambers and between the last chamber and the well were covered with Turkish toweling one layer thick.

With a fine camel's hair pencil, the upper surface of the abdomen of any ant used for individual experiments was marked with water-color paint. If more than one ant was used simultaneously for such experiments, each was given a distinctive hue. In all experiments with marked ants, any unmarked ant that visited the stage was immediately imprisoned.

The stage used consisted of a piece of white bristol board 15 cm. square; in the edges of two opposite sides perpendicular slits were made 2 cm. from each corner, for the purpose of attaching inclines to the stage. The center of this platform was attached, by means of a pin, to the cork of a bottle about 12 cm. high. Unless otherwise stated, a new stage was used for each series of experiments.

All the inclines were made of the same bristol board as the stage and were about 3 cm. wide and usually 30 cm. long. For special purposes inclines were made by pasting two of these end to end. They were also modified in other ways. When an incline led from a stage downward, it was always attached so as to project 2 cm. above the stage except when a dark chamber was used. When the incline led from the stage upward it was always attached so as to project 2 cm. below the stage. The dark chamber consisted of an inverted pasteboard box 8 x 4 x 1 cm. A flap about one centimeter wide and attached above was cut out of one end, and was pressed inwards to furnish a door through which the ants could enter the dark chamber. In order to observe what was happening on the under side of the stage and incline, a small mirror, inclined at the proper angle, was placed on the island, at one side of the stage.

Unless otherwise stated, preparatory to each series of experiments, the nest with its entrance open was placed on a LUBBOCK island for one or two days in order to familiarize the ants with the island.

*Historical Résumé.*—Students of ant behavior may be conveniently grouped into four schools: first, those who claim that ants lead a purely reflex life; second, those who hold that ants lead a purely instinctive life; third, those who grant that ants possess a limited amount of intelligence; fourth, those who insist that ants are endowed with anthropomorphic intelligence.

The first school, of which BETHE ('98, '00, '02) is the most noted modern member, claims that these animals are mere machines which respond to certain stimuli, always with the same fixed action or set of actions. Some of these machines are, indeed, quite complex; but so is the linotype. And as the linotype, in mechanical response to a variety of definite stimuli, turns out line after line, no two of which are exactly alike, just so the most complex activities of the invertebrates are but unconscious mechanical responses to diverse stimuli. In other words, the life of these creatures is a life of mechanical responses or tropisms. For them there is no content of consciousness. Heliotropism, galvanotropism, stereotropism, polarized trails, etc., explain all their behavior. They do not learn. All reflexes may not be possible at birth, because the physical mechanism is not yet perfected; but once the mechanism has responded, thereafter under the same conditions, it always responds to the same stimulus in the same way.

The second school, to which I, hesitatingly, assign PIERON ('04, '05), admits that reflex actions, some of which are connate and some of which are deferred, do not fully explain the habits of ants. According to them, the so-called instincts of these creatures are decidedly plastic. They profit by experience; but not by associating present sensations with revived sensations, nor by inference, nor by any of the higher forms of rational thought, but by what MORGAN ('00), THORNDIKE ('98), and others have called the method of trial and error.

The third school, to which belong EMERY, FOREL, LUBBOCK ('81), WASMANN ('98, '00, '02) and others, holds that ants have elementary feelings, ideas, and even what the English have called a simple association of ideas, but that they do not have rational thoughts and emotions.

The fourth school, including L. BÜCHNER ('80), HUBER ('10), MACCOOK, ROMANES ('92) and others, insists that there is difference only in degree between human consciousness and the consciousness of lower animals.

To separate the third from the fourth school is to make a distinction which savors more of convenience than of scientific accuracy; for it is probably true that an idea differs from a product of rational thought, not in kind, but in degree.

*Acknowledgments.*—The studies on the behavior of ants, of which this contribution is the first fruit, were begun about five years ago, while I was connected with Clark University of Atlanta, Georgia. They were continued at the University of Chicago during the summer and autumn of 1906 and the winter of 1907. I take this opportunity to express my gratitude to the University of Chicago for the scholarship privileges granted me, without which the publication of this contribution would have been much delayed. I also wish to acknowledge my indebtedness to the members of the Zoölogical and Psychological Departments for their encouragement, and especially to Dr. C. M. CHILD for his sustained interest in my work and for suggestive criticisms, and to Dr. F. R. LILLIE for his assistance in revising the manuscript.

## I. EXPERIMENTS ON TROPISMS.

BETHE'S insistence ('98, '02), in spite of the opposition of WASMANN ('98, '99, '01), BUTTEL-REEPEN ('00) and FOREL ('01), that ants are merely reflex machines, led me to plan the series of experiments discussed in this section. The purpose of the experiments was to see what rôle, if any, tropisms play in the homing of ants. These homing activities were selected for study because they could easily be investigated under controlled conditions sufficiently simple to yield reliable results. Only such forms of stimuli were investigated as might possibly influence the normal activities of the ants.

*Heliotropism.*—"The essential feature of heliotropic reaction" says LOEB ('06, p. 124), "consists in the fact that the light automatically puts the plant or animal (Eudendrium, Spirographis) into such a position that the axis of symmetry of the body or organ, falls in the direction of the rays of light." Light may play an important rôle in the life of an organism without that creature being heliotropic. "Heliotropism (LOEB '06, p. 135) covers only those cases where the turning to the light is compulsory and irresistible, and is brought about automatically or mechanically by the light itself."

A large number of experiments were made to see what part heliotropism as defined by LOEB plays in the home-going of ants. In each experiment one or more cardboard stages and inclines were used. Illumination was furnished, in some cases by diffuse daylight through a window, and in others by a 16 c. p. incandescent light. For each experiment a new cardboard stage and inclines were used. Pupæ and ants were placed on the stage and the ants allowed to find their way home.

These experiments fall into the following groups:

1. Those in which the ants in passing home must pass obliquely towards the source of light, then parallel to the rays but away from the source.
2. Those in which the ants must pass obliquely away from the source, then parallel to the rays and towards the source.
3. Those in which the ants must pass obliquely away from the source and then at right angles to the rays.
4. Those in which the ants must pass obliquely towards the source of light and then at right angles to the rays.
5. Those in which the path was practically equally illuminated on all sides.
6. Those in which the ants must pass obliquely towards the source of light, then parallel with the rays and towards the source, then at right angles to the rays, then parallel with the rays and away from the source.
7. Those in which the ants must pass obliquely away from the source, then parallel with the rays and away from the source, then at right angles to the rays, then parallel with the rays and towards the source.

In the sixth and seventh cases two inclines and two stages were used. The stages were connected by an incline and one incline led from stage number two to the ground. The pupæ and ants were placed on stage number one.

All of the above experiments were performed with each of the following species: Cremastogaster lineolata Say, Forelius maccooki McC., Lasius niger L., Myrmica punctiventris Rog., Pheidole sp.?, Prenolepis imparis Say, Tapinoma sessilis Say, Formica pallide-fulva Latrl., Formica fusca var. subsericea Say, Dorymyrmex pyramicus Rog., Aphænogaster lamellatus Mayr, Monomorium minutum, Mayr. In most of these cases experiments were performed with several different colonies of the same species.

If ants are heliotropic in the sense of LOEB, they should move from or to the light, in the direction of the rays, until the edge of the stage is reached; then they should pass to the under (shaded) side of the stage, or else remain on its margin until the direction of the rays of light is changed.

But under each of the seven conditions mentioned above, and with each of the species observed, the neuter (worker) ants when first put on the stage made random movements in every possible direction. After a time in almost every case (over 95 per cent), some one or more ants would find the way from the stage to the nest and back. Such ants then began to convey pupæ to the nest regularly. Gradually they were joined by others. The time required for ants to find the way home varied greatly; not only for different species, and for different colonies of the same species, but for the same colony at different times. That, however, is an irrelevant matter. The essential thing is, not how long did it take them, but which way did they go? In the few exceptional cases mentioned above, after a number of random movements, the ants ceased to search for an outlet and settled down quietly upon the stage. In such cases they usually collected the pupæ in the center of the stage and huddled over them. This getting lost was not confined to any particular species and it was only an occasional thing; no species got lost each time it was used.

It is thought that the above experiments prove conclusively that heliotropism does not influence the home-going of neuter ants. This is in harmony with LOEB's conclusions, for he says ('02, p. 196), "I have never found true heliotropism in the workers."

When winged females were placed on the stage with the pupæ, they would pass sometimes to the under side of the stage, sometimes they would roam about until they found the way home, and in some cases they actually assisted in carrying the pupæ home.

In a very few cases (less than 1 per cent) males placed on the stage with the pupæ flew away; but in almost every case they rushed to the under (shaded) side of the stage. Sometimes these males again returned to the top of the stage; but in no case observed by me, did any of these males reach the nest again until carried there by the workers.

*Geotropism.*—Any animal moving under the influence of geotropism is automatically forced to orient its body so that its axis of symmetry is at right angles to the horizon; or, if that be impossible, with that axis parallel with the component of gravitation which lies in the plane along which the animal is moving.

In the majority of experiments on heliotropism, the apparatus was so arranged that the ants were forced to go down hill to reach the nest. To determine whether geotropism led them downward, the apparatus was so adjusted that the ants had to go up-hill to reach the nest. The neuter ants readily learned the way home.

Ants that never had been trained to go down-hill to the nest, learned to go up-hill to the nest about as quickly as ants of the same kind had learned to go down-hill. Ants, however, that had previously been trained to go down-hill, often took an unusually long time to learn the way home up-hill. This delay was due to the fact that such ants would over and over again attempt to go home the way they had previously learned. Repeatedly they would partly ascend the incline and then return to its foot and reach down as though seeking something that they could not find. About the same number failed as in the experiments on heliotropism.

To test this point further, two stages were used. Stage number two was four inches higher than stage number one and was connected with it by an incline twelve inches long; an inclined plane twenty inches long connected stage number two with the LUBBOCK island. Thus, in order to get home, the workers, which (with the pupæ) were placed on stage number one, had to pass first up-hill, then across a horizontal plane and then down-hill. It took all of the ants a much longer time to learn this way than the more simple route of the other experiment and the percentage of total failures was almost doubled; but a very large majority (fully 90 per cent) of the ants found the way home. In these experiments I used the same species that were used in the experiments on heliotropism.

These experiments, it seems to me, prove conclusively that geotropism does not guide the worker ants home.

*Chemotropism.*—The results of numerous investigators demonstrate the presence of well developed olfactory organs in ants. It is also well established that the organ of that sense is the flagellum of the antenna.[1] This possession of well developed olfactory organs makes it possible for ants to be chemotropic. BETHE ('98, '02) has gone so far as to assert emphatically that the home-going of ants is the result of chemotropism. According to him, ants leave behind a polarized odor-trail which mechanically leads them to and from the nest. He thinks that this trail is double, the outgoing ants being guided by one line and the ingoing ants by the other. He also believes that burdened and unburdened ants are affected in different ways by the same trail, burdened ants being

---

[1] MISS FIELDE ('03) goes further than this. She claims to have proved that the eleventh segment of the antennæ is for detecting the nest aura, the tenth for detecting the colony odor, the ninth for detecting the individual track, the seventh and eighth for detecting the inert young, and the fifth and sixth for detecting the odor of enemies.

driven toward and unburdened ants away from the nest. He further states that burdened ants so scent the trail that ants which come in contact with it can tell whether the ants that passed that way were burdened or unburdened.

WASMANN ('99) raises the following objections to BETHE's polarized odor-track hypothesis: (1) An ant leaving the nest for the first time could not be led home by its own trail. (2) If it did so return the two superimposed trails would so confuse the outgoing ants that they could not find their way. (3) There would be much confusion along the narrow paths of some ants. (4) Many ants in going home do not adhere slavishly to the common path. (He even cites a case of a whole colony moving from one nest to another across an unscented path.) (5) Ants frequently straighten their trails. (6) Unburdened ants find their way home as readily as burdened ants. (7) Ants conveying burdens from the nest pass outward as well as unburdened ants. My observations on ants in the field and in the laboratory support all of the above contentions of WASMANN.

Although WASMANN opposes BETHE's polarized odor-track hypothesis, yet, practically, his view is not very different from that of BETHE. In attempting to explain how ants know which way to go, WASMANN ('01) expresses the belief that their "footprints" have an odor-shape which, combined with the relative intensities of the odor-tracks, enables the ant to tell in which direction the nest lies. On a trail leading from the nest, the nearer the nest the more intense would be the nest-odor of the footprints; on an ingoing trail the reverse would be the case.

Time and again, in the field and in the laboratory, I have noticed ants straighten their trails. This militates against the idea of their home-going being an olfactory tropism, but not against WASMANN's hypothesis nor against the idea that it is a non-tropic reflex caused by odors.

Over a hundred experiments were performed by me to test BETHE's and WASMANN's hypotheses. Although they are unlike, there is a similarity about them which makes it possible to use the same kind of experiments in testing each. The experiments used were of two kinds. In the first, a cardboard stage with one incline leading down to the island was used. On the stage were placed a great many pupæ, larvæ or eggs and several worker ants. After the ants had conveyed all of the pupæ, larvæ or eggs into the nest, both ants and pupæ, larvæ or eggs were replaced on the stage. After this had been repeated several times, so as to make sure that the ants were thoroughly acquainted with the trail, the incline was reversed, so as to place the original nest-end at the stage, and the stage-end near the nest. Although this was tried several dozen times, and with all the species used in the experiments on heliotropism, the ants continued as though nothing had happened. At first I was inclined to think that these experiments disprove BETHE's contention, but a little reflection showed that they do not; for, if there is a double polarized trail one path of which leads the ants to the nest and the other from it, reversing the incline would still leave a double polarized trail of the same functional type.

This failure to reach a solution led to a different type of experiment. As in the first series, a cardboard stage from which an incline led down to the island was used. A great many pupæ, larvæ or eggs, and workers were placed on this stage. After these burdens had all been carried to the nest, they, with several workers, were replaced on the stage. In a shorter time than before the pupæ were all carried by the workers down the incline to the nest. This was repeated until I thought the ants were thoroughly acquainted with the stage and incline; then a second incline was so placed as to lead from the opposite side of the stage to the LUBBOCK island. If, after the lapse of a few minutes, no worker descended this second incline, I concluded that the ants were thoroughly acquainted with the path down the first incline to the nest. If they proved to be acquainted with the path, I then placed the first incline, which had become scented by the passing to and fro of the ants, where the unscented one had been and placed the unscented incline in the place formerly occupied by the scented one. Thus there was an unscented path in the place of the old trail and the old scented path was in a new position. Now if ants are guided home solely by the sense of smell, then one of two things should happen: they should spend approximately as much time learning the way down the new incline as they did learning the way down the former; or else, in their random movements, they should happen upon the scented incline and go down it. In reality they did neither of these things. They almost immediately went down the unscented incline which occupied the former position of the scented incline. About a hundred experiments of this sort were performed with Myrmica punctiventris Rog., Pheidole sp. ?, Prenolepis imparis Say, Tapinoma sessilis Say and Formica fusca var. subsericea Say. In each case the result was practically the same as stated above. In many cases, on first reaching the unscented incline there would be a momentary hesitation as though they had met an unfamiliar stimulus; but there was no prolonged disturbance. In addition to these experiments with ants acting in concert, similar experiments were tried with marked individuals of Myrmica punctiventris Rog., and Formica fusca var. subsericea Say. The results were the same.

A slight variation of the above experiment was tried with the same species of ants. Instead of substituting a new incline for the old, the stage was revolved through an angle of 180 degrees and the same incline retained in its original position. This gave an unscented path from the pupæ to the incline. With no, or, in some cases, little hesitation the ants found the way to the incline. Rarely would an ant go along the scented path instead of the unscented one that led to the incline. In these experiments where ants worked in concert, two or three large spatulas of ants were placed on the stage. Thus, where the colony was large, it was highly improbable that all the ants would be conveying pupæ at the same time. Even after the experiment had been repeated several times, the chances are that there would still be some ants that had never made the trip. The ants that went along the path that led away from the incline may have been ants that had not yet learned the way. I also tried substituting a new stage for the old. The results were the same as above.

Now both BETHE'S and WASMANN'S hypotheses demand a scented path over which ants must pass. The unscented path down which these ants passed was twelve inches long. These experiments do not prove that ants are unaffected by odors, nor do they indicate that odors are not utilized by ants in finding their way home; but they do demonstrate that the home-going of ants is not controlled solely by the olfactory sense. They militate against both BETHE'S double polarized trail hypothesis and WASMANN'S assumption that the footprints have an odor-shape which guides the ants home. The results of these carefully planned experiments harmonize with observations made by myself and others in the laboratory and field.

MISS FIELDE ('03) watched some specimens of Stenamma fulvum pass back and forth across a trench of water in order to convey their pupæ into their nest. They traveled back and forth across the water for thirty hours until all of the pupæ had been removed. She performed two such experiments with the same colony. To see if the ants left a scented trail on the water, she experimented as follows: (1) She removed a few drops of water from in front of an ant which was returning to the island. Out of thirty-one ants thus treated, twenty-one continued across and ten turned back. (2) She passed a knife-blade through the water and around an ant returning to the island. Out of ten ants experimented on none turned back. (3) She covered the surface of the water with dust, and after the ants had been passing for some time, removed the dust. The ants were not in the least affected. These results led her to conclude that in crossing the water the ants were depending upon something more than mere footprints.

Frequently I have noticed individual ants of most of our common species cross the water ditch that surrounds the Lubbock island. Occasionally I have had whole colonies escape in that way, but it has always happened when I was absent. On one occasion I had a colony of Forelius maccooki MacCook escape in that way. In this colony there were at least twice as many eggs, larvæ and pupæ as workers and winged females. Since no pupæ, larvæ or eggs were left behind, and since all of the workers do not usually take part in carrying pupæ, some of these ants must have crossed the water several times.

Wasmann ('01) states that if the surface-sand be removed from the vicinity of the nest of busy Formica sanguineas, the ants continue to pass back and forth without noticing the change. In the same paper Wasmann relates that he noticed another set of ants, laden with cocoons, travel eighteen meters from one nest to a former nest. On this occasion the ants neither used their antennæ to smell the way nor followed in each other's tracks. Each ant marched along independently as though it knew the way

These observations of Fielde and Wasmann serve to emphasize the statement made above, that the home-going of ants is not controlled solely by the olfactory sense.

Pieron ('04) from experiments[2] of a different kind came to the

---

[2] Pieron's experiments bearing on this point may be epitomized as follows: (1) He passed his finger across the path. The ants on each side halted and usually spread out along the line of disturbance,

conclusion that odors play a part in the life of ants, but that it is not by them that ants are guided on their journeys.[3] This is a much broader statement than that made above; indeed, it seems much broader than either his or my experiments warrant. Even though ants, favored by the muscular and tactile impressions furnished by the mandibles and feet, can still move with much precision when deprived of the use of eyes and antennæ, yet we have no more right to say that light and odors play no part in the home-going of normal ants than we have to say that, because blind men can move with much precision to and from home, vision plays no part in the home-journey of the normal man. What his and my experiments demonstrate is that odors do not play the sole rôle in the home-going of ants.

## II. EXPERIMENTS ON THE HOMING INSTINCT.

Most educated people once believed and many untrained people still think that there is a mysterious power, the homing instinct, which unerringly guides certain animals on their journeys. This "power" differs from a tropism in being guided by an inner rather than an outer stimulus. It was my purpose in the experiments of this chapter to discover whether ants possess a homing instinct.

The fact that ants lose their way militates against the idea that they have a homing instinct. Many a time after a rain, I have caused ants to lose their way by placing them and their pupæ on a stone situated within a few feet of their nest. At times the whole lot would roam aimlessly about; more often a portion would roam at random while the rest would busy themselves placing the pupæ under the stone on which I had placed them, or else under any other cover that they happened across; at yet other times a portion would finally reach the nest, while the rest would wander off.

finally some would strike the trail and the line of march would be renewed. (2) He moistened the path with a decoction of ants from an alien colony. The ants retreated precipitately. (3) He moistened the path with pure water. It had no effect on the ants. (4) He brushed odoriferous herbs across the path. The ants hesitated a moment then passed on. (5) He displaced the dust of their path with a twig. They were not disturbed. (6) He placed a piece of paper across the path of home-going ants. On this paper he scattered bits of turf and other detritus. When an ant had mounted this trap, Pieron gently transported the whole to a new situation in a place similar to the path along which the ants had been moving. In each case the ant continued in the direction it was going for a distance about equal to that between the trap in its original position and the nest opening.

[3] According to my understanding, Pieron's conclusion is so out of harmony with what his experiments warrant, that I have thought it wise to give, in this footnote, his exact words: "On en peut conclure que l'odorat doit jouer un rôle dans la vie de ses fourmis, mais ce n'est pas sur lui qu'elles se guidant dans leur passage." *Loc. cit.*, p. 176.

Not only have I caused ants to lose their way in the woods, but I have seen them lose their way on my LUBBOCK islands, which lack two inches each way of being two feet wide by two and a half feet long. Often, when I had disturbed a nest to remove the pupæ, the ants would rush out upon the island in all directions. After the excitement was over, many, sometimes all, of these ants would find their way back to the nest. In a large number of cases, however, instead of going home, a large number would congregate in groups on different parts of the island. These groups would usually be located on the peripheral ditch. There the ants would remain huddled together until discovered by ants that had spontaneously left the nest to seek what was to be found. Then they would be carried back to the nest.[4]

In my numerous experiments with individual, marked ants, I have incidentally obtained abundant evidence of the ease with which ants can be caused to lose their way. It was not an uncommon thing for an individual to fail completely to find its way home from one of my stages on the LUBBOCK island. After numerous random movements such an ant would usually settle down on some part of the stage or else busy itself rearranging the pupæ in the center of the stage. In almost all such cases, individuals from the same colony would learn the way to the nest and pass and repass the lost one, which seemed to have given up all attempts to reach the nest. In many cases the lost ant was finally carried to the nest by some other ant. This has happened in almost all the species examined; but it happened more frequently with Myrmica punctiventris Rog. than with any other. I have seen individuals lost within a foot of the nest on a piece of cardboard only six inches by six inches, and connected with the LUBBOCK island by an incline only twelve inches long!

To test this matter further the following experiment was devised. Myrmica punctiventris Rog. was selected, partly because of the slowness of its movements and partly because experience had taught me that individuals of that species were easily lost. The

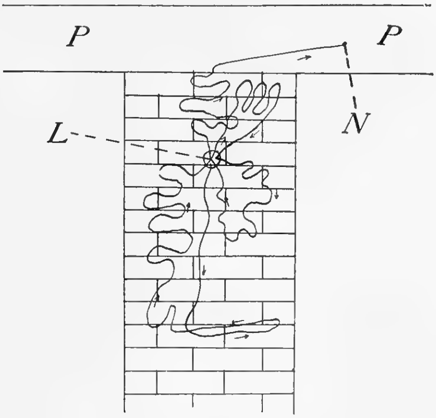
---

[4] If, as many claim, ants can communicate by means of their antennæ and say at least "Follow me," it might be asked parenthetically why did not these ants use their antennæ and tell those lost ants to follow them, instead of laboriously carrying them home one by one? For over two years I have had colonies of many of our common ants in the laboratory, and so far as my observation goes, whenever an ant wants another ant to go to a particular place, it picks it up and carries it there. Not only have I seen them thus carry workers, males, and even young females into the nest, but I have seen them thus carry workers and lay them down on a pile of pupæ. In no case have I seen any certain evidence of an antennal language. However, this is a problem that I intend to investigate more carefully in the near future.

nest containing the colony was placed on a new island. At the end opposite to that near which the nest was located was placed a new stage from which a new incline led to the island. On this stage I placed a large number of pupæ and workers. At once the workers began to move about the stage with pupæ in their mouths. Many fell off the stage. Many of these gathered in groups near the ditch; a few went to the nest. This experiment was begun at a quarter past nine in the morning. Occasionally a worker would partly descend the stage and then reascend. Up to ten o'clock, when I was called away, no worker had passed from the stage, down the incline to the nest. When I returned at half past two o'clock, the pupæ had been gathered into the center of the stage and the ants were resting on them. From this time until 4:40 o'clock the stage was watched continuously but no change occurred. When I returned at a few minutes before eight in the evening, everything was as I had left it at twenty minutes to five. I kept watch over these ants until ten minutes of ten without noticing any change excepting an occasional movement by one of them. Thus these ants were lost and remained so for at least thirteen hours, although their home was less than two feet away. When I returned next morning both ants and pupæ were in the nest, but how they got there I do not know. This result cannot be attributed to timidity or fright, for previously the same colony had been successfully used in seven experiments and each time the pupæ were taken home; but in each of those cases the ants had been given an opportunity to become familiar with the island.

But the facility with which ants lose themselves is not the only thing that fails to harmonize with the idea of a homing instinct; for the windings and twistings of the paths of many ants militate against that idea. Two summers ago, while in Elberton, Georgia, I noticed a sinuous line of ants leading from a nest of Forelius maccooki MacC. to a piece of honey-soaked paper and back. The paper was only three feet from the nest and situated in a level yard which was free from grass and weeds. The tortuous path the ants were following was at least fifteen feet long; it went all the way around the steps of the schoolhouse, although there were no topographical reasons why it should not have passed under the steps direct to the nest. At that place the steps were high enough for a boy to pass beneath them. Now had those ants possessed a homing instinct, they would have gone in a practically straight line from the paper to the nest and back again.

To test this matter further many experiments similar to the following one were tried in the field. I am uncertain of the species of the ant used in this experiment, but it was one of the small southern camponotids. The ant had its home in the baseboard of our front porch. At the time this experiment was begun, many of them were busy moving to and from some aphids that were feeding on the leaves of a vine that shaded the portico. By searching, I soon found a leaf upon which there was only one ant. This leaf was removed and inserted, by the petiole, in a notch in one of the brick supports of the veranda. The hole in which I had placed the leaf was only two feet from the nest opening. The ant acted as though dead for a while and then it thoroughly explored the leaf. From the leaf it mounted the pillar and went downwards (away from the nest) almost to the ground. It then went first to the right and then to the left and then zigzagged upwards again to the leaf. After again exploring the leaf it returned to the pillar and, after passing up and down several times, returned to the leaf. After another exploration of the leaf it returned to the wall and after a little meandering returned to the leaf. After another exploration it returned and zigzagged slowly upwards until it reached the baseboard. Then it at once increased its speed and hastened to the nest (Text Fig. 1). The leaf was placed



TEXT-FIG. 1. Path of ant in finding its way home; see text. *L*, leaf; *N*, entrance to nest; *P P*, porch. The arrows indicate the direction in which the ant moved.

in the hole at half past two o'clock. When the ant entered the nest the clock struck three. A half hour to find a nest that was only two feet away!

It is believed that these experiments show conclusively that ants do not possess a homing instinct.

## III. EXPERIMENTS ON THE POWER OF ANTS TO PROFIT BY EXPERIENCE.

If ants are guided in their home-goings neither by tropisms nor other forms of reflexes nor by a homing instinct, the probability is that they learn the way home. To test this two classes of experiments were performed. In the first class ants were allowed to work in concert (which is the normal way); in the other class, marked individual ants were induced to work alone or else in company with only one or two marked fellows. The cases where the ants worked in concert will be discussed first.

On the LUBBOCK island, which contained the nest of the colony to be tested, was placed a new cardboard stage from which a new cardboard incline led to the island. Ants and pupæ were placed on top of the stage. As a rule, the workers immediately began to move about at random. Some species moved slowly others more rapidly, and yet others so impetuously that many would fall off the stage. Some carried pupæ and others did not.

After a lapse of time varying with the species examined (for there is a marked contrast in the time it takes different species to solve the problem) usually at least one of the ants would find the way to the nest and back to the stage. As a rule it would carry a pupa the first trip, but sometimes it would go to the nest unburdened. The initial trip having been made, this ant would busy itself conveying pupæ to the nest; in this task it would soon be joined by several or many workers. These recruits were made partly from the ants on the stage and partly from ants roaming from the nest. During the first few trips most species moved slowly and cautiously as though they were feeling every step of the way. Later, they moved much more rapidly. Sooner or later (according to the activity of the species and the number of ants at work) all of the pupæ would be removed. In over a hundred experiments no live pupæ were left on the stage, excepting in cases where the ants failed to find the way home (which happened occasionally), or where I had added to their pupæ the pupæ of some other colony or species. In the latter case the alien pupæ were sometimes carried in and sometimes not. After the pupæ had all been removed, the ants would explore thoroughly both the stage and the incline. In some of these cases, after they had learned the way down one incline, I would add to the stage two or more inclines. In this case, when the pupæ had been removed, although no pupæ had been carried down these additional inclines, yet they would usually be thoroughly explored by the ants. After the exploration had been completed the ants gradually withdrew from the stage. It may not be out of place to state that if any of the ants originally placed on the stage failed to find their way home, they were carried there by the others.

After the workers had quieted down in the nest, the experiment was repeated; it was repeated not only once but over and over again, the series of experiments on the same colony often extending through several days. In the second experiment, in each of the several dozen series tried, the first ant usually reached the nest with a pupa in a much shorter time than did the first ant in the initial experiment of the series (Figs. 1, 3, 6).

In some experiments there was not much difference in the time of the two cases (Fig. 2) and in a few rare cases the time in the second case was even greater than at first (Fig. 4).

Frequently, in the midst of a series, the ants would act as though they had forgotten the way and had to relearn it (Fig. 5). This usually required much less time than at first. If any complications were introduced in the midst of a series the ants were sure to be delayed until they had mastered the situation (Figs. 3, 6). Sometimes they would fail. All of these points are brought out in Figs. 1 to 6, where the abscissas represent the number of each experiment in the series, and the ordinates the time in minutes that elapsed from the beginning of the series until the first pupa was carried into the nest. No one could watch the random movements made by the ants when first placed on the stage without being convinced that the finding of the nest the first time was merely a matter of chance; indeed, they sometimes failed completely to find it. The slow and exploring gait with which most species make the first few trips of the initial experiment of any series, when contrasted with the rapidity of the later movements, indicates that the ants learn the way home. The short period of time usually required for the first pupæ to reach the nest in the second or third and most of the subsequent experiments of a series, as contrasted with the long time required in the opening experiment of that series, suggests that the ants retain, for a while at least, what they have acquired. Indeed, there is hardly an experiment recorded in this paper, which does not indicate that ants profit by experience.

That ants can be trained is further evidence that they retain for a time what they acquire by experience. ERNST ('05) succeeded in training a Formica fusca to feed from his moving finger. He took a member of a colony of this species which had become somewhat familiar with man and confined it in a test-tube. In three hours after being confined to the tube it would feel with its antennæ the finger of the operator when presented to the open end of the test-tube. In order to tame it, food (honey, sugar) was offered it on the tip of the operator's finger, and in no other way. At the close of a month the test-tube was left open. With keen attention and with that tense attitude which would permit of immediate flight, the ant approached the opening and felt exploringly with its antennæ. On the second day its conduct was similar; but on the third day the ant wandered out for a distance of two centimeters. At the close of the second month the ant would feed from ERNST's finger, even when it was moving and the ant had to stretch halfway out of the tube in order to do so.

I have been able to train several ants to get to and from the stage used in my experiments in extraordinary ways. Two of these were trained to drop down; it might be nearer the truth to say that they trained themselves to jump down. One of these ants was a Myrmica punctiventris Rog. and the other was a Formica fusca var. subsericea Say. In each case the trick was learned in about the same way. A marked ant had been placed on the stage with the pupæ. Picking up a pupa it moved about at random and accidentally fell off the stage. Its impetuous dash was what carried Formica overboard; it is not possible to say what caused the fall of the more slowly moving Myrmica. Although the vertical distance from the stage to the island was four inches, the ant neither dropped the pupa nor seemed the least disturbed by the jar. It went at once to the nest, deposited the pupa and returned to the island, where it meandered from place to place, evidently not knowing how to return to the stage. With a pair of small forceps I picked it up gently and replaced it on the stage. It picked up a pupa, moved about the stage for a few moments, then dropped to the island and hastened to the nest with the pupa. Once more the ant was replaced on the stage, once more it picked up a pupa and dropped to the island. This was repeated over and over again.

In the case of Myrmica, I was careful always to pick it up at about the same place on the island. After I had picked it up about a dozen times, it would go from the nest direct to that place and wander about in a curve of short radii. When the forceps were presented the ant would mount them of its own accord and rest quietly thereon until transferred to the stage. Then it would pick up a pupa, drop off the stage and hasten to the nest. The ant always dropped off from the same side of the stage; but not from the same spot. Whenever it dropped, it was amusing to note the reflex tendency of its legs to cling to the support. Each time Formica would make several false starts before the successful drop was made. It would make a dash and perhaps the front part of the body would clear the edge, but the two hinder pairs of legs would hold fast to the stage. Recovering, it would make another start, and this time in all probability one or both hinder pairs of legs would retain the ant on the stage. But persisting in its efforts, it would finally make the drop through ten centimeters of vertical space—an enormous drop for a creature so small. Towards the latter part of the experiment the ant took much less time to overcome the reflex tendency of its legs to cling to the support. Formica continued this dropping until, by accident, I pinched its body with the forceps, and after that, not only would it not mount the forceps; but, when they were brought near, it would dash about in such a lively manner that it was impossible to capture it without injuring it.

Myrmica never dropped off in this headlong manner; on the contrary it usually dropped off sidewise, but like Formica it had much trouble in overcoming the reflex tendency of its legs to cling to the support.

In addition to proving that ants retain what they learn, this experiment lends credence to those anecdotes in which ants are reported to have voluntarily dropped from ceiling to table and from leaves to the ground (ROMANES '92, pp. 134, 135).

On another occasion I trained an ant to use a section-lifter as an elevator on which to pass to and from the stage. This time it was a specimen of Formica fusca var. subsericea Say. On this occasion two marked workers, A and B, were being experimented upon at the same time. The one I have called A readily learned the way down and up the incline; but to B this was an insoluble problem. It continued for a long time to move at random over the stage, reaching down over first one edge and then over another, as though it were reaching for a support that was not to be found; but nothing prompted it to pass down the incline. In experiments where the time required to learn the trick was not the point to be investigated, I had sometimes helped ants to learn the way by forcing them with forceps or spatula, to move in the right direction. I thought I would thus help B to learn. So with my forceps I pushed it along. Several times I succeeded in getting it to the incline, but nothing that I did would induce it to go down. I had failed, but this was not the first time that I had failed in similar attempts with other ants.

Prompted by another thought, I shoved the section-lifter under the ant and transferred it to the island. The ant then stepped off and carried the pupa into the nest. As soon as B returned to the island, I shoved the section-lifter under it and transferred it to the stage. B stepped off and picked up another pupa. With the section-lifter I again transferred it to the island. After this had been repeated several times, the moment I presented the section-lifter, whether on the island or on the stage, the ant immediately mounted it and rested quietly thereon until it had been removed to the stage or to the island; then it stepped off and picked up a pupa or else went into the nest. I usually held the section-lifter from two to four millimeters above the surface of the island or stage. In this manner the industrious creature passed to and from the stage about fifty times in something less than two hours.

Whenever I presented the section-lifter to other ants of the same colony, they would attack it, or avoid it, or else mount it and roam over blade and handle and sometimes even my hand. When the same section-lifter was presented to A (the one that all this time had been conveying pupæ down the incline) it would avoid it and pass on.

Thus I had two individuals of the same colony, at the same time and under identical external conditions, responding to the same stimulus in quite different ways. To the one the incline had no psychic value, to the other it was a stimulus to pass to and from the stage. To one the section-lifter was a repellent stimulus, to the other an attractive stimulus. Each had acquired a different way of accomplishing the same purpose and each had retained and utilized what it had gained by experience.

Not only do ants retain, for at least a few hours, what they have learned; but a habit once formed is hard to break. From time to time I have performed experiments for the purpose of breaking up habits. Often I have failed, my patience not being a match for the persistence of the ant; in other cases, by patient persistence, I have succeeded. I desire to relate one such case.

A minute before ten on the morning of September 23, I placed a Formica fusca var. subsericea Say, together with some pupæ, on a new cardboard stage, from which an incline led to the island. For my purpose, it was necessary for the ant to learn the way down and up the incline, but down the incline it would not go. After passing by the incline several times, the ant passed underneath the stage and down the bottle, which formed the central support of the stage, to the island and thence to the nest. Hoping that it would even now learn the way down the incline, I replaced the ant on the stage. Six times it was replaced on the stage, six times it went down the bottle. To those who believe that the movements of ants are tropic responses to odors, it may be of interest to state that each time the ant went down the bottle by a different path, usually more or less spiral. Now the experiment contemplated demanded that that ant learn the way either down or up the incline. Knowing by experience that ants sometimes go out by one path and return by another, I thought that possibly this ant might learn the way up the incline. So when the ant came out this time I let it alone. It made no attempt to ascend the incline, but after a little meandering, it ascended the bottle to the stage and descended the same way, with a pupa, to the island.

In order to prevent further use of this path, I painted the neck of the bottle with cedar oil and then replaced the ant on the stage. This was at half past ten in the morning. In a very short time it learned to carry the pupæ down the incline, but at first the ant always went first to the bottle and then to the incline. It was not until two o'clock in the afternoon that it learned to go down the incline without first going to the bottle. And even after that it would occasionally go to the bottle. To learn the way up was even more difficult. Whenever the ant returned from the island to the nest, it would go almost everywhere except to the foot of the incline and roam about until replaced on the stage or incline. If placed on the incline at its foot, it would ascend; but it was not until six minutes to three that the ant, of its own accord, went to the incline and ascended it to the top. Then it returned to the island and meandered. At three o'clock it ascended the incline to the stage. Thus it took it several hours to unlearn the old way and learn the new.

Although the new adjustment was slowly formed, once formed, it persisted. At a quarter past three the ant was imprisoned. At one minute to seven, when the experiment was resumed, it still retained the new adjustment. At eight o'clock it was imprisoned for the night. At twenty minutes to nine the next morning the experiment was resumed. The ant still retained the new adjustment, for in seven minutes it was busy carrying pupæ up and down the incline. And all of this seven minutes was not consumed in searching for the nest, for fully half of it was spent by the ant in stretching itself and cleaning its antennæ. Contrasting this three minutes with the several hours it took to learn the trick furnishes convincing evidence that ants retain what they acquire. It is unnecessary to describe any more special experiments along this line, for almost every experiment recorded in this paper proves that ants profit by experience.

In profiting by experience and retaining for a time what it has thus acquired, the ant resembles the fish (SANFORD '03), the frog (YERKES '03), the sparrow (PORTER '04), the chick (THORNDIKE '98, MORGAN '00), the rat (WATSON '03), the otter (HOBHOUSE '01, p. 155–184), the elephant (HOBHOUSE '01 pp. 164, 165, 169, etc.), and the monkey (THORNDIKE '98, HOBHOUSE, '01, pp. 167, 182, etc.). It thus appears that the ant is no more guided in its journeys by tropisms, other reflexes, or a homing instinct, than are vertebrates.

## TABULATED EXPERIMENTAL EVIDENCE.

To give detailed reports of each of the several hundred experiments upon which the above statements are based would require quite a volume. For the benefit of those who desire a more detailed statement than is given above, I close this section with the tabulated results of four series of experiments conducted with Prenolepis imparis Say, two with Formica fusca var. subsericea Say, and one with Myrmica punctiventris Rog. Prenolepis and Formica are fair representatives of the Camponotidæ, while Myrmica is a good representative of the Myrmicidæ. The shortest of these series extended over a little more than two days, the longest over a little less than nine days. Some of the series used extended over several times the longest time recorded here; but these serve as typical series. All of the experiments in each series were conducted upon the same colony; but each series represents a different colony.

### EXPLANATION OF ABBREVIATIONS IN TABLES I TO VII.

Column A. The number of the experiment in the series.
Column B. Minutes that have elapsed since the close of the last experiment.
Column C. Minutes that have elapsed from the beginning of the experiment up to the time the first ant reaches the nest (either burdened or unburdened).
Column D. Ditto. Second ant.
Column E. Ditto. Third ant.
Column F. Ditto. Until a line of ants is moving to and from the nest.
Column G. Ditto. Until all of the pupæ have been carried to the nest.

### TABLE I.

*Prenolepis imparis Say. Series 1.*

| A | B | C | D | E | F | G | |
|---|---|---|---|---|---|---|---|
| Exp. no. | Time since last exp. | Time of 1st ant | Time of 2d ant. | Time of 3d ant. | Time of ant col. | Total time of exp. | Remarks. |
| 1 | | 12 | | | 22 | 202 | Stage with one incline. |
| 2 | 226 | 9 | 9.5 | 9.5 | 13 | 14 | Do. |
| 3 | 10 | 0 | | | 1 | 6 | Do. |
| 4 | 4 | 0 | | | 0 | 9 | Do. |
| 5 | 11 | 1 | | | 1 | | Do. |
| 6 | 17 | 0 | | | 0 | 11 | Do. |
| 7 | 0 | 1 | 2 | | 3 | 9 | New incline substituted for old. |
| 8 | 0 | 0 | | | 0 | 10 | Same apparatus as above. |
| 9 | 26 | 0 | | | 0 | 17 | Do. |
| 10 | 2269 | 0 | | | 0 | 18 | Do. |
| 11 | 2 | 1 | 2 | | 3 | 27 | Used new stage but old incline. |
| 12 | 2 | 10* | | | 34 | 54 | Removed old incline and put new incline in new place. |
| 13 | 37 | 0* | | | 8 | 25 | Same apparatus as used in 12. |
| 14 | 2 | 1 | | | 1 | 21 | Do. |
| 15 | 0 | 0 | | | 0 | 28 | Do. |
| 16 | 4 | 0 | | | 8 | 31† | Besides the old incline a second is put on opposite side of stage. |
| 17 | 9 | 0 | | | 0 | 11‡ | Same conditions as above. |
| 18 | 443 | 0 | | | 0 | 21 | Do. |
| 19 | 3 | 1 | 6 | 6 | 8 | 28° | Substitute a new incline for the one down which they had been going; left other incline on opposite side of stage. |

Any time less than one-fourth minute is called 0.

* Many of the workers passed at once to where the incline had formerly been attached, and up to the end of the experiment some would always go to that place first and then from there to the new incline.

† Two pupæ were carried down the new incline, the rest down the old.

‡ Three pupæ were carried down the new incline, the rest down the old.

° Three pupæ were carried down the old incline, the remainder down the new incline which occupied the position of the incline down which they had learned to convey pupæ to the nest.

TABLE II.

*Prenolepis imparis Say. Series 2.*

| A<br>Exp. no. | B<br>Time since last exp. | C<br>Time of 1st ant | D<br>Time of 2d ant. | E<br>Time of 3d ant. | F<br>Time of ant col. | G<br>Total time of exp. | Remarks. |
|---|---|---|---|---|---|---|---|
| 1 | | 34 | 36 | 69 | 93 | 194* | Stage with incline *A* on left. Daylight. |
| 2 | 1 | 0 | | | 0 | | Do. Daylight. |
| 3 | 540 | 15† | | | 60 | | Do. Night. |
| 4 | 590 | 0 | | | 0 | 15 | Do. Daylight. |
| 5 | 1440 | 0 | | | 0 | 40‡ | Do. Daylight. |
| 6 | 0 | 2 | 9 | 10 | 12 | 47° | Same stage, incline *A* on right, new incline *B* placed on left. |

* This experiment furnishes a good example of the impossibility of predicting what an ant will do when presented with a new problem. A worker spent several minutes wedging a pupa into the space between the underside of the stage and the incline. Having succeeded it moved off; but in a few moments returned, pulled out the pupa and carried it back to the stage. In less than two minutes it returned and replaced the pupa in the crevice between the incline and stage.

While this was going on, worker number two carried a pupa and laid it on the incline near the bottom. One hundred and fifty mm. higher up the incline it placed another pupa. Then, after carrying pupa number two up and down the incline twice, it laid it on the incline thirty mm. higher than the first. Likewise it placed a fourth pupa twenty mm. below the second. While doing so, it accidentally knocked pupa number three off of the incline. It carried the fifth pupa down the stage to the nest, but in doing so knocked another pupa off of the incline. This was the second pupa carried to the nest from the stage. The pupæ that fell to the island were carried to the nest by stragglers from the nest.

† These were working by incandescent light and at night; the two previous experiments had been performed during the daytime.

‡ While the ants were passing to and fro, the incline was so adjusted as to form a vertical gap about five mm. high between the base of the incline and the Lubbock island. This did not disturb the ants in the least.

° One worker carried a pupa down incline *A* to the nest, all of the other pupæ were carried down the new incline *B*, which occupied the same position that incline *A* occupied at the time the ants learned the way down it. One worker ascended incline *A* from the island and descended incline *B* with a pupa which it carried to the nest.

## TABLE III.

*Prenolepis imparis Say. Series 3.*

| A<br>Exp. no. | B<br>Time since last exp. | C<br>Time of 1st ant. | D<br>Time of 2d ant. | E<br>Time of 3d ant. | F<br>Time of ant col. | G<br>Total time of exp. | Remarks. |
|---|---|---|---|---|---|---|---|
| 1 | | 12 | | | 21 | 71[*] | Stage with incline *A* on the left. |
| 2 | 73 | 0 | | | 10 | 14 | Do. |
| 3 | 1 | 0 | | | 0 | | Do. |
| 4 | 35 | 0 | | | 0 | 11[†] | Same stage, incline *A* on right, new incline *B* on left. |
| 5 | 4 | 0 | | | 0 | 35[‡] | Same as above only incline *B* has vertical gap, 1 mm., between it and island. |
| 6 | 40 | 0 | | | 0 | 42 | Do, but with vertical gap 4 mm. |
| 7 | 47 | 0 | | | 0 | 30 | Do. |
| 8 | 1490 | 2[°] | | | 3 | | Do. |
| 9 | 17598 | 10[§] | | | 12 | 28[**] | Nest higher than stage; incline *A* on left of stage. |
| 10 | 1 | 0 | | | 0 | 39 | Do. except that stage was revolved 180°; inc. *A* on the left. |
| 11 | 5 | 1 | 2 | 3 | 16[††] | | Do. but incline *A* on the right and incline *B* on the left. |
| 12 | 21465 | 4 | 5 | 6 | 54[‡‡] | | Nest lower than stage; incline *A* on left; 16 c. p. lamp near *A*. |
| 13 | 0 | 3 | 5 | 6 | [°°] | 135 | Do. but the light was placed near incline *B*. |

[*] In four minutes a worker had passed down the incline and laid a pupa upon the top of the nest. For some time it continued to store pupæ in that place and was soon joined in the occupation by a few other workers. Later stragglers from the nest carried these pupæ into the nest.

[†] All of the pupæ were carried down incline *B*. A worker ascended incline *A* to the stage and carried a pupa down incline *B* to the nest.

[‡] Two of the pupæ were conveyed down incline *A* to the nest, the remainder were carried down incline *B*.

[°] Immediately several workers picked up pupæ and started down incline *B*, but when they reached the gap, they turned around and returned to the stage.

[§] While some were seeking a way home, others were storing pupæ under the foot of the incline plane. These pupæ were finally taken to the nest.

[**] The ants went practically direct from the pile of pupæ to the incline. No pupæ were stored under the incline.

[††] The workers, one by one, passed unburdened to the nest and left the pupæ alone on the stage. Fully eleven minutes elapsed before they returned to the stage and began to carry the pupæ home. One worker passed down incline *A* to the stage and then carried a pupa up incline *B* to the nest. All of the pupæ were carried up incline *B*, which occupied the same position that had been occupied by the incline along which they had learned the way to the nest.

[‡‡] All of the workers passed, unburdened, to the nest and over thirty minutes elapsed before any worker returned to the stage for pupæ. All the pupæ were carried down incline *A*.

[°°] The pupæ were carried down incline *A*. All of the work seems to have been done by one worker; the others, after once reaching the nest, remained therein.

## TABLE IV.

*Prenolepis imparis Say. Series 4.*

| A<br>Exp. no. | B<br>Time since last exp. | C<br>Time of 1st ant. | D<br>Time of 2d ant. | E<br>Time of 3d ant. | F<br>Time of ant col. | G<br>Total time of exp. | Remarks. |
|---|---|---|---|---|---|---|---|
| 1 | | 8 | 10 | 12 | 16 | 69 | Stage with incline *A* on left side. |
| 2 | 1 | 2 | 4 | 6 | | 100 | Do. |
| 3 | 1 | 0 | | | 0 | 60* | Incline *A* on right, inc. *B* on left. |
| 4 | 6 | 0 | | | 0 | † | Do. revolved the stage through an angle of 180°. |
| 5 | 1085 | 0 | | | 0 | 150† | Do. |
| 6 | 8 | 0 | 4 | 13 | 20 | | Do. |
| 7 | 1260 | 0 | | | 0 | | Do. |
| 8 | 51 | 1 | 2 | 4 | | | A vertical gap of 3 mm. between base of incline *B* and island. |
| 9 | 2880 | 4 | | | 9 | ‡ | Do. but 16 c.p. lamp near incline *A*, incline *B* on opposite side. |
| 10 | 0 | 2 | 8 | 8 | 8 | 40° | Do. but 16 c.p. light placed near incline *B*. |
| 11 | 3 | 0 | | | 0 | 60 | Incline *B* removed, light placed where incline *B* had been. |
| 12 | 1271 | 0 | | | 0 | § | Incline *A* on right, incline *B* on left, 16 c.p. light near *B*. |
| 13 | 0 | 4 | | | 4 | 26¶ | Do. but 16 c.p. light is placed near *A*. |
| 14 | 4260 | 12 | 14 | 16 | 91 | 155** | Do. but placed dark chamber on stage. |

* Over 100 pupæ were used. Eight were carried down incline *A*, probably all by the same worker. The remainder were carried down incline *B*.

† All were carried down incline *B*.

‡ The pupæ were all carried down incline *A*.

° The workers were, at the beginning, much disturbed. The first three pupæ were carried down incline *B*. By that time a line of workers had begun to pass down incline *A*. After that occasionally a pupa was carried down incline *B*.

§ All of the pupæ were carried down incline *B*.

¶ At first an occasional worker went down incline *A*, while a line of workers was passing down incline *B*. Gradually the number going down incline *A* increased until there were lines of workers moving down both inclines.

** The majority of the workers began almost at once to store pupæ in the dark chamber. One worker soon found the way to the nest with a pupa, and after that made regular trips. It was not until all of the pupæ had been removed from the open and placed in the dark room that a line of workers began to convey pupæ to the nest.

TABLE V.

*Formica fusca var. subsericea Say. Series 1.*

| A<br>Exp. no. | B<br>Time since last exp. | C<br>Time of 1st ant. | D<br>Time of 2d ant. | E<br>Time of 3d ant. | F<br>Time of ant col. | G<br>Total time of exp. | Remarks. |
|---|---|---|---|---|---|---|---|
| 1 | | 1 | 2 | 2 | 3 | 23 | Incline *A* on left side. |
| 2 | 5 | 5 | | | 5 | 10 | Do. |
| 3 | 0 | 3 | | | 4 | | Do. |
| 4 | 0 | 0 | | | 0 | 13 | Do. |
| 5 | 3 | 0 | | | 0 | 27 | Do. |
| 6 | 0 | 0 | | | 0 | 30 | Do. |
| 7 | 240 | 1 | | | 1 | 17* | Incline *A* on the right, incline *B* on the left. |
| 8 | 53 | 5 | | | 10 | 33 | Do. but both stage and incline new. |
| 9 | 6661 | 11 | 13 | 15 | 18 | 65 | Incline *A* on the right, no other incline used. |
| 10 | 1 | 6 | | | | | Do. |
| 11 | 5 | 2 | | | | | Do. |
| 12 | 33 | 5 | | | | 30† | Incline *A* on the left, incline *B* on the right. |
| 13 | 2400 | 14 | | | | 54 | Incline *A* on the right, incline *B* not used. |
| 14 | 4 | 16 | | | | | Do. |

* Three pupæ were carried down incline *A*, the rest down incline *B*. The workers moving down incline *B* rushed along, the ones that went down incline *A* moved very slowly.

† The pupæ were all carried down incline *B*.

TABLE VI.

*Formica fusca var. subsericea Say. Series 2.*

| A<br>Exp. no. | B<br>Time since last exp. | C<br>Time of 1st ant. | D<br>Time of 2d ant. | E<br>Time of 3d ant. | F<br>Time of ant col. | G<br>Total time of exp. | Remarks. |
|---|---|---|---|---|---|---|---|
| 1 | | 4 | 5 | 7 | 17 | 43 | Incline *A* on the left. |
| 2 | 4 | 1 | 2 | 2 | 2 | 28 | Do. |
| 3 | 1 | 0 | | | 0 | | Do. |
| 4 | 3444 | 1 | | | 10 | 28 | Do. |
| 6 | 5760 | 17 | 42 | 43 | 67 | | 2 stages, one higher than other; incline *A* leads from 1 to 2, incline *B* from 2 to the island. |
| 7 | 427 | 1 | 4 | 35 | | | Do. |
| 8 | 620 | 21* | 29 | 31 | 50 | 95 | Do. |
| 9 | 145 | 1 | 3 | 4 | 5 | 69 | Do. |
| 10 | 59 | 1 | 2 | 2 | 4 | | Do. |
| 11 | 194 | 18† | 24 | 26 | | | Do. |
| 12 | 720 | 1 | 2 | 4 | | | Do. |
| 13 | 120 | 1 | 3 | 4 | | | Do. |
| 14 | 244 | 2 | | | 3 | ‡ | Do. but incline *C* substituted for *A* and incline *A* placed to lead from stage 1 to island. |

* At first the ants stored all of the pupæ in the crevice between incline *A* and stage number one. After that had been accomplished, they began carrying them to the nest.

† This was conducted at night, by incandescent electric light; all of the other experiments of the series were conducted by daylight.

‡ The pupæ were carried up incline C to stage number two, across stage number two to incline *B*, down incline *B* to the nest. No pupæ were carried down incline *A*.

TABLE VII.

*Myrmica punctiventris Rog. Series 1.*

| A<br>Exp. no. | B<br>Time since last exp. | C<br>Time of 1st ant. | D<br>Time of 2d ant. | E<br>Time of 3d ant. | F<br>Time of ant col. | G<br>Total time of exp. | Remarks. |
|---|---|---|---|---|---|---|---|
| 1 | | 35 | 120 | 122 | 152 | 192 | Inc. *A* on right side. |
| 2 | 214 | 8 | 9 | 10 | 40 | 105 | Do. |
| 3 | 818 | 2 | 2 | 2 | 5 | 100 | Do. |
| 4 | 155 | 0 | | | 0 | 35* | Incline *A* on the right; incline *B* on the left. |
| 5 | 26 | 0 | | | 0 | 39† | Do. |
| 6 | 13 | 1 | | | 6 | 30‡ | Incline *A* on the left; incline *B* on the right. |
| 7 | 3142 | 5 | 6 | | 7 | 75° | Do. |
| 8 | 25820 | | | | | § | New stage, inc. *A* on left; placed on new island. |
| 9 | 1440 | 5 | | | | | Same apparatus as in ex. 8. |
| 10 | 1521 | 1364** | | | | 1395 | Same stage; incline *A* on right; dark chamber on top of stage. |

* One pupa was conveyed down incline *B*, all the others down incline *A*. One worker ascended incline *B* to the stage and carried a pupa down incline *A*.

† One pupa was conveyed down incline B, the remainder down incline *A*.

‡ All of the pupæ were conveyed down incline *B*.

° A very large majority of the pupæ were carried down incline *B* to the nest. One pupa was carried down incline *A* to the nest and several were carried down incline *A* and stored under the base of the incline.

§ Up to bedtime the pupæ had not been carried to the nest. Thus the ants were lost for over 12 hours.

** In the course of half an hour all of the pupæ had been stored in the dark chamber. There they were left, while the workers, one by one, straggled back to the nest. After the lapse of 21 hours and thirty minutes, the pupæ were still in the dark chamber. I then removed the dark chamber and placed workers from the nest on the stage.

## IV. IMPRESSIONS THAT INFLUENCE HOME-GOING ANTS.

I have endeavored to show that ants find their way home by virtue of something which they acquire by experience and retain; in other words, that they acquire from their environment impressions which influence their home-going. I now propose to examine the nature of these impressions.

Most recent students of ants write as though these impressions were composed solely of olfactory elements. One group of writers, represented by BETHE, claims that the home-going of ants is the result of olfactory reflexes; another, represented by WASMANN, claims that olfactory percepts are important.

Scattered through the literature are passages which indicate that some authors are not fully satisfied with this view. LUBBOCK

('81, p. 262) showed that, under certain conditions, Lasius niger will move a short distance along an unscented path. WASMANN ('01), although believing that the footprints possess an odor-shape which enables ants to tell which way to go, gives several examples of ants going a short distance along paths that have not been scented with their trail. VIELMEYER ('00), in his study of Leptothorax unifasciatus, claims that, when near the nest, light and shadows assist the ants in finding their way, and more than twenty years before that LUBBOCK had stated that "In determining their courses ants are greatly influenced by the direction of the light." PIERON ('04), although admitting that odors play an important rôle in the life of ants, was influenced by his discovery that ants sometimes move along paths that have not been scented by trails to conclude that odors play no part in guiding them home. According to him, their home-going is controlled by a tactile sense and muscular memory.

As far as I can understand PIERON, his hypothesis is as follows. On the outgoing trip the muscular movements made induce in the nervous mechanism a condition which enables the ant to return to the nest, in a reverse order, over the same pathway by which it journeyed forth. That tactile impressions are, and that muscular impressions may be, factors in the impression that guides ants harmonizes with my experiments; but that the muscular movements play any such rôle as is here indicated seems improbable. PIERON's hypothesis implies that an ant returns to its home in practically the path by which it went out. I have conducted a large number of experiments which show conclusively that this is not always the case.

1. I have already mentioned the case of the ant which would drop, with a pupa in its jaws, from the stage to the island; but which, on returning from the nest, would wander about the island until I presented a pair of forceps. It would then mount the forceps and rest quietly thereon until I had placed the tip of the forceps on the stage. It would then step off and pick up a pupa and take a flying leap from the stage to the nest.

2. I had a specimen of Formica fusca var. subsericea Say, which regularly descended from the stage to the island on the under side of the incline, but on returning to the stage this ant always moved along the upper side.

3. Another specimen regularly descended to the island by way

of the incline and returned to the stage up the bottle by which the stage was supported at its center. This it did until half the pupæ had been conveyed to the nest.

4. On several different occasions, where I had attached a second incline to a stage from which ants had been conveying pupæ down another incline to the nest, I have noticed that an ant would occasionally ascend to the stage by the second incline, pick up a pupa and then pass down the other incline to the nest.

5. During the first part of my experiments I was not looking for data along this line, but towards the close I devoted five hours an evening for two weeks to an investigation of the problem. Formica fusca var. subsericea served as a subject. I placed a number of pupæ and a marked worker on a stage from which an incline led to the island. I found that in each case the ant had to learn the way, not only from the pupæ to the incline and down it to the island and thence to the nest, but that it had also to learn the way from the nest to and up the incline. And it usually took a much longer time to learn the way from the nest to the stage than it did to learn the way from the stage to the nest. Now if PIERON's hypothesis were true, the muscular memory of the ant should have carried it back to the stage in practically the same path by which it had passed from the stage to the nest. But such was not the case. On leaving the nest, the ant would wander first in one direction and then in another, often returning to the nest. It acted as though hunting for something it could not find. At times it would fail entirely to find its way back.

6. In my experiments on the rôle light plays in the home-going of ants, I gathered some data on this point. With the light in a certain position, the marked ant was allowed to learn thoroughly the way to and from the stage to the nest. Then the light was placed on the opposite side of the stage. The ant was always much disturbed by the change and it always took it a long time to find the way to the nest. But, having reached the nest, if PIERON's hypothesis be correct, its muscular memory should have guided it immediately back along the path by which it reached the nest. The ant, however, always had a hard time finding the way back to the stage and often it failed completely.

*Experiments with Odors.*—Having observed that ants can find their way about without eyes and without antennæ, PIERON concludes that odors play no part in the home-going of ants; but, as

I have already stated, this no more proves that normal ants do not utilize odors in their home-going than does the fact that blind men are able to find their way about demonstrate that normal men do not use visual sensations in their journeys.

Most writers lay great stress upon the odor of the trail, and FIELDE claims that a special organ (the ninth joint of the flagellum) exists for the detection of the track-odor. If I interpret my experiments aright, it is not the scent of the trail merely, but the odor-peculiarities of the pathway as such, that form a part of the impression which enables ants to pass home. The readiness with which ants react to any strange odor that is added to their pathway lends support to the view that the odors of the pathway itself form a part of the psychic impression of home-going ants. PIERON himself says that ants traveling in a common road are arrested by unexpected odors; they flee from odors of their enemies and cross with little difficulty scents of vegetable origin. To my mind, this statement of PIERON'S supports the view just presented.

To test this matter in the laboratory, several experiments like the following were tried. A colony of Formica fusca var. subsericea Say was divided and each nest placed in the same relative position on different LUBBOCK islands. On each island was placed a cardboard stage from which an incline led to the island. Each of these inclines led from the same relative position on the stage and in the same direction. On each stage was placed a large number of pupæ and a marked worker. After each worker had thoroughly learned the way to and from the stage to the nest, the experiment proper was performed. The ant that was carrying pupæ from stage number one was the subject of the experiment proper. The ant on stage number two being used, in the manner hereafter mentioned, as a control.

Special inclines were made by placing across the middle of the white slip used for ordinary inclines a transverse band, three-fourths of an inch wide, of some odoriferous substance. The chemicals used for this purpose were xylol, oil of cedar and oil of cloves. When the ant on stage number one had become so well acquainted with the way home as not to be disturbed by the substitution of a new incline of the same kind for the old, the old incline was replaced by one of these special inclines. In each case the ant was very much disturbed, but in the case of both the xylol and cedar oil, after a while, the ant began to go back and forth across the band conveying pupæ to the nest. In a short time after the first few trips had been made across the band, the ant would be making its journeys to and from the nest as rapidly and regularly as down the old incline. Then a new special incline or a plain incline of the ordinary kind was substituted for the one just used and that one transferred to the control stage. In each case the animal used for control was much disturbed, which demonstrated that, from the ant's standpoint, the transverse band of volatile substance was still on the incline. Evidently that odor or better that volatile substance had become for ant number one a familiar element of the homeward path. This experiment then shows that the volatile chemical peculiarities of the path form a portion of the impression experienced by ants on their journeys (Figs. 9, 18).

*Experiments with Tactile Stimuli.*—That tremors affect the home-going of ants is evidenced by the fact that a comparatively slight tap on the stage will cause an ant to halt and a severe jar will so disturb it as often to make it necessary for the ants to relearn the way home (Fig. 12, *D*).

A number of experiments were performed for the purpose of discovering whether ants are affected by the surface character of the pathway. In this case a worker was trained to go down and up a smooth black incline. After it had reached the condition where it was not disturbed by the substitution of another smooth black incline for the old one, a black incline with a velvety surface was substituted for the smooth black one. Myrmica punctiventris Rog. was much disturbed by the change (Fig. 10, *g*), but Formica fusca was not (Fig. 18, *M*; 14, *P*).

It seems legitimate to assume that tremors and jars probably give kinesthetic stimuli and that the velvety surface gives a tactile stimulus. Such being the case, kinesthetic impressions probably form part of the mental furniture of all ants examined by me and at least some ants have tactile impressions.

*Experiments with Optic Stimuli.*—To see if optical impressions are received by ants two kinds of tests were conducted: experiments with ants working in concert, and with marked individuals.

In experiments of the first type a cardboard stage from which a cardboard incline led to the island was used. A 16 c.p. incandescent electric lamp was placed, sometimes near the side to which the inclined plane was attached, and sometimes near the opposite side. After the ants had thoroughly learned the way home, a new incline was attached to the side of the stage which was opposite the one to which the old incline was attached. If after a lapse of five minutes no ants went down this second incline, conditions were considered right for the test. The light was now transferred to the opposite side of the stage. In each case the halting movements of the ants showed that they were disturbed (Fig. 6). In most cases, some of the ants would finally go down the new incline and in a few cases, after the lapse of several minutes, all of them would go down the new incline. These experiments were tried on all of the ants used in the experiments on heliotropism (p. 371).

Similar experiments were conducted with marked individuals of the species, Formica fusca var. subsericea Say, Myrmica punctiventris Rog. The results harmonized with those derived from experiments conducted with ants working in concert (Fig. 14, *B*; Fig. 17, *B*, *H*, *M*); only, in almost every case, after a greater or less lapse of time, the ant would usually find its way down the old incline to the nest; and after a still greater lapse of time find its way back to the stage.

Fig. 16 illustrates how ants are disturbed by altering the position of the light better than a multitude of words. From the beginning to *B* the ants had been working by daylight, the light coming from two windows, one on the south and one on the west. From *B* to *C* the ants were working at night, the illumination being furnished by electric lights and coming from the northeast. From *C* to the end, the conditions were the same as from *A* to *B*.

To determine whether this effect was due to the intensity of the light, to the direction of the rays or to heat, the following series of experiments were conducted with Formica fusca var. subsericea Say.

That the effect described above was not due to heat, was proved in the following manner. A cardboard stage was arranged with its left side connected to the table by a cardboard incline. At the right and left of this stage was placed a heat-filter, consisting of a tall museum jar 34 cm. x 16 cm. x 7 cm., filled with cold distilled water. At the beginning of the experiment, a 32 c.p. incandescent lamp was placed behind one of these filters (usually behind the one near the incline). After the ants had traveled the path long enough to make the trips regularly and rapidly, the lamp was transferred to a point behind the opposite filter. In every case the workers were much disturbed in the manner stated above. Since the heat had been excluded, it is evident that the disturbance was the result of some form of light stimulus. This was repeated with seven different colonies of Formica fusca.

To determine whether the intensity or the direction of light was the determining factor, a different kind of experiment was used. The stage and incline were arranged as before. Sometimes the heat-filters were used, but more often they were not. To furnish illumination, four different candle powers (4, 8, 16 and 32) of incandescent electric lamps were used, one at a time, in a darkened room. At the beginning of the experiment a lamp of a certain candle power was placed near the side of the stage to which the incline was attached. After the ants had thoroughly learned the way home, a different candle power was substituted for the first. After the lapse of a few more minutes this lamp was transferred to the opposite side of the stage. Shortly it was returned to its former position. A few minutes later a different candle power was substituted for this. This performance was repeated over and over again until each lamp had thus been used one or more times. It was found (Fig. 17) that substituting a lamp of one candle power for one of a different power had no disturbing effect on the actions of the ants; but that by any marked change in the angular position of the light, no matter what the candle power, the ants were very much disturbed. This warrants the conclusion that when light is present the direction of its rays plays a prominent rôle in the home-going of ants whose eyes are normal.

LUBBOCK over twenty-five years ago stated this fact, but his observation has been either overlooked or ignored by recent continental writers.

*Experiments with Colored Pathways.*—The purpose of the experiments now to be described was not to determine whether ants have color vision, but simply to ascertain whether the color of the path plays a part in the home-going of ants. In these experiments the usual stage was employed; but the inclines were composed of colored papers of practically the same texture. Each incline was composed of one color. Of the color series I used, red, yellow, green, blue, purple; of the brightness series, white and black. When an ant had learned the way down a certain colored incline so well that it was not disturbed by the substitution of another of the same color, an incline of a different color was substituted for the old one. This was repeated until all of the colors had been used at least once. All ants were not affected in the same way by these changes. Myrmica punctiventris was slightly affected each time a change in color was made (Fig. 15); another ant (sp. ?) was disturbed by a change from black to white, but not by changes from one member of the color series to another. Formica fusca was not usually disturbed by any changes made but occasionally (Fig. 14) it was slightly disturbed. This shows that changes in color of the pathway do not disturb some ants at all[5] whereas other ants seem to be slightly affected by such changes;[6] while yet others are affected by changes in brightness but not by changes in hue.

*Experiments with Auditory Stimuli.*—This section is not intended to be an exhaustive discussion of the auditory sense of ants. It is, however, an attempt to collate our knowledge on the subject, to give additional experimental data and to harmonize the conflicting views.

About a century ago St. Fargeau, in his Hist. Nat. des Hymenopteres, asserted positively that ants hear (Lubbock '81, p. 221). But Huber (Nat. Hist. of Ants), Forel (Fourmis de la Suisse) and Lubbock ('81) conducted experiments to test the power of ants to hear and each decided that they were deaf to sounds that fall within the human auditory range.

Sir John Lubbock's experiments were especially well planned. He used sounds produced by a dog whistle, a violin, the human voice, a shrill penny pipe, and a full set of tuning forks. These experiments were tried both upon ants that were carrying pupæ home and upon ants confined to paper bridges. In no case did he get the slightest response to any of the sounds made. Since, however, he had discovered in ants what he thought was an auditory organ, he presumed that it was probable that ants both heard and produced sounds; but that they were tones that fell outside of the human auditory range.

The negative results of the experiments of these three authorities have caused most people to believe that ants cannot hear.

---

[5] Lubbock (*loc. cit.*, p. 198) performed an experiment which showed that the ants studied by him did not notice the color of the path. He placed some ants on a narrow bridge, which was supported by pins with their bases in the water. On this bridge he projected a spectrum and noticed that the ants acted as they did on the plain bridge.

[6] It is not improbable that these disturbances may have been due to a slight difference in the texture or odor of the different papers.

Yet, if they cannot hear, it is hard to understand why so many ants are provided with organs for producing sound. DAVID SHARP ('93) has proved conclusively that the Dorylidæ, the Poneridæ and the Myrmicidæ possess stridulating organs, each consisting of a file on the anterior portion of the tergum of the third abdominal somite, which file is rubbed against the roughened underside of the second abdominal ring. He did not find any such organ in either the Camponotidæ nor the Dolichoderidæ and he was doubtful of its presence in the Cryptoceridæ. LANDOIS ('67) had seen such an organ about fifty years ago in PONERA.

SHARP'S work was strictly morphological, but physiological evidence that ants can make audible sounds is furnished by WROUGHTON ('92), FOREL (Fourmis de la Suisse), WASMANN ('91) and JANET ('94), each of whom has heard sounds produced by ants. WROUGHTON listened to Cremastogaster rogenhoferi, FOREL to Camponotus ligniperdus, JANET to Myrmica rubra L. and Tetramorium cæspitum L. and WASMANN to Myrmica ruginodis.

So far as I have been able to ascertain, WASMANN ('91) is the only European who has produced any experimental evidence against the negative results of HUBER, FOREL and LUBBOCK. He experimented with Formica rufa, which was confined in a LUBBOCK nest, the floor of which was covered with one mm. of dirt. Whenever he scratched on the glass with a needle, he found that the ants made responsive movements which demonstrated they were affected by the stimulus. Experience has taught me that the slightest touch upon any portion of my JANET nests is almost certain to be responded to by some movement of the ants within. It is to be regretted that WASMANN did not produce his sounds in some other way than by scratching on the nest; for, since there is a possibility that the scratching produced a slight tremor, a fair critic is bound to admit that the positive evidence furnished by this experiment is not of sufficient weight to offset the negative results of the three men mentioned above.

About eight years ago an American, LE ROY D. WELD ('99) performed a carefully planned series of experiments, which seem to prove that Cremasgaster lineolata, Lasius Americanus and Aphænogaster sp. can hear sounds that are audible to man. Some of these experiments were conducted under conditions that apparently precluded the possibility of jars from the sounding body reaching the nest by any other medium than the air. The sounds used were produced by a steel bar, a tin whistle, a wooden whistle, a middle A tuning fork and a milled disk rotating against the edge of a card. FIELDE and PARKER ('04) claim that ants do not react to aerial sound waves from a piano, violin, or GALTON whistle; but only to vibrations that reach them through some solid body.

Recently I have performed a series of experiments upon Formica fusca var. subsericea Say, and a variety of Formica sanguinea Latr. For these experiments the ants were housed in JANET nests, the covers of which were composed of orange colored glass. During the day, the experiments were never begun until the sun was several hours high; and at night, the experiments were not begun until the electric lights had been shining for at least three hours. These precautions were taken to eliminate the disturbing effects of a change in illumination. To lessen the possibility of jars from the sounding body reaching the nest through any medium other than air, the nests were placed on a layer of cotton batting half an inch thick. For the same reason, the legs of the table on which the nests rested were placed on thick wads of cotton batting.

The sounds used were produced by the Galton whistle, organ pipes and the human voice. Sometimes the whistle or pipe was held near the nest and in other cases a short distance away. The pipes were always held in such a position that the air when expelled from the pipe could not impinge directly upon the nest. These experiments were conducted during the winter and early spring.

They showed conclusively that each of the two species of ants mentioned was sensitive to vibrations of the air which to the human ear would be sounds. I obtained responses to notes as high as 4138 vibrations per second and as low as 256 vibrations per second. The responses, in the form of zigzag movements, were usually slight for pitches higher than 3000 vibrations per second and sometimes slight for other pitches; but, to most pitches under 3000 vibrations per second, the ants usually responded in a pronounced manner, usually darting about as though much excited.

After the ants had been subjected to the sounds for a long time they seemed to become fatigued, failing to respond in the least to pitches which would call forth pronounced responses from fresh ants. The fertile females seemed to be more intensely excited by the tones than the neuters. Several series of experiments were performed. Details of four typical series are recorded in the following table.

TABLE VIII.

*Series 1.*

| VIBRATIONS. | FORMICA FUSCA. | FORMICA FUSCA. | FORMICA SANGUINEA. |
|---|---|---|---|
| 3480 | Slight | Slight | Response |
|  | Marked | Slight | Marked |
| 3906 | ? | ? | Slight |
| 4138 | None | None | None |

*Series 2.*

| VIBRATIONS. | FORMICA FUSCA. | FORMICA FUSCA. | FORMICA SANGUINEA. |
|---|---|---|---|
| 256 | Marked | Slight | Marked |
| 3168 | Response | Slight | Slight |
| 3480 | Very slight | Very slight | Very slight |
| 512 | Marked | Marked | Marked |
| 316 | Slight* | Slight ? | Slight ? |
| 880 | Response | Response | Response |
| 3906 | Slight | Slight ? | Slight ? |
| 4138 | Very slight | None | Very slight |
| 4645 | ? | None | ? |
| 256 | Slight | None | Marked |
| 512 | Slight | Slight | Slight |

*Series 3.*

| VIBRATIONS. | FORMICA FUSCA. | FORMICA FUSCA. | FORMICA SANGUINEA. |
|---|---|---|---|
| 1760 | Marked | Response | Slight |
| 1056 | Marked | Slight | ? |
| 880 | Slight | Slight | None ? |
| 512 | Marked | Very slight | Marked |
| 362 | None ? | None ? | Slight? |
| 256 | None | None | Slight? |
| 3168 | Response | Response | None |
| 2816 | Slight | Slight | Response |
| 2640 | Response | Slight | Slight |
| 2280 | Marked | Marked | Marked |
| 2112 | Response | Response | Response |
| 1980 | Response | Response | Very slight |
| 1900 | Marked | Slight | Response |

*Series 4.*

| VIBRATIONS. | FORMICA FUSCA. | FORMICA FUSCA. | FORMICA SANGUINEA | FORMICA FUSCA. |
|---|---|---|---|---|
| 512 | Slight | Slight | Slight | None |
| 880 | Very slight | Very slight | Slight ? | None |
| 256 | ? | ? | Marked | None |
| 1056 | Marked | Marked | ? | None |
| 3168 | Slight ? | None ? | Slight ? | None |
|  | Slight | Slight ? | ? | None |
| 512 | Marked | Response | Marked | None |
| 362 | Marked | Slight ? | Slight | None |
| 256 | Marked | Slight | Marked | None |

* The fertile females gave a marked response.

EXPLANATION OF TABLE VIII.

Column 1. The number of vibrations per second.

Column 2. A colony of Formica fusca var. subsericea Say, containing three fertile females and about two hundred neuters.

Column 3. A colony of Formica fusca var. subsericea Say, containing about two hundred neuters and no fertile females.

Column 4. A mixed colony of Formica sanguinea Latrl. and Formica fusca. This colony contained about two hundred neuters, over two-thirds of which were fuscas. No females were present.

Column 5. A few workers of Formica fusca var. subsericea Say, the antennæ of which had been removed two days before.

Some may think the response of these ants was the result of tactile stimuli caused by shaking of the nest by the sound wave. To me it does not seem possible for the nests to have vibrated in response to each of so wide a range of pitches. However, to meet that objection, the following experiment was devised. I obtained some felt cloth two mm. thick and placed two layers of it in the bottom of each of the living chambers of a JANET nest. This nest rested on cotton placed on the table the legs of which rested on wads of cotton. After the ants had become accustomed to their carpeted floor, various sounds were made. This experiment was tried upon both Formica fusca var. subsericea Say and Formica sanguinea Latr. It is important to note that even with the false felt bottom to stand on, the ants could not reach the top of the nest with their antennæ. In each case the ants responded to the sound in the same manner as has been described above. Since the felt would prevent nest tremors reaching the ants, the response, it seems to me, must have been to air vibrations which the human ear would sense as sounds.

At present I have housed in a JANET nest a small colony of Camptonus herculeano-ligniperdus. This colony consists of eight winged females and about twice as many neuters. Usually one of the neuters mounts guard in the outer doorway. Whenever sounds similar to those mentioned above are made, this guard shows marked evidence of being disturbed. Under such conditions it makes agitated movements with its antennæ and often snaps with its jaws right and left. If the noise is continued, the guard is apt to rush back into the nest.

Undoubtedly, artificial colonies of each of these species of ants respond in a pronounced manner to atmospheric vibrations which to the human ear would be sounds.

When, however, I tested ants that were moving about outside the nest, I obtained no such marked reactions. Often I could detect no response whatever. But usually there would be a slight movement of the antennæ, or a slight but sudden acceleration of speed, or else a halting movement. Sometimes the ant would stop still. All of these movements were slight, usually so slight that they might easily be overlooked by an observer who was not expecting a response of some kind.

Even with single individuals confined to a test-tube which was suspended by a string (a method much used by WELD), I sometimes obtained no response. Indeed, I seldom received more pronounced responses than a slight movement of an antennæ, or a twitch of one or more legs, or a more tense attitude of the body. In most cases, however, I did get these slight movements, and, occasionally, I observed wide sweeping movements of the antennæ or other easily observed bodily movements.

The pronounced positive results obtained by WELD and myself do not seem to harmonize with the equally pronounced negative results obtained by HUBER, FOREL and LUBBOCK. One cannot believe that the American ants are physiologically as much unlike the European as these antagonistic results would seem to indicate. It seems to me that these contradictory results can be harmonized in the following manner.

LUBBOCK'S experiments were made either upon ants that were carrying pupæ home, or else upon ants that were confined to paper bridges. As has been stated above, my experiments show that under such conditions the ants usually do not respond at all to sounds, or else react with movements so slight that they might easily be overlooked by one not expecting movements of the kind made. I am fully convinced that experiments conducted upon European ants colonized in JANET nests, would yield the same positive results obtained by WELD and myself.

To harmonize FIELDE and PARKER'S ('04) work with mine is not an easy task. We agree that, up to about 4000 vibrations per second, ants respond to a long range of vibrations which a human ear would sense as sounds. They claim that these vibrations are responded to only when received through a solid medium; while my experiments seem to show that they are responded to when received through the air. Yet two of the species used by me (F. sanguinea and F. fusca var. subsericea) were also used by them. They used the piano, the violin and the Galton-whistle; I used organ pipes and the Galton-whistle. It seems to me that

I have taken even more precautions to preclude the possibility of the vibrations reaching the ants through a solid medium than they did. The only precaution they took was to rest the nest upon a thick layer of paper. I carpeted my nests with two layers of thick felt, placed a thick layer of cotton between the nest and the Lubbock island and thicker wads of cotton beneath the legs of the table upon which the island rested. The lowest note of the whistle used by Fielde and Parker was 10,000 vibrations per second, which is far above the highest pitch to which ants respond. The whistle I used ranged from 3480 to 51,000 vibrations per second. If the sound of the piano and of the violin were common in the room where the ants were kept they may have become too familiar to arouse responses. My ants were kept in a room facing a paved street. The noises of this street did not disturb them.

The more I meditate on Fielde and Parker's paper, the more I am inclined to believe that the lack of harmony between their results and mine is due to the difference in our technique. In their experiments the same note was sounded ten times in slow succession; in mine each note was sounded continuously or else in rapid succession for one minute or longer. I thought that, if ants can hear, the occasional production of a note might simply attract attention, while a continuous rapid repetition of the same would arouse some form of visible motor response. In my own experiments a note repeated a few times in slow succession would often cause no response, yet a prolongation of the sound or a continuous rapid repetition of the same would soon produce marked responses. If this contention be valid, we would expect Fielde and Parker's technique to yield nothing more than an occasional response. And this is the result they obtained; for on page 643 (*loc. cit.*) they say, "Now and then an ant would seem to respond to a given note, but in every case repetitions of the experiment gave a negative result.

Responses to light within and without the nest exhibit differences similar to those observed for sound. If light is admitted into a nest, the ants at once are much disturbed and show it by vigorous movements. Yet in the outer world, so long as the direction of the rays remains the same, ants are scarcely, if at all, affected by changes in the intensity of the light. Both light and sound are almost constant factors of the external world, but are rare phenomena in the confines of the nest. With ants, as with us, it seems that unusual stimuli cause unrest.

*Experiments on Direction and Distance.*—LUBBOCK ('81, p. 260) devised an experiment which shows that ants have accurate impressions of direction in a horizontal plane. This experiment, a portion of which I shall presently quote, has been repeated by me, with confirmatory results, on most of our southern species of ants. LUBBOCK writes as follows, "I then accustomed some ants (Lasius niger) to go to and fro over a wooden bridge, *b*, *c*, to some food. When they had got quite accustomed to the way, I watched when an ant was on the bridge and then turned it around, so that the end *b* was at *c*, and *c* at *b*. In most cases the ant immediately turned around also; but even if she went on to *b* or *c*, as the case may be, as soon as she came to the end of the bridge she turned around. I then modified the arrangement, placing between the nest and the food three similar pieces of wood. Then when the ant was on the middle piece, I transposed the other two. To my surprise this did not at all disconcert them."

LUBBOCK next tried a different experiment. By means of a pin through its center, he pivoted a disk of cardboard to the middle of the table. At one corner of the table he placed some food. When the ants had come to know their way so that they passed straight over the paper disk on their way from the nest to the food, he moved the disk around with an ant on it, so that the side that had been towards the nest was now towards the food. As in the above experiment, the ants turned round with the paper. He also repeated it with a table arranged to revolve in three concentric sections. The result was the same as above.

I think some of my experiments warrant the assertion that ants have an impression of vertical as well as horizontal direction.

In my experiments (excepting those on color and tactile phenomena) the stage and incline were made out of the same material, often being cut from the same piece of cardboard. The apparatus was so adjusted that when the ant reached the union of stage with incline, only two changes in movement were necessary in order to take the next lap of the journey; the ant must turn so as to receive the light rays on a different side than before, and it must move obliquely downward instead of moving in a horizontal plane. The apparatus was also so adjusted that if the ant turned at the parting of the ways and moved horizontally along the stage in the direction of the nest, it would receive the light rays on the same side of the body as it would in passing down the incline. The only new factor that entered the life of the ant that moved down the incline rather than horizontally along the stage towards the nest was the experience of moving downward. Vertical changes in direction must affect ants differently from horizontal changes in direction, otherwise there is no reason why the ant should pass regularly down the incline rather than horizontally along the stage towards the nest.

Again, after an ant had thoroughly learned the way down and up the incline, it would often not take the trouble to go all the way to the union of stage and incline, but, reaching the edge of the stage at a greater or less distance from its union with the incline, the ant would reach downward over the edge; if it could not touch the incline it would move nearer the junction of stage and incline and again reach downwards. If necessary, it would move nearer still. As soon as the ant could touch the incline, it would step off of the stage and move obliquely downward to the nest.

To test this matter further, the following experiment was devised. Underneath the incline of one of my stages was placed an adjustable support made by sticking a pin vertically into the cork of a small bottle. Since the lower end of the incline was free while the upper was attached to the stage, by moving this adjustable support more or less towards the base of the incline, a vertical gap of any desired size could be formed and maintained between the base of the incline and the island. After the ants had thoroughly learned the way to and from the nest, a small vertical gap, which was gradually increased until the ants on the island could no longer touch the base of the incline with their antennæ, was made between the foot of the incline and the island. Now so long as the ants could touch the incline with their antennæ, they would stretch upward until their forefeet touched the incline, then mount the incline and go to the stage. Ants coming down the stage acted the same way, only they stretched downward rather than upward. When, however, the base of the incline could no longer be touched by their antennæ, the ants would come to the place where the foot of the incline had been, elevate the front part of their bodies as much as possible and reach upwards with their antennæ. Elevating the base of the incline still more, I placed along the side of the path and parallel to it a stack of clean microscopic slides, one cm. high. This stack of slides was placed near enough to the incline for the ants, by stepping across a narrow horizontal gap, to pass easily from it to the incline. At once the ants mounted the stack of slides and went up the incline.

Does not this indicate that the ants have an impression of vertical direction? Does it not also indicate that they have an impression of distance? Otherwise, what makes them stop at that place and feel upward for the incline? It will not do to say that they stopped because the scented trail terminated there, for, even if it were not true that tracks of those ants cross that place in all directions, it has already been shown that the termination of a scented trail does not impede the progress of ants moving in a direction that is thoroughly known. Nor will it do to say that they halted and acted that way because they sensed the incline above them; for they do not react that way towards bodies held above them on other parts of the stage, nor do untrained ants react that way when they pass underneath the incline. In each of these test cases, ants may reach upward with the antennæ and then pass on; but they do not return to the spot over and over again and reach up as though they were hunting for something that was lost.

This view is supported by yet other experiments. In another connection, I have mentioned the case of a worker ant that learned to come to a certain point on the island, mount my forceps and be conveyed to the stage. After this mode of conduct had been thoroughly learned, the ant, on leaving the nest, would immediately go to this position on the island and meander in a small circle until my forceps were presented.

It was not an uncommon thing for an ant that knew the way up and down a certain incline, occasionally to miss arriving at the foot of the incline. In such cases, the ant would not, as a rule, roam here and yon, but would usually turn quickly and hunt for the incline. If it missed it again, it would go back to some point in its path, often as far as the nest opening itself, and, taking a new start, arrive at the incline without further trouble. This mode of conduct not only indicates that ants use certain landmarks as such, a subject which will be referred to in the next section, but it also seems to harmonize with the views stated in this section.

Another common occurrence which puzzled me not a little may, perhaps, be best explained in this connection. In some experiments planned to solve a problem not discussed in this paper, two stages were used, from each of which an incline of the same kind led to the island. In one case the incline was attached to the right side of the stage and in the other to the left. Incline number two was nearer the nest opening than was incline number one. An ant that had thoroughly learned the way up and down incline number one, would occasionally start up incline number two. Sometimes it would continue on to the stage, but more frequently, when only part of the way up, it would turn about and return to the island and continue on to incline number one; either directly, or else after having first retreated to some point farther back on the trail. The same thing sometimes happened where two inclines were attached to opposite sides of the same stage.

From a psychological point of view, there were only two differences between incline number one and incline number two; incline number one was scented with the footprints of the ant, while incline number two was not; and incline number one was farther from the nest than incline number two. Since it has been shown that the substitution of an unscented incline for one scented by the tracks of ants is not a disturbing stimulus to ants that are moving in a well known path, the difference in the distance traveled seems the only thing that could have caused the inhibition.

The grouping of all these data in one section does not imply that they are of the same psychic order. Some may be simple and others complex. Some may even be the derivatives of others mentioned here. To discuss such issues is not the purpose of this section. Its sole aim is to show that the psychic impression that confronts the home-going ant is not a simple olfactory stimulus, as most writers seem to suppose, but that it is a complex impression composed of contributions from the olfactory (topochemical), visual, tactile and kinesthetic and auditory senses.

## V. HAVE ANTS ASSOCIATIVE MEMORY?

"By associative memory, I mean the two following peculiarities of our central nervous system: First, that processes which occur there leave an impression or trace by which they can be reproduced even under different circumstances than those under which they originated . . . . . The second peculiarity is, that two processes which occur simultaneously or in quick succession will leave traces which fuse together, so that if, later, one of the processes is repeated, the other will necessarily be repeated also. By associative memory we mean, therefore, that mechanism by means of which a stimulus produces not only the effect which correspond to its nature and the specific structure of the stimulated organ, but which produces, in addition, such effects of other causes as at some former times may have attacked the organism, almost or quite simultaneously with the given stimulus" (LOEB '02, pp. 213 and 214).

As to the criteria of memory, the same author writes (*ibid*, p. 218): "It will require more observations than we have made at present to give absolutely unequivocal criteria. For the present, we can say that if an animal can learn, that is, if it can be trained to react in a desired way upon certain stimuli (signs), it must possess associative memory. The only fault with this criterion is that an animal may be able to remember (and to associate) and yet not yield to our attempts to train it . . . . . The fusion or growing together of heterogeneous but by chance simultaneous processes is a sure criterion for the existence of associative memory."

If we consider the experiments herein described in the light of these criteria of LOEB, we must certainly conclude that ants have associative memory; for, as has been shown, ants learn by experience, retain what they learn in a way that can be recalled by the proper stimuli, and they can be trained to do certain things.

Some psychologists do not agree with LOEB that the mere ability to learn predicates memory. There is a method of learning depending on repeated blundering efforts with fortuitious successes that are gradually selected which LLOYD MORGAN calls the method of trial and error. Such a mode of learning, some say, does not indicate the existence of memory. Memory predicates the existence of ideas which are associated. In learning by trial and error, no association of ideas is involved; we have simply assimilation of a sense impression or impressions with an impulse. To use the words of THORNDIKE (*loc. cit.*, p. 71) "The ground work of animal associations is not the association of ideas, but the association of idea or sense-impression with the impulse."

HOBHOUSE ('01), who experimented on the same animals as THORNDIKE, differs from him in his conclusions. He thinks that the average laboratory psychologist has gone to extremes in his conclusions which the experiments do not warrant. He reminds us that, "A dog may show not merely highly developed hunting instincts, but real cleverness in the adaptation of past experience when it is a question of catching a hare, but may also be an intolerable dullard about opening a box . . . . . To test an animal's intelligence by mechanisms, seems to be about on a par with gauging the nature of a man's intelligence by certain puzzles, in which, as is well known, many able men are, indeed, dullards . . . . . What Mr. THORNDIKE's experiments prove so far is, not that cats and dogs are invariably educated by the association process, that is by habituation, but, on the contrary, that at least some cats and dogs conform, in at least one point, to the method of acquisitions by concrete experiences . . . . . In some cases they not only merely learn to meet a given perception with a given motor reaction, but also to combine and adapt their actions so as to effect physical changes which, as they have learned, aid them in gaining their ends."

HOBHOUSE further reminds us that habits are generally formed gradually by many repetitions and that, where the act is the result of habituation, the time curve should gradually descend. Indeed, THORNDIKE himself lays stress upon this same point; for he says (*loc. cit.*, p. 45): "And if there were in these animals any power of inference, however rudimentary, however sporadic, however dim, there should have appeared among the multitude some cases where an animal, seeing through the situation, knows the proper act and does it, and from then on does it immediately upon being confronted with the situation. There ought then to be a sudden vertical descent of the time curve. Of course, where the act resulting from the impulse is very simple, very obvious, and very clearly defined, a simple experience may make the association perfect and we may have an abrupt descent in the time curve without needing to suppose inference. But if in a complex act, one found such a sudden consummation in the associative process, one might well claim that reason was at work . . . . . The gradual slope of the time curve, then, shows the absence of reasoning. They represent the wearing smooth of a path in the brain, not the decisions of a rational consciousness."

If a gradual descent of the time curve be a sure test that a creature has learned by the method of trial and error and if an abrupt descent is an indication of perceptual learning, we must conclude that the ant's mode of learning is not the trial and error but the perceptual mode and that they have memory (Figs. 8, 10, 12, 18). I freely confess, however, that this seems to me a very unsatisfactory criterion. For this criterion to be of any real value, we would need some way to determine, from the animal's standpoint, what is complicated and what is not; and there is no known way.

There are, however, other considerations that lead me to believe that ants have memory. In memory we usually find a complex impression composed of contributions from more than one sense organ. In the section that precedes this, I have tried to show that home-going ants have a complex impression which is composed of contributions from several sense organs. Now the existence of this complex impression does not necessarily prove the existence of memory, but, it does demonstrate the existence of one of the usual physiological accompaniments of memory.

BUTTEL-REEPEN ('00) chloroformed some bees and found that they were no longer able to find their way home. This he considered a proof of memory. How, he asks, could they forget unless they had a psychic content to forget. Is it not reasonable to consider cases of "forgetting" that cannot be attributed to injuries received nor to retardation due to fatigue as evidences of memory? In my experiments, I frequently met cases of what might be called lapses of memory. Sometimes this would happen on the stage, at others on the island. The ant would move about at random as though it had forgotten the way. These lapses would increase the time ordinarily required for the trip, from one to three minutes. The subsequent trips were made as rapidly and as regularly as before. I have also met with cases of what might be called mistaken identity (Fig. 7). Recall the experiment with two stages, from each of which an incline descended to the island—the case when the ant occasionally went up the wrong incline—and you have a case of this kind.

Then, too, I have noticed cases which I think reveal ants as using a thing or things as a means of accomplishing a certain end, rather than responding to it as an end. Take the experiment mentioned in the previous section, where a high vertical gap was present between the foot of the incline and the island. The ants were coming repeatedly to the same point and reaching upward for something beyond their reach. In that place, a stack of clean glass slides was placed a little to one side of the path. At once the ants climbed the slides and mounted the incline. Similar stacks of slides placed just to one side of the path at other points along the trail were not thus mounted by the ants. The road by which the ants had learned to reach the stage from which the gap now separated them, had no vertical walls that needed to be climbed. This wall of slides was not placed across the path, but a little to one side of it. Immediately, the ants mounted it and thereafter used it as a means of passing from island to incline and from incline to island.

Then, too, it seems to me that ants use light as a means to an end. In a former section, an attempt was made to prove that light is not for ants a tropic stimulus, yet, by a repetition, under control, of one of LUBBOCK's experiments, I have shown that the direction of the rays of light does have a guiding influence.

In each of those experiments, I used a cardboard stage, which was connected with the LUBBOCK island by means of a single incline. In some experiments, I placed the light (a 16 c.p. incandescent electric lamp) near the side to which the incline was attached, in other cases the light was placed on the opposite side. There was no other light in the room. After waiting until the ant had thoroughly learned the way down the incline,[7] I transferred the light to the opposite side. Invariably, as shown by its movements, the ant would be very much disturbed by the change. Now to my mind, this disturbance seems due to the fact that the ants use the direction of the rays of light as reference data. In other words, the light is responded to as a means to an end and not as itself an end. If this contention be valid, then ants learn, not by the method of trial and error, but perceptually, and they have associative memory. As the result of careful observation, I am convinced that ants use such things as irregularities of the surface, edges of flat surfaces, the edges of shadows, etc., as reference data.

On several occasions, after a marked worker had been carrying pupæ for a long time, it was imprisoned from one to several hours and then returned to the stage. In some cases the ant failed completely to find the way to the nest, in a few others it went to the nest immediately; but in most cases, it took some time to find the way to the nest. Usually the time required to re-solve the problem was

---

[7] When the ant was not disturbed in its movements by the substitution of a new incline of the same kind for the old, the ant was judged to be thoroughly acquainted with the way. This was the test I always used in such cases.

shorter, often much shorter, than was needed by the ant the first time such a problem was presented. Aside from the differences of time required for different individuals to reach the nest, there were marked individual differences in their conduct. I noted five different modes of response: (1) An ant would take a pupa to the nest and remain therein instead of returning to the stage. (2) An ant would pass unburdened to the nest and remain therein instead of returning to the stage. (3) An ant would carry a pupa to the nest or to some point on the island and then return to the stage and make repeated trips. (4) An ant would pass, unburdened, to the nest, and then immediately return to the stage for a pupa and thereafter make regular trips. (5) Occasionally, a worker would pass, unburdened, to a point near the nest, then return to the stage for a pupa and thereafter make regular trips.

Such marked individual differences in conduct were noted between members of the same colony, under the same external environmental conditions. All of these individuals, at the time of their imprisonment, were thoroughly acquainted with the way between the nest and the stage. The difference cannot be attributed to fatigue, for they had been resting from one to several hours. It seems to me that these facts harmonize rather with the memory hypothesis than with either the "assimilation of idea to impulse" or to the "determination of stimulus" hypothesis.

If either of the two latter hypotheses is true, the following is probably a fair statement of the factors that guided my ants to and from the stage to the nest. The sensing of the pupa on the stage causes the ant to pick it up and move in a certain direction. The direction of the rays of light, etc., cause it to move to the point of union of stage and incline. Contact with that point, etc., cause it to turn and pass down the incline, receiving the light on a different side than before. At the base of the incline, contact with the zinc, etc., cause it to pass to the side of the nest, where other stimuli cause it to go into the nest, where yet other stimuli cause it to lay down its pupa. Now all of these several stimuli act on it in a reverse way and cause it to return to the stage. After the "assimilation of impulse and idea" or the "determination of stimulus" has been made, the animal moves along just as automatically as an animal in a tropic response. Each stimulus is responded to as an end in itself and not as a means to an end. Now, if I interpret my experiments aright, none of the ants examined acted this way.

They acted as though getting the pupæ under some shelter, preferably the nest, was the end in view, and as if all of their responses to stimuli were but means put forth to accomplish that end.

If either of these hypotheses applies to ants, a worker meeting a pupa anywhere in the open air, unless carried on by the momentum of other stimuli, should respond to it in the same way that it would had it encountered the pupa on the stage. Now what are the facts in the case? Whenever I place a pupa in the track of such a worker, as soon as the pupa was sensed it was picked up by the worker and carried to the nest; either back along the path just traveled or first to some reference point and thence to the nest. One might suppose that this is what would have happened had the ant encountered the pupa on the stage, for there is a general belief that the ant picks up the pupa, turns about at once and returns in its own tracks to the nest. With some species of ants, especially when they are working in concert, it is hard to decide whether this is the case or not; but even a casual observation of an individual of Formica fusca var. subsericea Say, working alone, will convince anyone that such is not the case. With the pupæ scattered here and there over the stage, the ant must hunt for them, and each pupa is approached over a different, more or less sinuous, line. When the pupa is reached, the axis of the ant's body may make almost any angle, from zero to one hundred and eighty degrees, with the line that leads from the pupa to the union of stage and incline. Hardly any two of these positions are alike. Whether or no, on picking up the pupa, the ant turns about at once is a secondary matter, dependent upon the position of the ant's head at the time. The species just mentioned rarely, if ever, returned in its own tracks from the pupæ to the union of stage and incline. What the ant really does is to pick up the pupa and move off in such a direction as to keep the light rays falling on that portion of the body which it has learned from other trips, must receive the rays of light if it is to reach the union of stage and incline. This may not take it direct to the junction but it will take it to some familiar point and from there it will take a beeline to the junction. In the test experiments, I took especial pains to place the pupæ in such situations that, to get to the nest, the ant must move in such a direction as to receive the rays of light on a different side of the body and at a different angle than would have been the case had the pupa been encountered on the stage. And yet the ant always went home without a moment's hesitation. To say that the pupa does not give the ant a stimulus to make a certain definite movement, but any movement necessary to take it home, is equivalent to saying that the ant responds to the stimulus as a means to an end.

There is yet another observation which deserves mention in this connection. In all my experiments with ants working in concert, when the pupæ had all been removed from the stage the ants would thoroughly search the stage and incline and then retire to the nest. Why did the ants stop going to the stage? Surely the same stimuli existed in the nest as formerly; the only new factor is that there are no more pupæ on the stage. This cessation of movement cannot be attributed to fatigue, for they act in the same manner after removing a small lot of pupæ as they do after removing a pile many times as great. It would be equally fallacious to assume that the pupæ on the stage influence the ants directly from afar, and that the lack of pupæ to furnish an immediate stimulus is the cause of the cessation; for ants roaming over the island in search of pupæ are not attracted by the pupæ. Many a time I have seen specimens of Lasius, and Formica pass repeatedly back and forth beneath the stage without being attracted by the pupæ on the stage; I have known Formica to ascend the incline and pass to within three centimeters of the pupæ and return to the island without sensing them. To test whether such ants were in a condition to be affected by the sensing of pupæ, I have placed pupæ in front of them as soon as they reached the island. Immediately such pupæ were picked up and carried to the nest. Nor would it be consistent to assert that the stimulus-to-return did not affect ants that returned unburdened to the nest; for after the pupæ were removed, each ant always made from one to a few round trips; and, furthermore, it frequently happened, when the stage was well supplied with pupæ, that an ant would pass, unladen, to the nest, and then immediately, or after a few moments, resume its periodical round trips.

I fail to see how these facts can be harmonized with either the assimilation hypothesis of THORNDIKE or with the determination of stimulus hypothesis, but they do harmonize with the assumption that ants have associative memory. It is not claimed that ants exhibit a high grade of intelligence in finding their way about. In my experiments, the first trip to the nest was always the result of happening to succeed after making many blunders. So far this accords with the observations made by all students of vertebrate animal behavior. During the first few trips, however, aided by memory, certain associations of ideas are formed which persist and enable the ant to orient itself. To men of THORNDIKE's conviction, this is a discordant note, but it accords perfectly with HOBHOUSE's view concerning vertebrates. Although this does not necessarily make the ant a self-conscious creature, it makes it much more than a mere reflex machine.

It is worth noting that in ascribing associative memory to ants, I am in perfect accord, not only with WASMANN, but also with such a stanch advocate of the tropisms as LOEB. In his chapter on "The distribution of associative memory in the animal kingdom" ('02, p. 224), LOEB says, "Although I heartily sympathize with BETHE's reaction against the anthropomorphic conception of animal instincts, I yet believe that he is mistaken in denying the existence of associative memory in ants and bees."

After the space occupied in attempting to show that the "assimilation" and "determination of stimulus" hypotheses do not adequately account for the conduct of home-going ants, I fear that by "associative memory" I may be misunderstood to mean some high type of rational life. Therefore, I wish to emphasize the fact that I use the term as LOEB uses it in the quotation with which this section opens.

## VI. DOES DIVISION OF LABOR AMONG ANTS SIGNIFY MUTUAL COÖPERATION?

In the course of my experiments many examples of division of labor have been noticed. I have known one set of workers to store the pupæ under the incline, or in a dark chamber, or on the stage in the open, while yet other workers conveyed them from these places to the nest. I have seen one set of workers lay pupæ down on the island, while a different set carried them into the nest. I have even seen cases where one set laid the pupæ down in the feed chamber, from which another set carried them into the nest proper. I have noticed similar examples of division of labor in most of the species experimented upon. It was with Prenolepis imparis, however, that I took pains to investigate it carefully. Here we have one set of workers bringing pupæ to a certain spot whence they are carried further by another set of workers. Each set does its share, and between them the work is quickly accomplished. Thus stated, these facts suggest the thought that these coöperating ants must have some kind of mutual understanding.

I am constrained, however, to add a statement which will give a different interpretation to the act. In all of the cases of coöperation observed by me, the pupæ were carried into the nest by workers which, roaming from the nest, by chance discovered them. The workers that stored the pupæ under the incline, those that hid pupæ in the dark chamber, and those that piled them in the open on the stage, were ants which, being unable to find the way home disposed of the pupæ in these special ways. Those that laid them on the island simply brought the pupæ thus far and laid them down. They did not go to the nest, nor did they touch with their antennæ any of the ants that subsequently carried these pupæ to the nest. In all of the cases mentioned, some worker or workers, roaming from the nest, discovered the pupæ and carried them home. The only observations that did not accord completely with the above statement, were those few cases in which the workers from the stage deposited the pupæ in a group of ants that was swarming against one side of the nest. In that case, it was impossible to be sure that some of those did not assist the stragglers from the nest in carrying the pupæ. Even in that case, I could detect no evidences of communication between the ants from the stage and those from the nest. These observations warrant the assertion that each case of division of labor observed by me was the result, not of mutual understanding, but rather of accidental coöperation.

On re-reading MOGGRIDGE'S (ROMANES '92, p. 98) account of ants dropping leaves for other ants to pick up, LESPE'S (*ibid.*, p. 99) account of "regular depots for their provisions," and BELT'S (*ibid.*, p. 99) account of ants casting down burdens for other ants to carry, I cannot help but feel that had these special cases been observed from the beginning, they would have proved to be of the same type as those described above. Any one acquainted with the habits of ants who reads MOGGRIDGE'S account of the coöperative dismemberment of a grasshopper by ants, is certain to be reminded that any large insect dropped in the midst of ants is sure to be independently attacked from all sides by ants which, acting as individuals, gnaw and pull away from the object.

MOGGRIDGE (*loc. cit.*, p. 98) tells us that the grasshopper was "too large to pass through the door, so they tried to dismember it. Failing in this, several ants drew the wings and legs as far back as possible, while others gnawed through the muscles where the strain was greatest. They succeeded at last in thus pulling it in." It is a pity this account is so meager. If there were only two ants to each member, one pulling it out and the other gnawing at the place of greatest strain, we would have an undoubted case of intelligent coöperation; whereas, if there were a large number of ants attacking each member, the fact that some happened to gnaw at the point of greatest strain does not prove intelligence. To repeat, there is nothing in the anecdote, as recorded, to show that this was was not a case of accidental rather than of mutual coöperation.

A case cited by ROMANES ('92, p. 99) is so remarkable that I quote it in full. "In Herr GREDLER's monastery, one of the monks had been accustomed for some months to put food regularly on his window sill for ants coming up from the garden. In consequence of Herr GREDLER's communications, he took it into his head to put the bait for the ants, pounded sugar, in an old ink stand, and hung this up by a string to a cross piece of the window and left it hanging freely. A few ants were in the bait. They soon found their way out over the string with the grains of sugar and so their way back to their friends. Before long a procession was arranged on the new road from the window sill along the string to the spot where the sugar was, and so things went on for two days, nothing fresh occurring. But one day the procession stopped at the old feeding place on the window-sill and took the food thence without going up to the pendant sugar jar. Closer observation revealed that about a dozen of the rogues in the jar above were busily and unwearyingly carrying the grains of sugar to the edge of the pot and throwing them over to their comrades down below."

Remarkable? Yes; but before passing judgment, let us recall a few results of experiments. It is a common occurrence to have different ants of the same species doing different things at the same time. I have had a portion of the ants of a colony busy conveying pupæ into an artificial nest, while the remainder were industriously excavating holes in the sand. Likewise, in my cardboard stage experiments, I have observed at one and the same time, one set of ants storing pupæ under the incline, another set conveying pupæ to the nest, and yet another set piling the pupæ in the center of the stage.

Time and again, when ants were busy conveying pupæ from the stage to the nest, I have dropped pupæ in the path of ants returning from the nest. I have tried this experiment with all the species of ants considered in this paper; and, without exception, the pupa was picked up and carried into the nest.

In the light of these facts, let us consider Herr GREDLER'S account. In this case the ants had learned the way from the sugar, by way of the string, wall, window-sill and wall to their nest. Now had a small number of these ants begun to pile the sugar on the edge of the bottle, from which most of it would surely have fallen to the window-sill, the case would have been similar to the one where one portion of one of my colonies conveyed pupæ from the stage to the nest, while another portion piled the pupæ at a certain place on the stage. But the falling of a portion of the sugar to the window-sill, which was a portion of the pathway of the ants returning from the nest, would introduce a modifying variation. As soon as a returning ant encountered a grain of sugar, it would pick it up and carry it to the nest. And if the grains fell from the rim of the bottle fast enough, we should soon have no ants taking the trip up the string. Thus would be produced a behavior which simulates mutual coöperation. Since Herr GREDLER failed to observe the stages by which the continuous line of ants was transformed into two distant yet coöperating lines, this anecdote has no value as evidence proving that ants rationally coöperate.

To sum up the results of this section, it is quite probable that division of labor of the type mentioned above is of rather common occurrence among certain ants; but until new data are forthcoming, we must consider all such cases as coincidences, rather than as proofs of rational coöperation.

## VII. CONCLUSIONS.

1. In their journeys, the movements of ants are not tropisms.

2. Ants are not as slavishly guided by the scent of their footprints as is usually believed, for all of the species examined by me could be trained to pass over at least twelve inches of an unscented path. This discovery furnishes an easy means of investigating many problems in ant psychology.

3. LUBBOCK was right when he said, "In determining their course ants are greatly influenced by the direction of the light."

4. The color of the pathway has no, or little, effect on the home-going of ants. There are a few doubtful cases where the hue may have had some effect. There are many in which pronounced changes in the brightness of the pathway seem to affect the ants.

5. In their wanderings, ants are influenced by olfactory (*i.e.*, topochemical), optic, auditory, kinesthetic and tactile stimuli.

6. Ants seem to have fairly definite impressions of direction in both horizontal and vertical planes, and also impressions of distance.

7. They are enabled to take long round trips by learning by experience and retaining what they thus learn.

8. They have associative memory.

9. Such cases of division of labor as ROMANES—quoting from MOGGRIDGE, LESPES, BELT and Herr GREDLER—describes in his "Animal Intelligence," are to be looked upon as cases of coincidence rather than as examples of mutual coöperation.

10. In their home-goings, ants display marked individual variations.

11. They are not guided by a homing instinct.

12. While conducting these experiments, I have made many observations, unrecorded in the body of the text, which show that WHEELER is right in emphasizing the high development of the female, for the winged females often take part in the regular duties of the nest. I have had them learn the way home from new situations and assist the workers in carrying the pupæ home.

13. The males seem unable to solve even the simplest problems.

14. The major workers of Pheidole, which ERNEST ANDRÉ claims function as soldiers and do not take any active part in the ordinary work of the nest, frequently assist the workers in making excavations and, occasionally, assist in conveying pupæ from one place to another. I have never noticed one continue to carry pupæ for any considerable length of time. This statement is based upon numerous observations which were omitted from the body of the text on account of lack of space.

15. Ants are much more than mere reflex machines; they are self-acting creatures guided by memories of past individual (ontogenetic) experience.

## LITERATURE CITED.

Bethe, A.

'98. Durfen wir den Ameisen und Bienen psychische Qualitaten zuschreiben? Abs. in *Amer. Nat.*, vol. 32, pp. 439–447.

'00. Noch einmal über die psychischen Ruditaten der Ameisen. *Arch. f. d. ges. Physiol.* (*Pflüger*), 79 Bd., Hft. 1-2, pp. 39–52.

'02. Die Heimkehrfähigkeit der Ameisen u. Bienen zum Theil nach neuen Versuchen. *Biol. Centralbl.*, 22 Bd., no. 7, pp. 193–215; no 8, pp. 234–238.

Buchner, L.

'80. Mind in Animals. Trans. by Annie Besant. *London.*

Buttel-Reepen.

'00. Sind die Bienen Reflex-maschinen? Experimentelle Beiträge zur Biologie der Honigbiene. *Biol. Centralbl.*, Bd. 20, pp. 97–109, 130–144, 177–193, 209–224, 289–304.

Claparède, E.

'03. The Consciousness of Animals. *Intern. Quart.*, vol. 8, pp. 296–315.

Ernst, Christian.

'05. Einige Beobachtungen an kunstlichen Ameisennestern. *Biol. Centralbl.*, Bd. 25, pp. 47–51; Bd. 26, pp. 210–220.

Fielde, A. M.

'01. Further Study of an Ant. *Proc. Acad. Nat. Sci. Phil.*, vol. 53, pp. 521–544.

'03. Experiments with Ants Induced to Swim. *Ibid.*, vol. 55, pp. 617–624.

Fielde, A. M. and Parker, G. H.

'04. The Reaction of Ants to Material Vibrations. *Ibid.*, vol. 56.

Forel, Aug.

'01. Die Psychischen Eigenschaften der Ameisen und eniger anderen Insecten. *Tagebl. v. Intern. Zool. Congr.* no 3, pp. 5–6.

'03. Ants and Some of Their Instincts. *Monist*, vol. 14, pp. 33–66; pp. 177–194.

Hobhouse, L. T.

'01. Mind in Evolution. *New York. The Macmillan Co.*

Huber, P.

'10. Recherches sur les Moeurs des Fourmis Indigènes. *Paris.*

Janet, Ch.

'94. The Production of Sound Among Ants. Abs. in *Amer. Nat.*, vol. 28, pp. 270–271.

Landois, H.

'67. Die Ton- und Stimm-apparate der Insecten in anatomische, physiologiger und akustischer-Beziehung. *Zeit. f. wiss. Zool.*, Bd. 17, pp. 105–186.

Loeb, Jacques.

'02. Comparative Physiology of the Brain and Comparative Psychology. *New York, G. P. Putnam's Sons.*

'06. The Dynamics of Living Matter. *New York.*

Lubbock, Sir John.

'81. Ants, Bees and Wasps. *London. Kegan, Paul and Co.* 10th Edition.

Morgan, C. Lloyd.

'00. Animal Behavior. *London. Edw. Arnold.*

Pieron, H.

'04. Du rôle sens musculaire dans l'orientation des fourmis. *Bull. Inst. Gen. Psyc. Paris.* T. 4, pp. 168–187.

Porter, J. P.

'04. A Preliminary Study of the Psychology of the English Sparrow. *Am. Jour. of Psychology*, vol. 15, pp. 313–346.

Romanes, G. J.

'92. Animal Intelligence. *New York. D. Appleton and Co.*

Sanford, E. C.

'03. The Psychic Life of Fishes. *Inter. Quart.*, vol. 7, pp. 316–333.

Sharp, D.

'93. On Stridulation in Ants. *Trans. Entom. Soc. London.* 1893, pt. II, pp. 199–213.

Thorndike, E. L.

'98. Animal Intelligence. *Psychological Review, Monog. Suppl.*, vol. 2, no 4.

Vielmeyer, H.

'00. Beobachtungen über das Zurückfinden von Ameisen (Leptothorax unifasciatus Str.) zur ihrem Neste. *Ill. Zeit. f. Entom.*, Bd. 5, pp. 311–313.

WASMANN, E.
'91. Zur Frage nach dem Gehorsvermogen der Ameisen. *Biol. Centralbl.*, Bd. 11, pp. 26–27.
WATSON, JNO. B.
'03. Animal Education. *Univ. of Chicago Press.*
WELD, LE ROY.
'99. The Sense of Hearing in Ants. *Science.* n. s., vol. 10, pp. 766–768.
WROUGHTON, ROBERT.
'92. Our Ants. *Jour. Bombay Nat. Hist. Soc.*
YERKES, R. M.
'03. The Instincts, Habits and Reactions of the Frog. *Psychological Review. Monog. Suppl.* no. 17; *Harvard Psychological Studies*, vol. 1.

## EXPLANATION OF FIGURES.

In all of the figures the successive ordinates represent minutes of time. In Figs. 1 to 6 (see text, p. 382) each abscissa represents an experiment in the series tabulated and each ordinate the time in minutes that elapsed in that case from the beginning of the series until the first pupa was carried to the nest. These experiments were conducted on ants acting in concert, the purpose being to see if ants retain what they gain by experience. In the remainder of the figures the abscissæ represent successive trips to the nest. When a line terminates in an arrowhead, that indicates a failure. In all curves any time less than a quarter of a minute is considered zero.

## PLATE II.

FIG. 1. Learning curve of Myrmica punctiventris Rog., acting in concert, showing how easily it is affected by even slight changes in the environment, and that it has not a homing instinct.

1. June 21, 7:30 a.m. Apparatus, a cardboard stage connected on the right to the island by means of a cardboard incline (*A*).
2. Do. 2:45 p.m. Same apparatus as before. The ants have had a rest of two hours and thirty-five minutes.
3. June 22, 11:08 a.m. Same apparatus as before. The ants have had a rest of twenty hours and twenty-three minutes.
4. Do. 2:35 p.m. Same apparatus as before. The ants have had a rest of one minute.
5. 3:56 p.m. Same apparatus as above. The ants have had a rest of twenty-six minutes.
6. Do. 4:48 p.m. Same stage as before, but the scented incline is placed on the left side of the stage and a new unscented incline (*B*) placed where the scented incline had been. The pupæ were all carried down the new incline. No larvæ were carried down the old incline; one worker started down the old incline and then returned to the stage. Occasionally, a worker would ascend the old incline from the island. The ants had rested one minute.
7. June 23, 10:40 a.m. Same apparatus as before. Workers carry the pupæ down incline *B* to the nest; other workers convey pupæ down incline *A* and store them under its foot, thence stragglers from the nest convey them to the nest. The ants had rested twenty-nine hours.
8. July 11, 9:15 a.m. A new cardboard stage, a new incline and all (even the nest) was placed on a new island. The figure indicates a failure but does not indicate how great. Those ants were lost for over twelve hours. At 9:50 p.m. when I left the laboratory, they were resting quietly on the stage. Sometime before 8:30 the next morning they found the way to the nest (see text, p. 379).
9. July 13, 7:54 a.m. Same apparatus as above. The ants had rested a day and had had a chance to become acquainted with the island.
10. July 24, 9:15 a.m. A cardboard stage from which one incline passed to the island. A dark chamber opening upon the stage and also upon the incline, was placed over the top of the incline. All the pupæ were stored under the dark chamber, none were carried to the nest. The workers went to the nest and left the pupæ on the stage. The ants had rested eleven days and seventy-four minutes.

FIG. 2. Learning-curve of Prenolepis imparis Say, showing that the homing of ants is not a chemotropism and that ants can learn a new way home when the way they once knew has been removed.

1. June 24, 7:38 a.m. A new cardboard stage with a new incline (*A*) attached to the left side.
2. Do. 2:46 p.m. Same apparatus as above. The ants had rested three hours and forty-six minutes.
3. Do. 3:10 p.m. Same apparatus as above. The ants had rested ten minutes.
4. Do. 3:20 p.m. Same apparatus as above. The ants had rested four minutes.

5. Do. 3:40 p.m. Same apparatus as above, only I added incline *B* to the right side of stage, so that now incline *A* is on the left and incline *B* on the right. The ants carried the pupæ down *A*, none were carried down *B*.

6. Do. 3:58 p.m. Same apparatus as above. The ants had rested seventeen minutes.

7. Do. 4:20 p.m. Same apparatus as before, only inclines *A* and *B* were made to change places. All the pupæ were carried down *B*, none were carried down the scented incline *A*. The ants had rested one minute.

8. Do. 4:40 p.m. Same apparatus as above. No pupæ carried down *A*. The ants had rested one minute.

9. Do. 5:06 p.m. Same apparatus as above. The ants had rested one minute.

10. June 26, 7:12 a.m Same apparatus as above. All the pupæ were carried down *B*, a few unburdened workers occasionally promenaded on *A*. The ants had rested one day, thirteen hours and forty-nine minutes.

11. Do. 7:42 a.m. Used the same stage but turned it bottom side up, thus making practically a new stage. The same inclines were used in the same position, *A* on the right and *B* on the left. All the pupæ were carried down *B*, none were carried down *A*. The ants had rested two minutes. (An unburdened worker went down *B* to the nest one minute after the ants were placed on the stage.)

12. June 26, 8:11 a.m. Same stage, but inclines *A* and *B* are both removed and a new incline *C* placed where *A* had been; this left no incline at the place where the ants had been descending and an unscented incline on the other side. The ants pick up pupæ and go immediately to the place where *B* had been. Failing to find *B*, they become much confused. They return over and over again to that point and reach down as though hunting for something. Finally they carry the pupæ down *C* to the nest. The ants had rested twenty-nine minutes.

13. Do. 9:42 a.m. Same apparatus as above. Several workers convey pupæ to where *B* had been. The ants had rested two minutes.

14. Do. 10:09 a.m. Same apparatus as above. The ants had rested two minutes.

15. Do. 10:30 a.m. Same apparatus as above. The ants had rested one minute.

16. Do. 11:02 a.m. Same apparatus as above, only I added a new incline *D* to the left side of the stage. The majority of the pupæ were carried down *C*; only two pupæ were carried down *D*. The ants had rested four minutes.

17. Do. 11:24 a.m. Same apparatus as before, only *C* and *D* were interchanged, so that we now had the unscented path *D* in the path the ants had been traversing. The majority of the pupæ were carried down *D*, only three were carried down *C*. The ants had rested nine minutes.

18. Do. 6:55 p.m. Same apparatus as above. The ants had rested one hour and two minutes.

19. Do. 7:18 p.m. Same stage, but I replaced *C* by *D* and placed a new incline *E* where *D* had been. The majority of the pupæ were carried down *D*. The ants had rested two minutes.

FIG. 3. Learning-curve of Prenolepis imparis acting in concert, showing lapse of memory, the effect of light rays, interruptions of the path, etc.

1. June 27, 9:42 a.m. A new cardboard stage with new incline *A* descending from its left side to the island.

2. Do. 10:55 a.m. Same apparatus as above. The ants had rested two minutes.

3. Do. 11:20 a.m. Same apparatus as above. The ants had rested one minute.

4. Do. 12:15 a.m. Same apparatus as above. The ants had rested thirty-five minutes.

5. Do. 12:30 p.m. Same apparatus as before, only there is a vertical gap of 1 mm. between the foot of the incline and the island. The ants had rested four minutes.

6. Do. 1:15 p.m. Same apparatus as before, but the vertical gap is increased to 4 mm. The ants had rested ten minutes (see text, p. 410).

7. Do. 2:35 p.m. Same apparatus as before, only the 4 mm. gap was horizontal instead of vertical. The ants had rested forty-two minutes.

8. June 28, 10:55 a.m. Same apparatus as before only the ants must cross a horizontal gap of 4 mm. to a pile of slides and down them to the island. The delay was caused by the gap. They went down to the gap and there hesitated, many returning to the stage. This was unexpected, since only yesterday they had been trained to cross a horizontal gap of that kind. The ants had rested twenty-two hours and twenty minutes.

9. July 10, 7:16 a.m. A cardboard stage from which an incline ascends to the nest. The ants had rested thirteen days, twenty hours and eleven minutes.

10. Do. 7:55 a.m. Same as above. The pupæ had rested four minutes.

11. Do. 8:46 a.m. Used same stage and incline but rotated the stage through 180°. Incline in same position. This gave an unscented path from pupæ to the incline. The ants went direct to the incline. The ants had rested one minute.

12. Do. 9:30 a.m. Same stage, substituted incline *B* for *A* and placed incline *A* on the opposite side of the nest. The ants had rested five minutes. (At the beginning a worker went, unburdened, up incline *B* to the nest, but did not return to the stage.)

13. July 25, 7:30 a.m. A stage from which incline *A* descends from the left side to the nest. It was illuminated by a 16 c.p. incandescent lamp placed near to the off-side of the incline. The ants had rested fifteen minutes.

Fig. 4. Learning-curve of Formica fusca var. subsericea Say, acting in concert; showing the effect of frequent changes of environment.

1. July 1, 8:30 a.m. A cardboard stage with an incline attached to the left side.
2. Do. 9:00 a.m. Same as above. The ants had rested ten minutes.
3. Do. 9:10 a.m. Same as above. The ants had rested one minute.
4. Do. 9:33 a.m. Same as above. The ants had rested one minute.
5. Do. 10:33 a.m. Same as above. The ants had rested three minutes.
6. Do. 11:00 a.m. Same as above. The ants had rested one minute.
7. Do. 3:30 p.m. The same stage used in the above, but a new incline *B* is substituted for incline *A*. *A* is then attached to the opposite side of the stage. The majority of the pupæ were carried down incline *B*. At first, occasionally, a worker would carry a pupa down *A*, but in each case that worker moved much slower than those moving down *B*. The ants had rested four hours.
8. Do. 4:40 p.m. A new stage and a new incline. The ants had rested one hour.
9. July 6, 11:24 a.m. A new stage with a new incline on the right side (the other inclines had been on the left side). The ants had rested four days, fourteen hours and thirty-four minutes.
10. Do. 12:28 p.m. Same apparatus as above. The ants had rested one minute.
11. July 6, 2:25 p.m. Same apparatus as above. The ants had rested five minutes.
12. Do. 3:00 p.m. Same stage, but incline *A* was placed on the opposite side of the stage and a new incline *B* placed where *A* had been. The pupæ were all carried down *B* to the nest, occasionally a worker would carry a pupa partly down *A* and then return to the stage. The ants had rested thirteen minutes.
13. July 10, 7:55 a.m. A new stage with a new incline attached to the right side of the stage. The ants had rested four hours and twenty-five minutes.

Fig. 5. Learning-curve of Prenolepis imparis Say acting in concert, showing unexpected variations in the mode of response.

1. July 9, 7:31 a.m. A cardboard stage with an incline *A* attached to the left side.
2. Do. 10:46 a.m. Same apparatus as above. The ants had rested one minute.
3. Do. 8:05 p.m. Same apparatus as above. The workers had rested over nine hours.
4. July 10, 6:30 a.m. Same apparatus as above. The ants had rested eight hours and ten minutes.
5. Do. 7:55 a.m. Same apparatus as above. The ants had rested ten minutes.
6. Do. 9:35 a.m. Same stage, a new incline *B* is substituted for *A* and *A* is placed on the opposite side of the stage. The ants had rested ten minutes.

Fig. 6. Learning-curve of Prenolepis imparis Say acting in concert, showing the effect of the direction of the rays of light and the result of placing a dark chamber over the top of the incline.

1. July 9, 7:06 a.m. A cardboard stage with incline *A* on left side.
2. Do. 8:16 a.m. Same apparatus as above. The ants had rested one minute.
3. Do. 9:55 a.m. Same apparatus as before. The ants had rested one minute.
4. Do. 10:45 a.m. Same apparatus only the stage was revolved through an angle of 180°, but the incline was left in the same position. Thus there was an unscented path from the pupæ to the incline. The ants had rested six minutes.
5. July 10, 6:30 a.m. Same apparatus as before. The ants had rested twenty hours.
6. Do. 9:08 a.m. Same as above only the stage was revolved through 180°, *A* was left in the old place. Thus there was an unscented path from the pupæ to the incline.
7. July 11, 6:28 a.m. Same apparatus as above. The ants had rested twenty-one hours.
8. Do. 7:21 a.m. Same apparatus as above. The ants had rested fifty minutes.
9. July 12, 7:46 a.m. A new cardboard stage with a new incline leading down to the island. A 19 c.p. incandescent lamp was placed near the incline. The ants had rested one day and twenty-five minutes.
10. Do. 8:53 a.m. Same apparatus as before. The ants had rested three minutes.
11. July 13, 7:11 a.m. Stage with incline *B* on the right. 16 c.p. lamp on the same side as *B*. The ants had rested forty-nine minutes.

12. Do. 8:05 a.m. Same apparatus as above, only a dark chamber opening upon stage and incline was placed over the top of the incline. One set of workers conveyed pupæ to the dark chamber; another set, stragglers from the nest, conveyed them from the dark chamber to the nest. The delay represents the time that elapsed before a straggler from the nest discovered the pupæ in the dark chamber. The ants had rested nine minutes.

13. July 16, 7:39 a.m. Same as above. The workers had rested two days, twenty-one hours and fifty-nine minutes.

14. Do. 2:07 p.m. Same apparatus as above. The delay was caused because they stored all of the pupæ in the dark chamber before any were carried into the nest. The ants had rested four hours and a half.

FIG. 7. Learning-curve of an individual Formica fusca var. subsericea Say, showing lapse of memory, etc.

Apparatus. Two cardboard stages, *1* and *2*; inclines *D* and *E* leading to the island from each, respectively. The feet of the inclines were side by side. Each was attached to the right side of the stage. The marked worker was placed on stage 2 (see p. 412).

*A*. On trips 6 and 7 the pupa was taken from stage 1 to the nest.

*B*. On trip 12, do.

*C*. The worker ascends and descends incline *D*, then ascends and descends incline *E*, then ascends to stage 2 and carries a pupa to the nest.

*D*. On trip 36 the pupa was taken from stage 1.

*E*. On trips 43–45, do.

*F*. On trip 50, do.

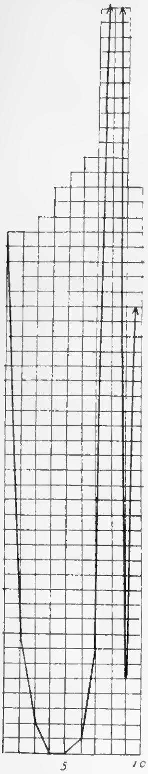


*Fig. 1*

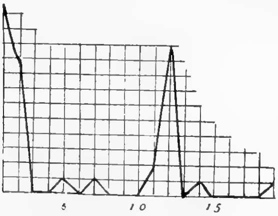


*Fig. 2*

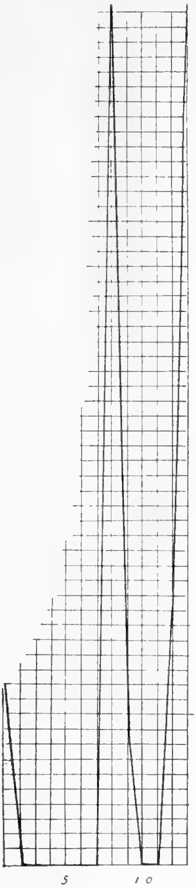


*Fig. 3*

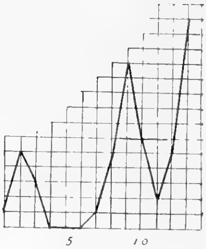


*Fig. 4*

*Fig. 5*

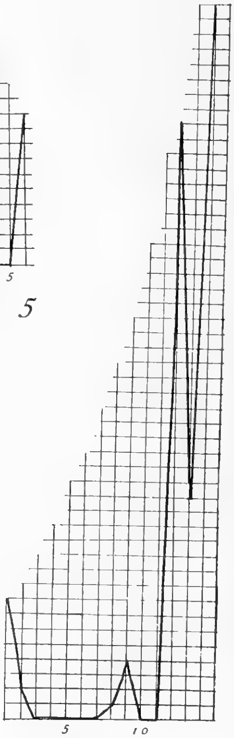


*Fig 6*

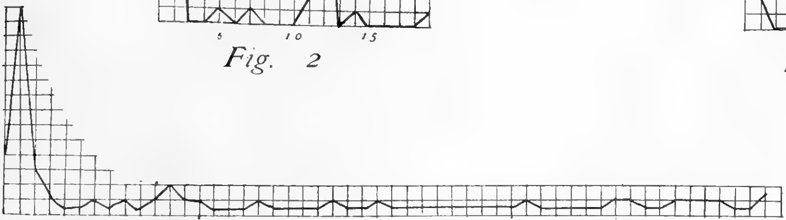


*Fig. 7*

## PLATE III.

FIG. 8. Learning-curve of an individual Myrmica punctiventris, showing its reactions to colored pathways.

Apparatus, cardboard stage with a red incline leading down to the island; illuminated by diffuse daylight.

*a.* While the worker was on the stage a new red incline was substituted for the old.
*b.* Do. Green for red.
*c.* Do. Purple for green.
*d.* Do. Blue for purple.
*e.* Do. Yellow for blue.
*f.* Do. White for yellow.
*g.* Do. Red for white.
*h.* Do. White for red.
*i.* Do. Smooth black for white.
*k.* Do. Black with velvety feel for smooth black.

FIG. 9. Learning-curve of an individual Formica fusca var. subsericea Say, showing its reactions to odors encountered in its path.

Apparatus, a cardboard stage with an incline passing down to the island. On this stage the pupæ and a marked worker were placed. The worker had made several trips before the first trip plotted here.

*A.* While the worker was on the stage, I substituted for the incline one with a transverse band of xylol across its middle.

*B.* I replaced the old incline.

*C.* While the worker was on the stage I substituted the incline with the transverse band of xylol.

*D.* While the worker was on the stage the incline with the xylol band was transferred to the control stage and allowed to remain there eight minutes. The ant used for control was much disturbed. During the eight minutes it mounted the incline several times, but would not cross the band.

*E.* The incline with the xylol band is reattached to stage 1. During the eight minutes that have elapsed the marked ant has made several trips down an unscented incline which was attached to the stage when the incline scented with xylol was removed.

*F.* The incline with the xylol band is transferred to the control stage and causes the same disturbance as before.

FIG. 10. Learning-curve of a Myrmica punctiventris, showing its reactions to light rays and to tactile stimuli.

Apparatus, a cardboard stage with an incline *A* passing from left side to the island. Near the left side of the stage was placed a 16 c.p. incandescent lamp. The room was darkened.

*a.* While the worker was on the stage the 16 c.p. lamp was transferred to the right side of the stage.

*b.* While the worker was on the stage, the incandescent lamp was extinguished and the curtain of a window thrown up so as to illuminate strongly the left side with daylight.

*c–d.* Experiment was interrupted for six minutes.

*d.* The same stage, but illuminated uniformly by diffuse daylight instead of by an incandescent lamp in a special position. A smooth black incline leads from the stage to the island.

*e.* While the worker was on the stage the white incline was substituted for the black.
*f.* Do. Smooth black incline for white.
*g.* Do. Black incline with velvety feel for the smooth black.

FIG. 11. Learning-curve of an individual Formica fusca var. subsericea Say, showing its reaction to a colored pathway.

Apparatus, a cardboard stage with red incline leading down to island, illuminated with diffuse daylight.

*a.* While the worker was on the stage a new red incline was substituted for the old. The paper on this incline was somewhat wrinkled.

*b.* Do. Green for red.

FIG. 12. Learning-curve of an individual Formica fusca var. subsericea Say, showing effect of a jar upon its behavior, etc.

Apparatus, a cardboard stage with a white incline leading from its right side to the island. A heat-filter composed of a tall rectangular museum jar filled with water was placed near both the right and left sides of the stage. Behind the heat-filter on the right was placed a 32 c.p. incandescent lamp. Excepting for this light the room was dark.

*A*. Placed a new white incline on the opposite side from the first incline.

*B*. While the worker was on the stage the 32 c.p. lamp was placed behind the heat-filter on the side where the second incline was.

*C*. While the worker was in the nest the light was replaced on the same side as the first incline.

*D*. While the worker was on the stage I substituted a new white incline for the old. In doing so the stage was jarred considerably.

*E*. Do. White for black.

*F*. Replaced the worker on the stage.

*G*. While the worker was on the island, I substituted a white incline for the black.

*H*. Do. New white for the old.

Fig. 13. Learning-curve of an individual Myrica punctiventris, illustrating one of those occasional cases in which it took the ant much longer to make the second trip to the nest than it did to make the first.

Apparatus, two cardboard stages, each with an incline leading down to the island. Pupæ are placed on both stages. The marked worker is placed on stage number one.

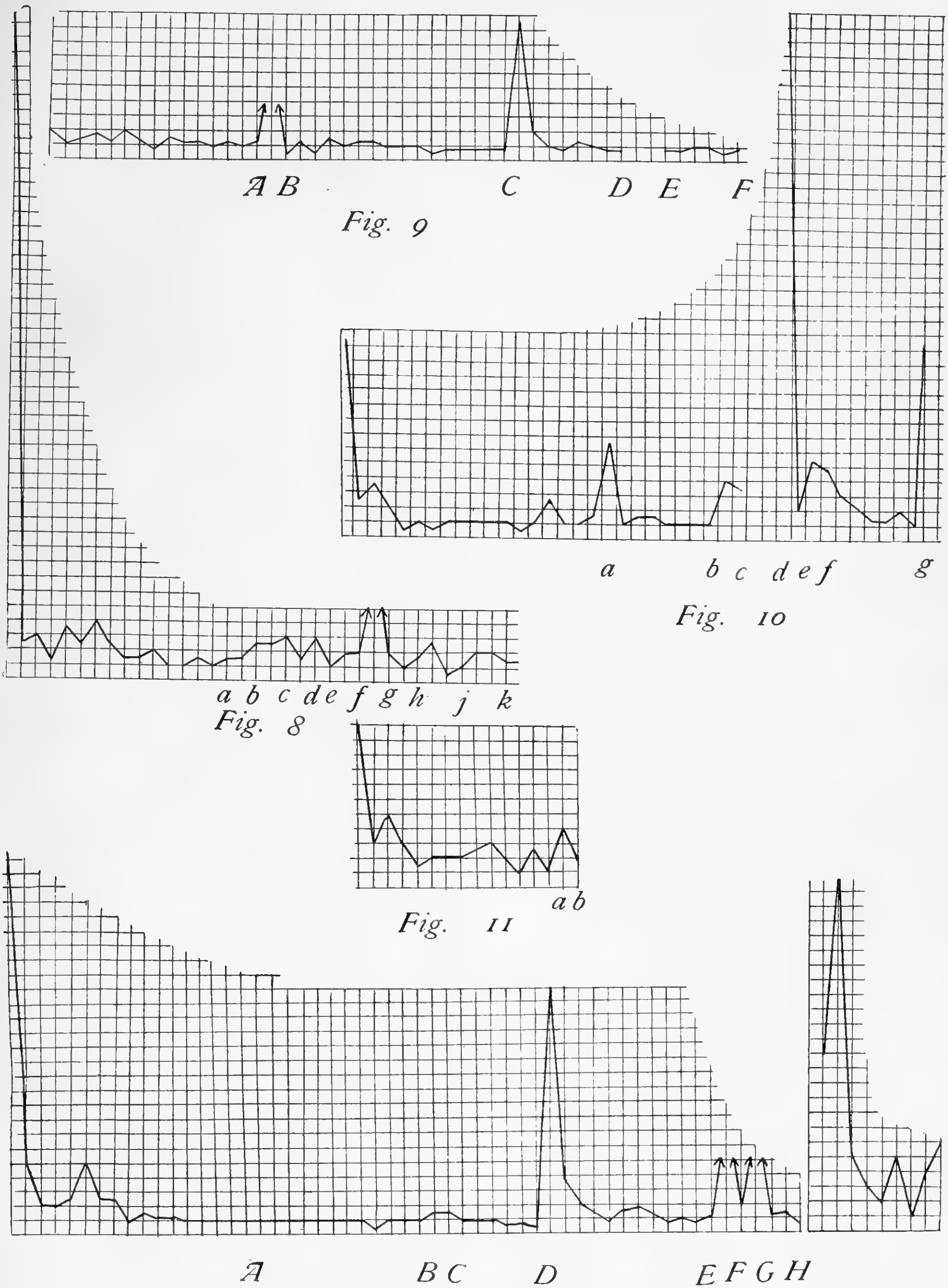


Fig. 9

Fig. 10

Fig. 8

Fig. 11

Fig. 12

Fig. 13

## PLATE IV.

FIG. 14. Learning-curve of an individual Formica fusca var. subsericea Say, illustrating its reaction to changes in the direction of light, to colored pathways, and to tactile stimuli.

Apparatus, a cardboard stage with a white incline leading from the right side to the island. A 16 c.p. lamp is placed on the same side of the stage as the incline. Throughout the whole of this part of the experiment the worker ascended to the stage on the top side of the incline, and descended to the island on the lower side.

*A.* Placed a new white incline on the side opposite the old incline.

*B.* While the worker was on the stage, the 16 c.p. was transferred to the opposite side of the stage.

*C.* Replaced the light on the same side as the incline.

*D.* While the worker was on the stage, I transferred the light to the opposite side of the stage.

*E.* I replaced the light in former location.

*F.* While the worker was on the stage, I substituted a smooth black for the white incline.

*G–H.* The experiment was interrupted from 7:41 p.m. to 8:41 a.m.

*H.* The same stage, but a red incline is substituted for the white and no artificial light is used. In this section of the experiment the worker goes in almost a straight line from the foot of the incline to the side of the nest and then to either the right or the left (for it does not always follow the same line) to the nest; but in returning to the incline it meanders a great deal.

*I.* While the worker was on the stage, I substituted a new red incline for the old red one.

*K.* While the worker was in the nest, a green incline was substituted for the red.

*L.* While the worker was on the stage, a purple incline was substituted for the green.

*M.* While the worker was on the stage, I substituted a yellow for the purple incline.

*N.* While the worker was on the stage, a blue incline was substituted for the yellow.

*O.* While the worker was on the stage, a smooth black incline was substituted for the yellow.

*P.* While the worker was on the stage, a black incline with velvety feel was substituted for the smooth black.

FIG. 15. Learning-curve of an individual Myrmica punctiventris, showing its reactions to colored pathways, etc.

Apparatus, a cardboard stage with an inclined plane leading down to the island. Illumination, diffuse daylight. During the first twenty-three trips the pupæ were carried only so far as the base of the incline; from there other workers conveyed them to the nest.

*A.* While the worker was on the stage a new white incline was substituted for the old.

*B.* Do. Smooth black for white.

*C.* Do. Black with velvety feel for smooth black.

*D.* Do. Red for black.

*E.* Do. Green for red.

*F.* Do. Purple for green.

*G.* Do. Yellow for purple.

*H.* Do. Blue for yellow.

*J.* Do. White for blue; placed a 16 c.p incandescent lamp on the same side of stage as the incline and darkened the room.

FIG. 16. Learning-curve of an individual Formica fusca var. subsericea Say, showing the effect upon its behavior of a change in the direction of the light rays.

Apparatus, cardboard stage with incline descending to the island.

*A.* Between 24 and 25 the experiment was suspended for one hour.

*B.* Between 49 and 50 the experiment was suspended for four hours and twenty-six minutes.

From *B* to *C* the ant was working at night by lamplight and the direction of the rays was from the northeast. The rest of the work was done by daylight and the direction of the rays of light was from the south and west (see p. 400).

*C.* Between 66 and 67 the experiment was suspended for eleven hours and twenty-six minutes.

FIG. 17. Learning-curve of an individual Formica fusca var. subsericea Say, showing its reactions to changes in the direction of the rays of light.

Apparatus, a cardboard stage with a white incline leading from the right side to the island. A 4 c.p. incandescent lamp was placed near the right side of the stage; otherwise the room was dark.

*A.* While the worker was on the stage, I substituted a 32 c.p. lamp for the 4 c.p.

*B.* While the worker was on the stage, I transferred the 32 c.p. to the left side of the stage.

*C*. Do. The 32 c.p. to the right side.
*D*. While the worker was on the stage, I substituted an 8 c.p. lamp for the 32 c.p.
*E*. While the worker was on the stage, I transferred the 8 c.p. lamp to the left side.
*F*. Do. 8 c.p. lamp to the right side.
*G*. While the worker was on the stage, I substituted a 4 c.p. for the 8 c.p.
*H*. While the worker was on the stage, I transferred the 4 c.p. to the left side.
*I*. Do. 4 c.p. lamp on the right side.
*K*. While the worker was on the stage, I substituted a 32 c.p. lamp for the 4 c.p.
*L*. While the worker was on the stage, I placed the 32 c.p. at the back of the stage.
*M*. Do. 32 c.p. at the front of the stage.

FIG. 18. Learning-curve of an individual Formica fusca var. subsericea Say, illustrating its reactions to odors of the pathway and to tactile stimuli.

Apparatus, cardboard stage with white incline on the left. Illumination by incandescent lamps; practically uniformly illuminated.

*A*. While the ant was in the nest, a new white incline was substituted for the old.
*B*. The old incline was substituted for the new.
*C*. While the worker was on the stage, a new white incline was substituted for the old.
*D*. Do. an incline with a three-fourths inch transverse band of oil of cloves across its middle was substituted for the other.
*E*. Replaced the old incline.
*F*. Do. an incline with middle three-fourths inch band of xylol for the other.
*G*. Do. with fresh xylol band.
*H*. Do. with fresh band of cedar oil.
*I*. Do. with fresh band of oil of cloves.
*K*. Do. with unscented white incline.
*L*. Do. with smooth black incline.
*M*. Do. with black incline with velvety surface.

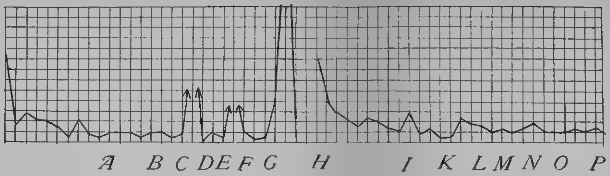


Fig. 14

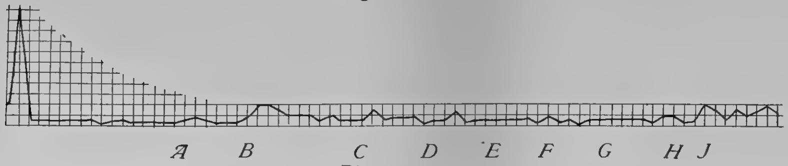


Fig. 15

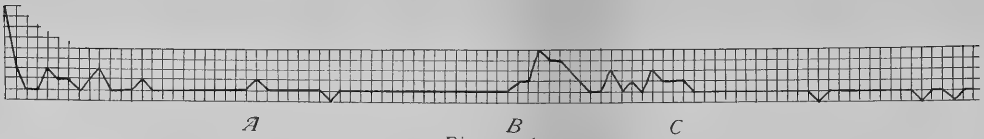


Fig. 16

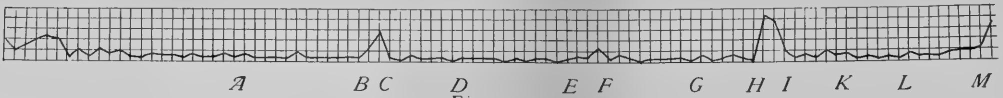


Fig. 17

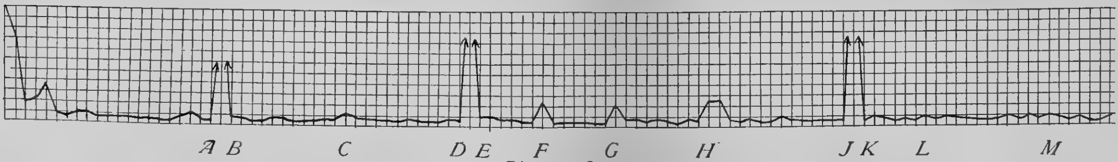


Fig. 18

# THE BEHAVIOR OF THE PHANTOM LARVÆ OF CORETHRA PLUMICORNIS FABRICIUS.

BY

E. H HARPER.

(From the Zoölogical Laboratory of Northwestern University, Evanston, Ill.)

WITH FIVE FIGURES.

This paper describes some features of the behavior of the larvæ of Corethra plumicornis Fabricius var. Americana, one of the short-beaked mosquitoes. Some observations upon the pupæ are included. The larvæ of Corethra have attracted much attention among naturalists. They have been called the phantom larvæ on account of their transparency. They are of predatory habit, lying in wait and feeding upon small crustacea, Culex, etc. The clear, open water is their preferred habitat. The writer has found them in great numbers in a pond where predatory aquatic insects abounded. Their daily depth migrations under the combined influence of light and gravity are a prominent feature of their reactions.

Their behavior is modified in correlation with their transparency, the absence of appendages, and their air sacs. Their transparency secures them immunity. Their relation to the inorganic environment is largely automatized through the air sacs. They are thus enabled to maintain their position, through the static function of the air sacs, at any level adapted to their physiological state. The air sacs also serve a purpose dynamically in producing certain automatic movements. There are two pairs of these, anterior and posterior, through which the specific gravity may be altered. Their immunity is associated with a lying-in-wait habit, with discontinuous movements of intensive rather than extensive type. The absence of appendages, besides being the cause of the absence of certain familiar reactions (thigmotropic), is further associated with an unconventional type of locomotion and orientation to stimuli, which invites comparison with the current explanations of the tropisms.

## THE TROPISMS. THEORIES OF ORIENTATION.

In the treatment of the reactions of the lower animals many writers have apparently considered the direction of movements as the only feature worthy of attention, with the consequent reduction of the reactions to positive and negative tropisms. A universal form of movement as a mode of orientation to stimuli has even been formulated, which is supposed to sufficiently describe *a priori* the behavior under stimulation. The animals are regarded in reality as passive factors in the result, having their movements imposed upon them. This conception of an animal's movements manifestly is a homologue of the notion of spontaneous generation. The movements are virtually represented as directly produced by the action of the environment.

Other writers have shown clearly what scarcely needs to be pointed out, that an animal's behavior is as characteristic as its structure. One of the first fruits of comparative study of behavior has been to replace the old notion of the production of movements by the action of the environment, akin to the spontaneous generation of organisms, by descriptions which are in some cases as definite as those of anatomical structure which we possess. This later view finds in animal behavior an external exhibition of regulatory activity, and treats movements as self-regulative rather than externally controlled.

The most extreme exhibition of this later tendency is a proposition to explain tropisms on a basis of accidental orientation, or trial and error, rather than to allow the directive action of external stimuli. But this view repudiates the adaptive character of directed movements as clearly as did the belief in movements produced directly by the action of the environment. The theory is that under stimulation animals make varied movements. Those that are in such a direction as to lead to decrease of stimulation, are continued because of the absence of stimulus to further change. In the older view orientations were forced by the environment. According to this point of view orientation is regarded as accidental. Such a roundabout method as is implied in the selection of varied movements is manifestly less self-regulative than a more direct response to a stimulus would be. It means that the animal in question is regarded as having no power of immediately regulating its actions with reference to the direction of an external stimulus.

The apparent desire to be rid of the directive influence of external stimuli and exalt the animal's self-regulative power, lands one in the difficulty of seeming to diminish the animal's self-regulative capacity, by explanations which fortunately do not affect the *modus vivendi* of the animals under discussion.

The principle of trial and error in its application to the behavior of some of the lowest forms, has been applied with greatest plausibility to animals whose movements are of an undifferentiated type, as in many Protozoa. The fact that behavior may be of various degrees of differentiation has an important bearing on these problems. In the undifferentiated activities of Euglena or Paramœcium the same movement comprises both internal and external factors and can be interpreted only by analysis into its components. Thus the protozoan, while continually swerving aborally along its spiral path, and thus coming into contact with an ever-changing environment, may broaden the spiral by swerving still further aborally in answer to an external stimulus. So in the same movements are blended spontaneous trial movements and directed ones; locomotion of a peculiar, adaptive type, food-taking, and it may be, an avoiding reaction. But in any form having a differentiated type of behavior, the different forms of reaction occur separately.

It is manifest that an undifferentiated movement cannot be regarded as a pure tropism, for the latter is defined as the result of an external stimulus alone. The pure tropism can only be found in a differentiated type of behavior and is to be regarded as a product of evolution from behavior of the undifferentiated sort. The difficulty in harmonizing the behavior of Paramœcium with the accepted and simple type of the tropism found in more specialized animals, upon which the "local action" theory of tropisms has been based, is the point here emphasized, that the movements of Paramœcium do not show the tropism in pure form, but an undifferentiated type of activity. Moreover the apparent simplicity of tropisms should give no comfort to the other school who regard movements as directly produced by the environment, when they are reminded of the probable phylogeny of the tropism. Simplicity and directness are the outcome of an evolutionary process, not signs that the organism is acted upon as iron filings are by a magnet.

It is scarcely necessary to point out this similarity between external behavior and other physiological processes. Just as functions become localized in organs and become more definite, as well as susceptible of analysis, so in behavior increasing definiteness and specialization of functions in separate forms of activity are met with in the ascending scale of animal life.

## CLASSIFICATION AND DESCRIPTION OF MOVEMENTS.

In classifying the activities of the Corethra larvæ we recognize, in addition to the ordinary kind, the occurrence of automatic movements due to alteration of specific gravity, by means of the air sacs. Observation of the muscular movements leads to classifying them in several groups according to their form: (1) locomotion, (2) food-taking, (3) convulsive wrigglings which have the appearance of spontaneous overflows of energy, (4) cleaning movements. The muscular movements are all produced by the lashing of the body, which is destitute of locomotor appendages except a ventral, caudal fin composed of a row of bristles.

Each separate movement is effected by a single lashing motion of the body and is followed by an interval of rest. Under a certain condition of stimulation, to be considered later, they may move continuously for a short time. Occasionally under ordinary conditions a movement is followed in close succession by a second, rarely by a third. In a hundred successive movements, frequently a third of them occur in twos.

Another characteristic of the locomotion is a lack of symmetry. After a movement the larva is found at a little distance pointing in a new direction. In a recorded series it is found to point successively in all directions (Fig. 3). In rapid flight, under the condition of stimulation which causes continuous motion, they move in a fairly straight, but zigzag path.

Still another general quality of the movements is their energetic character. Each one starts from rest and lack of momentum is compensated by the energy put forth. One half of the musculature is ordinarly involved. Fatigue may be readily produced by mechanical stimulation.

The movements at times acquire a degree of regularity, most pronounced in the active state of the animal. An observed case of unusually high frequency may be instanced, in which the number of movements per minute for ten consecutive minutes was 21, 21, 20, 21, 22, 22, 22, 20, 19, 23.

*The Method of Locomotion.*—MIALL speaks of the movements as having the quickness of a deflection of the magnetic needle. The unit of movement in locomotion consists (1) of a side sweep of the posterior half and a similar but less pronounced stroke of the head in the same direction. The head may also move up or down. The side sweep of the tail may be carried till the end touches near the middle of the body or it may be of much less extent. (2) After the contraction the body straightens quickly, but not bending to the opposite side. The drifting motion that results is nearly always accompanied by rotation, with the head in such cases always turned away in the direction opposite to that of the contraction (Fig. 1). A parallel position may be maintained, but there is never rotation of the head in the direction of the contraction. A consideration of the factors shows that the lateral sweep of the head and tail to the same side would have opposite effects upon the tendency to rotate. The return movement of the tail appears most effective in producing the rotation. It seems to be due to elasticity alone. The extent of the movement varies from a slight twitching of the two ends up to a movement with rotation to 180°. Locomotion is thus seen to be in the nature of a recoil or reaction to the single muscular contraction. The lashing of the body is like that of cilia, driving the body in the opposite direction.

FIG. 1. Diagram of locomotion. *A*, pigmented air sacs.

MIALL speaks of the movements as due to the sculling motion of the tail. That description does not include the action of the anterior end. The body tapers posteriorly. The muscles are mainly segmental, binding together adjacent segments. The side stroke of the more powerful anterior end though less extensive is effective in locomotion. It appears more effective in the contraction, the posterior end in the return movement.

*Food Taking.*—While locomotion is in the nature of a recoil, in food taking this is not the case. Food is seized only when nearby without preliminary movements. A glass capillary rod will often be seized repeatedly by a hungry animal. Either a food reaction or an avoiding reaction may be given if the rod is presented to either end. When it is presented at the posterior end, in case the food reaction is given, the animal bends its head around, and continuing to bend it moves directly to the object with a suddenness that is hard to follow (Fig. 4). If the rod is presented at the side of the head it simply bends the head to one side, turning on its long axis to get the object in its mouth. In both the food reaction and the avoiding reaction the contraction of muscles occurs on the stimulated side. But in the food reaction only the head bends toward the object, while in the avoiding reaction both ends take part, the tail being chiefly instrumental in causing the animal to recoil from the stimulating object. Accessory movements may occur after food-taking; the larva sometimes shakes its prey after capture.

*Other Movements.*—The other class of movements referred to as convulsive or wriggling may also be made to include those directed at the animal's own body, which appear like cleaning movements. In wriggling the ends contract oppositely forming an S, and repeating this a number of times, with twisting on the long axis. These wrigglings sometimes occur after a longer period of quiescence than usual. They appear like ebullitions of superabundant energy.

## REACTIONS OF THE LARVAE—APPLICATION OF THE "LOCAL ACTION" THEORY OF TROPISMS.

Locomotion is of the same form whether due to external stimulation, or spontaneous. It may therefore be positive, negative or indifferent with reference to the environment and have the same form in each case. Food-taking, as was seen, on account of the difference in form should be classed separately. According to the theory of tropisms, a mode of orientation was formulated for all animals. As applied to the earthworm, the theory is given as follows in DAVENPORT's summary of LOEB's views. It is very true that an explanation which is applicable to the earthworm is not invalidated because of its partial or complete failure to apply to some other form. It may, however, serve to emphasize the description of the facts to compare the mode of orientation in these two widely different forms, inasmuch as the explanation has been given a quasi universality in its mode of statement. We quote it in abridged form. The earthworm is attuned to light of low intensity. Therefore under unilateral stimulation, the muscle tonus on the more illumined side is reduced, with the result that the less illumined side, having its normal tonus, is caused to contract more and leads to negative orientation towards the rays of light. *Mutatis mutandis*, the same explanation would apply to positive orientation.

If this explanation is applied to the Corethra larvæ, it is found that under unilateral stimulation they too contract the muscles of the less illumined side. The similarity ends here, for the resulting movement in Corethra is toward the light and these animals are photopositive, while the earthworm is negative. Corethra is "attuned" to light of rather high intensity. According to the theory the muscle tonus of the more illumined side ought to be increased. But owing to Corethra's system of locomotion this would drive it away from the light. The reason for this difference in behavior is in brief that the motion of translation is in the earthworm caused immediately by the action of the muscles, while in Corethra it is caused by the recoil from the muscular movements (Fig. 5). On the other hand the positive reaction of food taking would conform to the conventional explanation as in this case it is the stimulated side which contracts. But this fact weakens the significance of the classification of movements in the same category as positive which differ in a quite opposite way in their form. It is clear that the classification of movements as + and − has involved the tacit assumption that since movements are forced by the environment anyway, their direction is the only thing worth considering. It is manifest from these examples that the mode of the reaction is peculiar to the system of behavior of the larva. We are compelled to look to the structure and behavior of the animal as a whole for explanation of its conduct. As a matter of fact Corethra shows a highly adaptive behavior, in which all the modes of reaction fit together and are explicable only in relation to one another.

Again, the theoretical mode of orientation of the tropism scheme may be applied to a negative response of Corethra, called forth, for example, by mechanical stimulus. The conventional negative response of turning away from a localized stimulus is brought about by contraction of the muscles of the unstimulated side. Corethra has as definite an avoiding reaction as any, but gets away by contracting the stimulated side, even in this way bringing its body at first into closer contact with the stimulating object. It is evident that it is not the mode of orientation which is uniform in different animals, but the result. The recognition of unconformity in the process of orientation in different animals emphasizes the self-regulative capacity of animals, and the difference between their movements and those of passive machines. In any case the most direct mode of orientation which is consistent with the animal's own system of movements is followed. Hence it is proper to speak of movements as directed, remembering that activity, not passivity, is implied in the process.

## APPLICATION OF THE TRIAL AND ERROR THEORY TO THE REACTIONS.

It is frequently maintained or implied that reactions to external stimuli lie at the foundation of behavior. But not all or even the larger part of an animal's movements are referable to external stimuli. In the case of Corethra the possibility of distinguishing the different movements with reference to their exciting cause is favored by their discontinuity. A significant addition to recognized forms of reaction among the lower animals are the trial movements emphasized by JENNINGS and others. Such movements make up by far the larger part of an animal's behavior, as is recognizable in a roughly quantitative way in Corethra, since the separate movements of the larva stand out distinctly and give opportunity to relate them to their antecedent causes, in a way which is perhaps more obvious than in an ordinary, continuously moving, restless water insect. In Corethra, while external, localized stimuli give rise to oriented movements, internal or unlocalized stimuli give rise to movements indefinite in direction but adaptive in bringing the organism into as wide contact with the environment as possible. As was pointed out above, wider range of vision is secured in these larvæ by the asymmetrical character of their movements, which causes them to face successively in different directions, an adaptation which is in accord with the lying-in-wait habit.

A series of movements A, B, C, D, may be pure overflows of energy, undirected by external agents; E may be directed at food; F may be an avoiding reaction; G, H, I, J, may be again overflow movements. It is seen that A, B, C, D, are random in direction and cause the animal to point successively in different ways, which, it may be surmised, has importance at least in the search for food. E and F on the other hand, are directed by external stimuli and are characterized by their definiteness and even precision. The trial and error principle cannot be recognized in such a series for the reason that the fundamental assumptions of the trial and error scheme do not hold. The random movements A, B, C, D are not made under external stimulation. The orientation in the movements E and F is not accidental, but immediate and directed.

## REACTION TO MECHANICAL STIMULI AND VIBRATIONS.

The sensory apparatus of the larvæ is highly specialized. Animals which make continuous movements through the water have some sort of feelers located at the anterior end. Corethra in accordance with its discontinuous movements and lying-in-wait habit has no such feelers, but is armed from front to back with sensory bristles. It indeed bristles with warning organs which notify it of the slightest disturbance in the water. It is scarcely possible to bring a glass rod near it without causing it to move.

Very similar in point of utility are the chordotonal organs of simple nature which respond to vibrations.[1] One of the most striking responses of these organisms is produced by tapping an aquarium full of them. Like electric needles they instantly become deflected and usually oriented with the head away from the source of vibration. The response is a single lashing movement so directed that the heads of all point in a general direction away from the source of disturbance. This can be repeated again and again at short intervals. This negative response might be surmised to serve to notify of the approach of prey as well as of danger. In catching food, the prey is seized at close range by

---

[1] The chordotonal organs of Corethra are figured in numerous texts, taken from GRABER ('82). They can be seen with diagrammatic clearness in the living specimens, or by adding 1 per cent acetic methyl green. The anatomy of the sensory bristles was worked out by LEYDIG ('51).

a single pounce without any preliminary movement to get in position. It might seem from this that the nicely coördinated movement employed in seizing food is not in response to the visual impulse alone, but that the stimulation of the sensory bristles at the same time serves to intensify the visual impulse. The negative response may be called forth by stimulating with a fine glass rod tipped with sealing wax. When so stimulated on either side the animal makes a movement away from the stimulating object. It may thus be guided across a vessel in a zigzag path by alternately stimulating the opposite sides.

When the stimulus causing the negative response is repeated by a rapid succession of taps and intensified, the larvæ appear to become highly alarmed and project themselves with great force and rapidity in long zigzag paths by a rapid succession of movements. It is obvious that the intensified negative response is of no small importance and that the security of these animals does not lie wholly in their transparency.

Acclimatization to such stimuli as tapping on the aquarium jar is soon produced by repetition of the stimulus at closer intervals. The responses become weaker until only a slight ducking of the head is produced and finally no further response is made. The dish in which the larva was placed was subjected to constant tapping at one point and the movements recorded on a sheet of paper by noting the position taken each time. The chart was then reduced to the form shown in the figure. It will be seen that the first eight or ten movements were all pointing in a general direction away from the source of the stimulus. A chart of the next movements shows them rather evenly distributed in all directions (Figs. 2–3).

## REACTION TO LIGHT.

In connection with the light responses of these creatures their daily depth migrations furnish the matter of greatest interest. It was noticed that Corethra's horizontal movements are restricted on account of its lying-in-wait habit. If one may speak of the orbit or range of an animal, it is of course a general fact that the orbits of animals are most extended horizontally. In the case of Corethra, however, the horizontal range is restricted, and the vertical range is important and is largely regulated by gravity. The pupa lacks the special adaptations of the larva and is more like an ordinary animal. Its reactions to light are more marked than those of the larvæ.

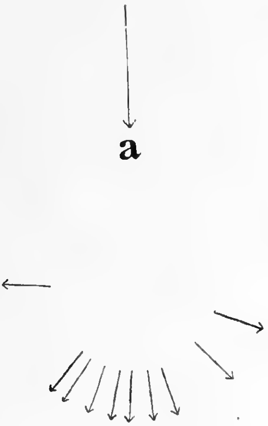


FIG. 2.

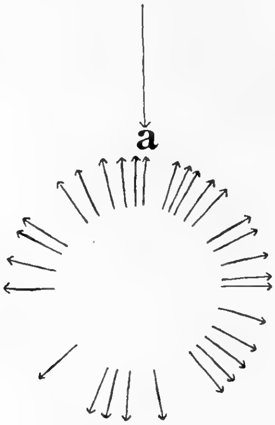


FIG. 3.

FIG. 2. Diagram showing directions taken in the first ten movements of a larva, produced while the jar was being tapped on side *a*.

FIG. 3. Diagram showing the directions assumed in the next thirty movements, made while tapping was continued at *a*, showing effects of acclimatization.

*Experiment 1.*—The latter show a distinct response which is most marked in animals just brought into the laboratory and attuned to the out-of-door intensity. These collect on the lighted side of an aquarium. For experiments larvæ were placed in a trough 4 x 4 x 18 inches, with glass ends and blackened interior, and lighted from one end, sometimes with sunlight and sometimes with a 32 candle power incandescent lamp. In the most marked responses noted the animals zigzagged to the lighted end in a few

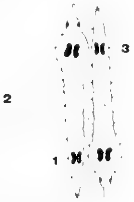


FIG. 4. Diagram of food reaction, showing movement in seizing an object applied as a stimulus at posterior end in position 1.

minutes. The mode of orientation has already been described. In such a case the less illuminated side contracted. The animal would be thrown around so that invariably, we may say, the other side would be presented to the light. Once in a while, of course, it might happen to get into the line of the rays, but the animal is, so to speak, always becoming oriented, and never except accidentally, for one resting interval, does it get into the line of the rays. On account of its unsymmetrical movements it is of course unable to take and keep such an oriented position (Fig. 5).

Fig. 5. Diagram showing positive phototaxis in Corethra. *L*, source of light.

The positive reaction changes gradually to negative as will be further shown in Experiment 6. Miall states that the animals prefer the upper lighted waters, but preferably in a place shaded somewhat by trees. The writer has collected them in great numbers from the surface waters of ponds at all seasons. In certain Wisconsin lakes, the writer is informed by Mr. C. Juday, Corethra larvæ (species ?) go down in the daytime and come up at night with great regularity and it is a very rare occurrence to find Corethra near the surface in the daytime. The writer has collected them in ponds whose water was shallow and also constantly quite turbid. In one pond whose greatest depth was four feet they were fairly abundant. In another with a depth of twenty-five feet they were very numerous. They could be obtained easily from the surface waters near the shore line in the daytime. Night was however the favorable time for collecting them, as they then came to the surface in great numbers. It is manifest that in the turbid waters of ponds they do not all seek such depths in the daytime as is the case in the clearer waters of some lakes. It is of course quite possible that the food supply also has something to do with the depth to which they go.

*Experiment 2.*—In order to determine the influence of light on their downward movements the experiment was next tried of lighting the water from above. The larvæ were placed in a tall cylindrical jar, on top of which was placed a dish of alum water. The experiment was tried in a darkened room and the larvæ were soon distributed through the upper portion of the jar. A 32 candle power bulb was then held over them. As soon as the light was turned on they began to swim downward. After a few minutes they had moved into the lower portion. All seemed to be affected by the light but in different degrees as indicated by the depths assumed. In some lots the animals went upward toward the electric light. There seemed to be differences in lots collected at different times.

*Experiment 3.*—The jar was next lighted from underneath. It was supported on a ring with a dish of alum water close beneath. When the animals had remained in the dark long enough to move upward the light was turned on beneath the jar. The larvæ at once moved downward as before and settled in the lower portion. In both experiments some came to rest on the bottom. This experiment indicates that the downward movement is not a negative light reaction, as the animals went toward the light.

*Experiment 4.*—Experiments 2 and 3 were next repeated with direct sunlight. For this purpose a cylindrical screen of black paper shaded the sides of the jar. In lighting from above the direct light was allowed to enter as far as possible but this was reënforced by reflection from a mirror. In lighting from beneath the light was reflected upward from a mirror. The experiments were carried on near a window where the rays were entering at a high angle. The results were the same as in 2 and 3. The same results as the above can be obtained more simply by placing the jar directly in the sunlight. These experiments also included the use of blue and red glass to transmit the rays. Red glass gave the same effect as darkness. The blue gave normal results.

*Experiment 6.*—The experiment was next tried with an aquarium of special form to show both the downward movement and the positive movement horizontally toward the light. For this purpose a deeper aquarium was used, two feet in depth, with the other dimensions six by twelve inches. The narrow ends were of glass. The rest of the interior was blackened. It was placed in the direct sunlight with the light entering from one end and the top covered. The larvæ moved downward and toward the lighted end, collecting in the lower lighted corner. When large numbers are used the result is very striking. Not all collect in this way, as a few will be scattered through the aquarium. With freshly collected animals the movements are rapid and appear hurrying in spite of the discontinuity. When the aquarium is turned end for end they begin to move in the other direction with great quickness. These experiments indicate that when the water is illuminated from whatever direction the larvæ follow their geotropic instinct to go downward. In darkness or weak light they are negatively geotropic or positively phototropic to weak light.

The positive response to strong light offers some difficulty since it would naturally be expected to cause the animals to go up as well as horizontally. The pupæ do move to the region of greatest intensity, up or down or to the side. In the larvæ the geotropism is the stronger. The musculature involved in downward movements is different in part from that employed in horizontal movements. The positive reaction changes to negative in from one to two hours or in some collections in less time. It should be observed however that the gathering on the lower lighted side of the aquarium precludes the explanation that the downward movement is due to a negative light reaction.

The case of Corethra perhaps presents some similarity to the nocturnal amphipods described by HOLMES, which were positively phototropic. PARKER ('01) ascribes the downward movement of Copepods in the daytime partly to negative phototropism. As shown by Experiment 3, the case of Corethra cannot be due to negative phototropism, although the depth migrations are not independent of light.

*Experiment 7.*—The first experiment was repeated with larvæ which had been kept in the laboratory several weeks and it was found that they reacted negatively to sunlight or artificial light and collected in the shaded portions of the aquarium. Repetition of Experiments 2 and 3 with them showed some manifestation of positive geotropism in strong light but the response was weakened. The movements of such animals are however quite sluggish and little can perhaps be inferred from their behavior beyond its subnormal character. The negative light response was not universal as a considerable proportion came to the lighted end and kept striking against the glass.

It may be asked, what interpretation is to be put upon the positive light response in its relation to the normal behavior. It is not to be concluded from the fact that they move downward in the daytime that the larvæ remain quiescent. Doubtless they are attracted by places of greater intensity, although prevented from going upward by their geotropism. At the depth then at which they remain in the daytime they may be inferred to seek the optimum intensity, which at nightfall or in cloudy weather includes movements upward as well. Their well developed eucone type of eyes, which are very rare in larvæ, are well adapted for vision at the lower depths, and their pigmented airsacs may have some specially important respiratory function, as MIALL suggests, enabling them to remain at these depths. Upon this point the writer has nothing to offer.

## AUTOMATIC MOVEMENTS DUE TO GRAVITY.

These animals are so balanced in the water by their air sacs that a slight change in their specific gravity causes them to rise or sink. When hungry they become more buoyant, as may be well seen in an aquarium full of them. A jar of Corethras will soon clean out the supply of small Crustacea. Let a scarcity of food arise and the behavior changes. They are all seen to be going through the same performance. Each larva rises automatically a little distance and then ducks down by one of its lashing movements, which are the same as the type described, except that the vertical component is a little greater than usual and is always directed downward. This performance of automatic rising and ducking down is repeated indefinitely. In the case of each individual it is quite rhythmical, the rate seeming to vary in different individuals in accordance with their degree of buoyancy.

Doubtless this behavior which occurs as a result of food scarcity is in a certain degree abnormal. But there is always a variation in specific gravity. In any lot of Corethras some may be rising from buoyancy and others falling, though in normal conditions the great majority appear nearly or quite motionless. The air sacs exert a dynamic function in causing righting movements, since they automatically bring the animal into horizontal position without muscular effort. After every downward movement this is noticed, in the automatic restoration of the horizontal position.

### THE PUPA.

There is a marked change of behavior in the pupa. Certain structural changes occur. They acquire a pair of broad flat caudal plates, by which they propel themselves by powerful strokes. They also acquire a pair of external floats at the forward end. The body becomes gradually more opaque. The pupæ stand almost erect and have a ventral flexure. The locomotion becomes rapid and more continuous, though a tendency to discontinuity persists. The negative reaction to jarring, etc., becomes more intense. Merely lifting the dish in which they are placed sets them off into rapid flight, a feature unnoticed in the larvæ. The positive light reaction also becomes well marked. They will move to the lighted end of the trough often without pause. If the pupa is stimulated at the posterior end it commonly makes a single movement. If stimulated elsewhere it usually makes a number of movements in quick succession, indicating a tendency to develop continuity of movement. If highly excited, as when the dish in which it is placed is lifted, its movements become really continuous. They have thus lost the two characteristic larval features of asymmetry and discontinuity. In these changes of behavior the pupæ approach more nearly to the ordinary type of behavior, showing the effects of the loss of transparency, which necessitates the development of pupal organs, such as the caudal plates and the floats, which are of use for only the few days of the short pupal period, but which greatly favor its security. Towards the close of the pupal period, it rises to the surface and when stimulated darts downward.

## THE APPLICATION OF THE TRIAL AND ERROR THEORY TO OTHER ANIMALS

As the trial and error hypothesis has received attention elsewhere in this paper, it may be well to indicate its application in other cases as understood by the writer, to avoid ambiguity. It is here used in the sense given by HOLMES ('06), implying varied movements under stimulation with accidental orientation. If used loosely as seems to be often the case, implying only failure to move in a direct line toward or away from a source of stimulus, it could very well be applied to Corethra in the case of some reactions (though the food reaction at least is very precise) inasmuch as its spasmodic and unsymmetrical movements do not carry it in a straight path.

In Paramœcium the application of the trial and error interpretation to its behavior under stimulation hinges on the question whether its avoiding reaction of backing and then turning always to the aboral side when stimulated is to be interpreted as a movement directed with reference to the stimulus or as simply a change of movement in a structurally determined direction, the aboral, evoked by the stimulus. As a matter of fact, the movement is determined functionally as much as structurally, since, as JENNINGS shows, Paramœcium is asymmetrical in the distribution of sensory areas. The oral groove is the sensory region *par excellence*, and so aboral turning may be regarded as a directed movement, in accord with the views of YERKES ('06).

JENNINGS' view is borne out by the fact that Paramœcium does show an apparent disregard to the direction of the stimulus, always turning aborally no matter whether stimulated locally in any region or all over the body and uniformly. It does not follow that when a stimulus is applied uniformly all over the body, it affects all parts alike, for there are marked differences in sensitiveness. The oral groove is the most sensitive region and receives stimuli of many kinds first, through currents drawn from in front, as JENNINGS shows. Or at any rate it may be most affected by stimuli applied anywhere and reaching it by conduction. MAST has discussed this point of view with respect to several forms of Protozoa ('06). In view of this, aboral turning would not be interpreted as a mere change of movement, but as a movement directed away from the stimulus. This would bring Paramœcium into line with other animals in respect to the nature of its avoiding reaction, and to the ordinary laws of attraction and repulsion exhibited by protoplasm toward the environment.

In respect to the application of the trial and error method of orientation to the earthworm by HOLMES, the views of the writer were expressed in a previous paper ('05).

The matter hinges on the behavior of the earthworm under relatively weak light, when it is not an exclusive factor in dominating behavior, since the directive influence of strong light is manifest. In the case of weak stimulation, in order to get a basis for trial and error it is necessary to assume that all the random movements the animal makes are due to light, so that the movements which lead to orientation may also be termed accidental as to direction. As a matter of fact, there is evidence that in weak light only those movements made by the worm while in the most extended state, when reaching out with its sensitive anterior end, are influenced by light. In this state of extension the light cells in the basal layer of the integument are most exposed and nearest the surface. In this condition it may react to light by backing or turning. After bringing up its body by the contraction of its longitudinal muscles, it initiates movements while in the less sensitive contracted state. These are of course less apt to be directed by the light, depending on its intensity.

## ADAPTIVENESS OF MOVEMENTS

The adaptiveness of the various features of the behavior of these animals appears as the culmination of a long regulative evolutionary process and we may ask, do the activities of this quite highly differentiated animal appear self-regulative or externally controlled when viewed as a whole? All the features of the behavior seem closely correlated. The transparency of the body makes possible the lying-in-wait habit in open water, with discontinuous movements. The lashing of the body gives a more powerful movement in view of the fact that it must start from rest each time, and is correlated with the absence of locomotor appendages. Further, the asymmetrical character of the movements compensates for lack of continuous range, by widening the range of vision, through causing the animal to move in a circle. The exposed habitat necessitates the high development of warning organs, whose stimulation leads to the intensified negative response, essential to safety. The highly developed eucone eyes, rarely found in larvæ, are highly adaptive to the open water habitat.

With the set of adaptions already mentioned, further adaptation to environment in changing physiological states may be secured by movements in a vertical path, and these movements are regulated under the combined influence of light and gravity.

The mode of orientation in the negative reaction and in the positive light response were shown to be unconformable to the conventional tropism schema, but adapted to the peculiar action system of this animal.

The great majority of the movements appear as spontaneous, overflow movements adapted to the needs of the animal by their special character, to bring it into contact with as wide an environment as possible. Such movements may be called trial movements. Finally in comparing the two kinds, the externally directed and the spontaneous, it was seen that each is purposive in its nature, but in a different way. The internally incited are varied so as to bring the animal into wider contact with the environment. The externally directed are not varied in direction, but precisely oriented and indicate the animal's capacity to regulate its movements beneficially by orienting itself immediately with reference to the direction of an external localized stimulus. The trial and error principle does not inhere in the externally directed movements. The basis of the trial and error theory of orientation lies in the assumptions contained in the phrase "varied movements under stimulation."

In the undifferentiated movements of the Protozoa there may be a blending of internal and external factors in the same movement, which can only be interpreted by analysis into its components. Results derived from the Protozoa should therefore be checked by comparison with animals showing a more differentiated type of behavior in which the various reactions, taking food, avoiding injury, spontaneous movements, etc., take place separately and may be recognized as such.

It will then be seen that the directive influence of external stimuli and the trial and error principle in behavior are not mutually exclusive, but complementary. But to make the trial and error principle include all behavior is as false as the tendency to regard reactions to external stimuli as the foundation of all behavior.

An amœba is first hungry and moves, before it can react to food, and so the more highly organized animal may exhibit its characteristic behavior under external conditions which are uniform and supply no stimulus to change of behavior, its energy overflowing in modes determined by the structure and changes in internal conditions.

## SUMMARY AND CONCLUSIONS.

1. Movements should be classified according to form. Classification according to direction into positive and negative, when the form differs, is inadequate. For example, in Corethra the positive reactions toward gravity, light and food differ in their form.

2. The movements of the larvæ are discontinuous, each consisting of a single lashing of the body and followed by an interval of rest. For this reason the separate movements may be more easily distinguished with reference to their exciting cause. A single stimulus is followed by a single movement ordinarily. By far the greater number of movements are pure overflows of energy, adaptive in nature, since their asymmetrical character causes the larva in a succession of such movements to face in all directions.

3. Those movements which appear to be externally directed, are characterized by precision and direct orientation with reference to the exciting stimulus. They conform in respect to the mode of orientation to the peculiar adaptive action system of the larva and are unconformable to the conventional mode of orientation laid down in the tropism schema.

4. The trial and error method is not exhibited in the orientations to external stimuli.

5. The horizontal range of these larvæ is restricted, as their ordinary movements involve little translation and some rotation. They may move in a zigzag path, which is tolerably straight, under stimulation.

6. The vertical range involves daily depth migrations under the combined influence of light and gravity.

7. The larvæ are positively geotropic and move downward when the water is illuminated whether from above or beneath. They move downward in the daytime on account of their positive geotropism in strong illumination. They move upward in weak light.

8. The larvæ are positively phototropic, when attuned to out-of-door intensity, in the sense that they move horizontally toward light, but not upward. The pupæ move in any direction toward light of greater intensity. Freshly collected larvæ gather in the lower lighted corner of an aquarium with side illumination. The positive reaction changes to negative after a time.

9. The larvæ are armed with segmental sensory bristles and also several pairs of chordotonal organs, and their orientations due to mechanical stimuli and vibrations are their most marked forms of response. The negative response may be accentuated by repetition and intensification of the stimulus, and lead to continuous movements of short duration, in a tolerably straight but zigzag path.

10. The movements are powerful, since they may involve one half of the musculature at each stroke. This compensates for lack of momentum due to discontinuity of movements. Fatigue is soon shown on continued mechanical stimulation. Acclimatization, distinct from fatigue, is shown.

11. The function of the air sacs is static, enabling the maintenance of position at various levels in accordance with the physiological state. They have a dynamic function in automatic righting movements and in producing buoyancy at times. Their respiratory function is undoubtedly of great importance in connection with their depth migrations.

12. The behavior of the pupæ becomes more conformed to an ordinary type, with loss of transparency and acquisition of special pupal organs. Movements are symmetrical and more continuous. Reactions are more pronounced.

Evanston, Ill.,
June 19, 1907.

## LITERATURE CITED.

Davenport, C. B.
'97. Experimental Morphology, vol. 1, pp. 209–210.
Graber, V.
'82. Die Chodrotonalen Sinnesorgane und das Gehör der Insekten. *Arch. f. Mikr. Anat.*, Bd. 21, pp. 65–145.
Harper, E. H.
'05. Reactions to Light and Mechanical Stimuli in the Earthworm Perichæta bermudensis, Beddard. *Biol. Bull.*, vol. 10, pp. 17–34.
Holmes, S. J.
'01. Phototaxis in the Amphipoda. *Am. J. Phys.*, Vol. 5. pp. 211–234.
'05. The Selection of Random Movements as a Factor in Phototaxis. *Journ. Comp. Neurol. and Psychol.*, vol. 15, pp. 98–112.
Jennings, H. S.
'06. Behavior of the Lower Organisms.
Lankester, E. R.
'64. On the Microscopic Anatomy of an Insect Larva, Corethra plumicornis. *Popul. Sc. Rev.*, vol. 4, pp. 605–611
Leydig, F.
'52. Anatomisches und Histologisches über die Larve von Corethra plumicornis. *Zeit. für Wiss. Zool.*, Bd. 3, pp. 435–451
Mast, S. O.
'06. Light Reactions in Lower Organisms. I. Stentor cœruleus. *Journ. Exper. Zoöl.*, vol. 3, pp. 359–399.
Miall, L. C.
'95. The Natural History of Aquatic Insects.
Needham.
'03. Aquatic Insects in New York State. *N. Y. State Mus. Bull.*, no. 68.
Parker, G. H.
'01. The Reactions of Copepods to various Stimuli and the Bearing of this on Daily Depth Migrations. *Bull. U. S. Fish Comm.*, pp. 103–123.
Yerkes, Robert M.
'06. Concerning the Behavior of Gonionemus. *Journ. Comp. Neurol. and Psychol.*, vol. 16, pp. 457–463.

# LITERARY NOTICES.

**Morris and McMurrich.** Human Anatomy; a complete systematic treatise by English and American Authors. Fourth Edition. Part III, The Nervous System, Organs of Special Sense. *Philadelphia, P. Blakiston's Son & Co.* 1907. $1.50.

In this fourth American edition of MORRIS's *Anatomy* the section on the Nervous System is revised by IRVING HARDESTY, that on the Eye by R. MARCUS GUNN, and the Ear, Tongue and Nose by ABRAM T. KERR. As a text-book it is to be warmly commended as giving an unusually large amount of descriptive detail, well coördinated and clearly written. The illustrations, most of which bear the descriptive legend in full on the figure, are good and judiciously chosen. The BNA nomenclature is used throughout, with however vernacular or older Latin terms added when necessary to avoid confusion. The mechanical excellence of the book is praiseworthy, and particularly the fact that it is printed on thin paper, thus avoiding the clumsy bulk which American text-book publishers usually inflict upon their patrons. The moderate price is also to be commended.

C. J. H.

**Baldwin, James Mark.** Mental Development in the Child and in the Races: Methods and Processes. *New York, The Macmillan Company.* Third Edition, revised, with seventeen figures and ten tables. Pp. xviii + 477. 1906. $2.25 net.

The fact that this book has been reprinted seven times is indicative of the interest which it has aroused and of its value. In its present form it is not essentially different from the previous editions, for, as the author remarks, "the revision has been mainly in matters of details of fact, and of exactness of exposition." Teachers of Comparative and Genetic Psychology will be grateful to Professor BALDWIN and to his publishers for again making available a text-book, which, despite its obscurities of style, is of great value to students.

## BOOKS AND PAMPHLETS RECEIVED.

**Paton, Stewart.** The reactions of the vertebrate embryo to stimulation and the associated changes in the nervous system. Reprinted from *Mitth. a. d. Zool. Station zu Neapel*, Bd. 18, Heft 2/3. 1907.

**Edinger, L.** A preliminary note on the comparative anatomy of the cerebellum. *Brain*, Part 116, pp. 483–486. 1906.

**Edinger, L.** Ein neuer Apparat zum Zeichnen und Projizieren. Reprinted from *Zeits. f. wissen. Mikros.*, Bd. 34, pp. 26–34. 1907.

**Edinger, L.** Bericht über das Dr. Senckenbergische Neurologische Institut, 1885–1906. With bibliography of contributions from the Institut.

**Levi, Ettore.** Contributo anatomo-comparativo alla conoscenza dei tratti tetto-bulbari. Reprinted from *Rivista di Patologia nervosa e mentale*, vol. 12, fasc. 3. 1907.

**Levi, Giuseppe.** Di alcuni problemi riguardanti la struttura del sistema nervoso. Reprinted from *Archivio di Fisiologia*, vol. 4, fasc. 4, pp. 367–396. 1907.

**Levi, Giuseppe.** Intorno alla cosidetta rigenerazione collaterale dei neuroni radicolari posteriori. Reprinted from *Monitore zool. Ital.*, vol. 18, no. 4, pp. 89–96. 1907.

**Froriep, A.** Ueber den Ursprung des Wirbeltierauges. Reprinted from *Münchener med. Wochen.*, no. 35. 1906.

**Froriep, A.** Ueber die Herleitung des Wirbeltierauges vom Auge der Ascidienlarve. Reprinted from *Verhandl. Anat. Gesell.*, 1906, pp. 145–151.

**Kappers, C. U. Ariëns.** Zur vergleichenden Anatomie des Vorderhirnes der Vertebraten. Reprinted from *Anat. Anz.*, Bd. 30, no. 19–20, pp. 496–509. 1907.

**Hawkes, Mrs. O. A. Merritt.** The cranial and spinal nerves of Chlamydoselachus anguineus (Gar.). Reprinted from *Proc. Zool. Soc., London*, 1906, pp. 959–991. 1907.

**Reese, Albert M.** The breeding habits of the Florida Alligator. Reprinted from *Smithsonian Misc. Collections*, vol. 48, Part 4, pp. 381–387. 1907.

**Bianchi, L.** Contributo alla dottrina delle afasie. Reprinted from *Annali di Nevrologia*, Anno 24, fasc. 5, 1906.

**Bianchi, L.** Sulle afasie. Reprinted from *Il Tommasi*, Anno 2, no. 11. 1907.

**Oppenheim, H. and Cassirer, R.** Die Encephalitis. Zweite, umgearbeitete Auflage. *Wien, Alfred Hölder.* 134 pp., 2 pl. 1907.

**Judd, C. H.** Psychology, General Introduction, vol. 1. *New York, Charles Scribner's Sons.* 1907.

**Judd, C. H.** Yale Psychological Studies. New Series, vol. 1, no. 2. 1907.

The Journal of
Comparative Neurology and Psychology

Volume XVII NOVEMBER, 1907 Number 6

# THE NERVES AND NERVE-ENDINGS IN THE MEMBRANA TYMPANI.

BY

J. GORDON WILSON, M.A., M.B. (Edin.)

*(Hull Laboratory of Anatomy, University of Chicago.)*

With Plate V.

In studying the membrana tympani we are struck by the unsatisfactory state of our knowledge in regard to the nerve supply and the nerve terminations in that structure. Jacques, writing in 1900, stated that our knowledge was still as it had been left by Kessel in 1870, accurate in most points so far as it went, but incomplete and unsatisfactory because of the technical methods then employed. This state of affairs he ascribes to the difficulty of the technique inherent in its structure and an inexplicable indifference to the organ in question. Jacques' paper was followed by an account by U. Calamida ('01). In both of these communications additions were made to our knowledge, but much was left indefinite and undecided. It may be, as acknowledged by Jacques, that it had been difficult to fix the exact position of the impregnated tissues. In neither case were drawings illustrating the conclusions published. The only paper with illustrations is that of Deinike ('05); but here only the horse and the ox have been studied.

My object in this investigation was to locate more exactly the course of the nerves, to show the mode of ending and to ascertain, if possible, the distribution in the membrane of the nerve trunks which pass to it.

The literature on this subject is by no means voluminous and is chiefly contained in the works of Kessel, Jacques, U. Calamida and Deinike. Kessel ('70) pointed out, (1) That the principal nerve enters at the upper and posterior segment lying between the cutis and membrana propria and accompanying the artery. It divides into two branches, one of which goes to the anterior segment, the other to the posterior and inferior segment. In addition, numerous small branches enter with blood vessels at different points of the periphery. The larger ramifications of these nerves, which lie between the cutis and the membrana propria, he calls the ground plexus. (2) From the ground plexus nonmedullated nerves pass to form a plexus along the blood vessels. These may end in the vessel wall or pass to help form the subepithelial plexus. In addition, from the ground plexus large fibers pass off in whose course he notes ganglion cells from which fibers pass both to the blood vessels and to the subepithelial plexus. From the subepithelial plexus fibers may be seen to pass between the epithelial cells; how they end was not known. (3) The mucous membrane lining of the membrana is well supplied with nerves; its subepithelial plexus receives its nerve supply both from the ground plexus and from the tympanic plexus.

JACQUES ('00), using intravitam methylene blue, agrees in the main with KESSEL, but states that, (1) The submucous plexus appears less developed than the cutaneous. (2) The plexus is most dense in the posterior superior quadrant. (3) The fibers of the plexus are nonmyelinated like those of the cornea. (4) Ganglion cells do not exist. The terminations he finds are complicated arborizations of the general type of peripheral sensory endings; certain fibers probably penetrate into the epidermis. He states that his researches must be regarded as incomplete, inasmuch as he has not been able to fix the exact position of the impregnated tissue.

U. CALAMIDA ('01 ) used the rapid GOLGI, the chloride of gold and the methylene blue (intravitam) methods. He agrees with JACQUES and distinguishes, (1) A subcutaneous plexus, lying between the cutis and the membrana propria, derived from the n. auriculo-temporalis and from the n. vagus, which consists of two parts: (*a*) a vascular plexus; (*b*) a subepithelial plexus. (2) A submucous plexus, lying between the mucous membrane and the membrana propria, supplied from the tympanic plexus as well as from the n. auriculo-temporalis and the n. vagus. It also consists of two parts: (*a*) a lymphatic plexus; (*b*) a subepithelial plexus. These two plexuses are connected both by the vascular plexuses and by independent fibers which pass from one to the other.

DEINIKE ('05) in his paper on the nerves of the membrana tympani of the horse and ox also refers to the difficulty of the technique "So viel ich mich auch bemühte, eine tadellose Färbung des nerven an Trommelfellen von Tieren mittlerer Grösse wie Hund, Katze u. a. zu erzielen, stets bleiben meine Versuche resultatlos" (p. 117). He describes the nerves as coming from the n. auriculo-temporalis and from the n. tympanicus. His account agrees in the main with that of JACQUES and CALAMIDA, but in addition he figures endings between the radiating and circular tissue and at the limbus; the former are plate-like bodies which probably act "Zur Bestimmung des Spannungsgrades des Trommelfells;" the latter correspond to endings in tendons elsewhere.

I have examined the membrana tympani of the dog, cat, rabbit, and monkey (Macacus rhesus), as well as several obtained from man. In the main they agree; points of variation will be pointed out later. The results, so far as man is concerned, are not complete and will be published later.

Those who have worked on the nerves of the membrana tympani will agree with JACQUES and DEINIKE that there are few parts of the body where one has so many difficulties to overcome and so many disappointments to encounter. Osmic acid is virtually useless, partly because so many of the nerves are nonmedullated and partly because of the abundance of fat-containing bodies lying on the cuticular part, which stain with osmic acid. Chloride of gold and GOLGI have in my hands proved very unsatisfactory. In my opinion the intravitam methylene blue method gives the best results, especially if the injection be made into an artery and fixed in ammonium molybdate. The method of DOGIEL is less satisfactory. In the human tissue where the ear cannot be procured immediately on death I have obtained results six or eight hours postmortem, by the following method: I immerse the drum in a mixture of methylene blue and weak osmic acid solution for two to four hours; it is then directly transferred to the ammonium molybdate solution. By this method the myelinated nerves are seen as dark brown fibers with a blue axis cylinder, and the nonmyelinated nerves blue; the rest of the membrane is light brown. While this method is not always successful it at times gives surprising results.

Under the term membrana tympani I include the pars flaccida (SHRAPNELL'S membrane) and the pars tensa. The nerve supply to the membrana tympani is for convenience grouped as follows:

I. Those entering at the region of the pars flaccida over the plicæ anterior and posterior.

II. Those entering at the insertion of the membrane (limbus membranæ tympani) into the sulcus tympanicus.

At both places the nerves, with a few exceptions to be noted later, enter from the external auditory meatus under that part of the cutis which is prolonged over the membrane. The relative number of fibers entering these parts appears to vary with the species of animal examined. Thus, in the dog (Figs. 1, 2 and 3) and the cat (Fig. 4), those entering at the periphery are very abundant and exceed in number those entering at the pars flaccida. In the monkey (Macacus rhesus, Figs. 5 and 6) there are fewer and smaller peripheral bundles, influenced, I believe, by the marked development externally of the tympanic bone which is prolonged at an acute angle to a higher level than the membrana tympani and forms a long osseous semicylindrical external auditory meatus of relatively small diameter. In man the distribution corresponds in many respects to that in the Macacus though more fibers enter at the limbus.

The bundles entering at the pars flaccida contain many medullated fibers and have a general direction downward toward the manubrium. Those entering at the limbus contain fewer medullated nerves and radiate inward toward the manubrium, the larger nerves following generally the direction of the radiating fibers of the pars tensa. As the nerve distribution varies in the pars tensa from the pars flaccida, it seems better to describe them separately.

*I. Pars flaccida.* The nerves pass down under the cuticular layer, not as one strand, but in detached bundles which freely communicate with each other (Figs. 3 and 6). Their course is directed toward the manubrium. The bundles pass over the plicæ anterior and posterior at varying points on to the upper part of the membrana tensa. Numerous branches are given off from these bundles which form a wide-meshed nonmedullated plexus (ground, or fundamental plexus of the pars flaccida). From this plexus numerous branches separate off which can be traced for a varying length as follows: (*a*) To the membrana tensa, where they enter the plexuses to be described later (Figs. 3 and 6). (*b*) Into the same or another bundle where they may pass upward or downward and soon become impossible to follow accurately (Figs. 3 and 5). (*c*) To form a subepithelial plexus. (*d*) To end in the subcutaneous tissue and in the epithelium. In addition we find nerves which form plexuses around the blood vessels.

The subepithelial plexus, composed of nonmedullated nerves, is very intricate and into it run not only nerves from the ground plexus but also nerves issuing directly from the nerve bundles. In it the entering nerves may divide into fine fibrils. Some of the fibers can be traced into the epithelium; others, after a long course, leave the subepithelial plexus and enter again into the ground plexus. Those penetrating the epithelium may do so singly or in groups, running between the cells interlacing with each other and ending in the upper layers in fine or bulb-like points.

In addition to the cuticular endings there are present many noncapsulated tree endings (Fig. 7). There are given off from the ground plexus nerve fibers of considerable diameter, which break up into an arborization differing in no respect from tree endings elsewhere, except that they are relatively smaller. They sometimes interlace intricately with each other. In their course they may give off nonmedullated branches which also end in arborizations, and in this way one nerve fiber may distribute its arborizations over a wide area. These arborizations are usually subcuticular.

Speaking generally, it may be said that the pars flaccida presents the picture of a membrane very rich in nerves not only because of the numerous branches passing down through it, but also because of its plexuses and abundant endings.

*II. The nerves of the pars tensa* enter chiefly from the external auditory meatus either over the pars flaccida or at the limbus. A few fibers pass in directly from the tympanic cavity.

(1) Those coming from the pars flaccida are directed toward the manubrium and reach it, not as one, but as several nerve bundles. These cross the plicæ anterior and posterior at various angles and at varying points, toward the manubrium which they reach along its upper third. The place at which the larger bundles cross varies in different animals—thus, in the dog and cat they cross over the capitulum or the anterior plica (Figs. 1 and 4); in

the monkey (Fig. 5) and man, over the posterior plica. The main trunks when they reach the manubrium may continue down one side or may divide and send a branch down each side, connected by a plexus of fibers across the external surface of the manubrium. From the large nerve bundles, branches pass off as follows: (*a*) Over the external and internal surface of the manubrium forming an external and internal manubrium plexus (Figs. 1, 5 and 4). (*b*) At intervals branches pass off which radiate toward the periphery (limbus tympanicus). Each of these with little or no medullary sheath, is of considerable size near the manubrium, but as at repeated intervals along its course it gives off branches, it finally arrives at the limbus as a very fine fiber. The branches which these radiating nerves give off are mostly nonmedullated; they frequently divide and interlace with each other to form in the membrana propria wide-meshed plexuses, the ground or fundamental plexus. This plexus lies among the circular and radiating connective tissue bundles and connects with the subepithelial and submucous plexuses.

(2) The nerves from the external auditory meatus at the limbus enter all around the periphery (Figs. 4 and 5). As they approach the limbus they divide and form a dense plexus with branches from the corresponding adjacent nerves. This annular or zonular plexus lies both external and internal to the limbus (Fig. 2). From this plexus or from the main trunks fibers pass (*a*) chiefly into the membrana tensa and (*b*) a few into the tympanic cavity (Fig. 4).

(*a*) Those passing to the membrana tensa are directed toward the manubrium lying among the radiating connective tissue bundles. At the periphery the nerves are of considerable size, but as they pass forward branches are given off which enter into the adjoining ground plexus so that when ultimately they reach the manubrium they appear as very fine fibers which pass into the plexuses on or around the manubrium (Fig. 1).

(*b*) Those passing into the tympanic cavity can be traced into the plexus in its mucous membrane.

The ground plexus is a wide-meshed interlacing of nerves lying in the fibrous tissue and corresponds to the ground plexus of the pars flaccida. The nerves which compose it come almost entirely from the external auditory meatus, those coming from the middle ear being few in number. It ought to be regarded as the chief distributing center for the epithelial plexuses and for the various varieties of endings.

From the ground plexus in the membrana tensa fibers pass off to form very intricate and dense subepithelial plexuses directly under the cuticular and mucous epithelium, but chiefly the former. From the subcuticular plexus fibers pass into the epidermis (Fig. 11). Some of these fibers may travel for a considerable distance among the deeper epithelial cells before they end, interlacing and surrounding them so that they may be said to form an interepithelial plexus. They end near the surface as fine interepithelial points or bulb-like bodies probably from a distension of their contents by the dye. No other endings are to be seen in the epithelium but these fine or bulb-like structures.

In the fibrous tissue the plexuses are abundant and intricate, and the fibers may show frequent divisions and interlacings. The following varieties of endings can be distinguished:

(*a*) The nerve fiber breaks up repeatedly into a number of fine fibrils which interlace and end as fine points or bulbs close to connective tissue cells (Fig. 9).

(*b*) A fiber divides into two branches each of which, after making several corkscrew turns, again divides; the resulting branchings surround a cell which stains like a connective tissue cell (Fig. 10a); or a fiber may divide into several fibrils which, after taking several corkscrew turns, form a long narrow plexiform ending between the connective tissue cells (Fig. 10b).

(*c*) A nerve breaks up into branches each of which ends in arborizations. These are especially abundant near the malleus and at the limbus (Figs. 7 and 8).

The nerves which enter from the tympanic cavity are relatively few in number and end in an epithelial plexus under the mucous membrane. This submucous plexus also receives branches from the ground plexus. As mentioned by JACQUES and CALAMIDA, no ganglion cells are present.

One cannot but note how analogous the distribution of the nerves in the membrana tympani is to that of the cornea. Here also we find a zonular plexus (plexus annulaire); a ground plexus (plexus fundamental) occupying the whole stretch of the cornea near the surface; and a plexus subepithelial and interepithelial with bud or point-like endings.[1] One is tempted to carry the

---

[1] POIRIER et CHARPY, vol. 5, p. 1040.

analogy further and to say that as in the cornea pain and not touch appears to be the sensation evoked,[2] so also in the membrana tympani one might expect that the slightest pressure would evoke unpleasant sensations—passing into pain—a fact well borne out by clinical observations.

The anatomical study of the endings in the fibrous tissue inclines one to support the opinion of DEINIKE that their probable function is to estimate variations in tension which the membrane undergoes. Their position and character seem well adapted to that end. The significance of these being determined, the function of the third variety of ending—the tree arborizations—would appear to offer here a suitable field for psychological investigation.

The nerve supply in the membrana tympani is usually given as coming from the n. auriculo-temporalis and the n. vagus. It was determined to ascertain the relative amount of distribution of each. The n. auriculo-temporalis in two dogs and two monkeys was sectioned. In one dog the nerve was cut as it emerges from under the mandible; in the other dog and in both monkeys the nerve was cut and removed along with a part of the n. mandibularis and the ganglion oticum at the base of the skull. After the operation each animal was kept alive for eight or ten days and then killed.

As the results from staining the membrana tympani with osmic acid and with MÜLLER's fluid and osmic acid had been unsatisfactory, it was determined to stain by the intravitam methylene blue method and then compare the results over a series of cases. As is well known, the ability of the nerve to react to this method disappears soon after section. As a preliminary it was ascertained that 48 hours after section in the dog, cat and rabbit definite changes were so apparent in the degenerated nerve when compared with the corresponding normal nerve as to leave no doubt that these were changes primarily in the nerve.

In every case both membranes were stained with methylene blue injected simultaneously into both carotids under the same pressure; then the tissue was fixed in molybdate in the usual way. At the same time the external cuticular layer and periosteum over the osseous part of the external auditory meatus of both ears was

---

[2] SHERRINGTON in SCHÄFER's *Physiology*, vol. 2, p. 987.

fixed in osmic acid. As the results were practically the same in all, those in the monkey only will be given.

A monkey (Macacus rhesus) had the left n. auriculo-temporalis cut as stated above; it was kept alive for eight days and then killed. On the right side numerous well-stained nerve bundles were seen passing from the pars flaccida over the plicæ, and from the limbus on to the membrana tensa, as in Fig. 5. On the left side no large bundles were seen, but a few fibers well stained and normal passed over the pars flaccida and distributed themselves irregularly over the membrana tensa, dividing in the fibrous tissue where they appeared to end. Under the high power it was possible to make out pale strands corresponding to the position of the nerve bundles of the right ear. In the cuticular layer from the osseous part of the external auditory meatus on the right side the medullary sheaths were normal; on the left side most, but not all, of the nerves showed the preliminary stages of nerve degeneration. It was also ascertained that in the monkey certain fibers came to the membrane along the posterior auricular branch of the n. facialis, which branch comes off after the n. facialis receives a branch from the ganglion jugulare n. vagi just above the stylo-mastoid foramen. So constant were these results that I feel justified in stating that the principal nerve supply to the membrana tympani is the n. auriculo-temporalis. Further, in the monkey at any rate, the nondegenerated fibers, which were few in number, had come from the n. auricularis posterior but were probably derived from the vagus as in man.

## LITERATURE CITED.

CALAMIDA, U.
Terminazioni nervose nella membrana timpanica. *Arch. Ital. di Otologia,* vol. 11, p. 326-329. 1901.

DEINIKE, D.
Ueber die Nerven des Trommelfells. *Arch. f. mikr. Anat.,* Bd. 66, S. 116-120. 1905.

JACQUES, P.
De la fine innervation de la membrane du tympan. XIII Cong. internat. du medicin. Sect. d'Otologie, p. 46, *Paris.* 1904.

KESSEL, J.
Das äussere Ohr. Handbuch der Lehre von den Geweben herausgeben von S. STRICKER, Bd. 2, S. 853, *Leipzig.* 1872.

## EXPLANATION OF PLATE V.

| | | | |
|---|---|---|---|
| *c.* | capitulum mallei. | *p:a.* | processus anterior. |
| *m.* | manubrium mallei. | *l.* | limbus membranæ tympani. |
| *p.m.* | prominentia malleolaris. | *e.a.m.* | meatus acusticus externus. |

FIG. 1. External surface of right membrana tympani of dog; nerves with their branches only partly shown. *n* and *n'*, two nerve trunks entering from external auditory meatus over pars flaccida; (*a*), branch from manubrium plexus to periphery; (*b*), branch from limbus towards manubrium. ZEISS comp. oc. 4; obj. 16 mm.

FIG. 2. Nerves (*n*) entering at inferior posterior quadrant of right membrana tympani of dog, from external auditory meatus. *mm*, position of limbus; *z*, zonular plexus. ZEISS comp. oc. 4; obj. 8 mm.

FIG. 3. Pars flaccida (*p.f.*) and pars tensa (*p. t.*) of dog, external surface, after malleus dissected off from within. *n*, nerves entering from external auditory meatus; *g.p.* ground plexus; *p*, plica membranæ tympani; *c*, branching cells in epidermis which readily stain with methylene blue. ZEISS comp. oc. 4; obj. 8 mm.

FIG. 4. Right membrana tympani of cat and adjacent part of middle ear, viewed from within. Through the transparent membrana tympani, nerves (*n*) are seen entering from external auditory meatus all around the periphery, breaking up at limbus (*l*) into zonular plexus with branches, of which only a few are shown (*n.c.*), to mucous membrane of middle ear and (*n.t.*) to membrana tympani. With this low power no branch can be distinguished passing from tympanic cavity to membrana tympani. ZEISS oc. 4; obj. $a_2$.

FIG. 5. External surface of membrana tympani of monkey (Macacus rhesus) after removal of surrounding parts, but still adherent to its bony attachments. The manubrium is seen through the membrane and the capitulum through the thin bone of external auditory meatus. Nerves (*n*) are seen entering over pars flaccida and posterior plica, and at limbus. *a*, principal artery to membrana tympani; *pp.*, plica posterior. ZEISS oc.; obj. $a_2$.

FIG. 6. Part of left membrana tympani of monkey (Macacus rhesus), showing nerves entering at upper segment and forming ground plexus (*g.p.*); *a—a'* indicate line of principal artery which divides at *a'* to send branches to each side of manubrium. ZEISS oc. 4; obj. 8 mm.

FIG. 7. Pars flaccida of dog immediately above plica posterior. Two nerves (*n* and *n'*) faintly medullated at first which end in interlacing arborizations in fibrous tissue under cuticular epidermis. ZEISS oc. 4; obj. 2 mm.

FIG. 8. The form of branched-ending seen most commonly under cuticular layer of pars tensa in the monkey. The nerves are nonmedullated. ZEISS. oc. 4; obj. 2 mm.

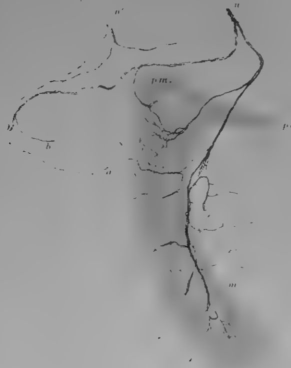
FIG. 9. Nerve (*n*) dividing and forming plexus in connective tissue of pars tensa of dog. ZEISS oc. 4; obj. 8 mm.

FIG. 10a and b. Two varieties of nerve endings in fibrous tissue of pars tensa of dog: (a) Nerve (*n*) divides into two branches each of which, after making several corkscrew turns, again divides to surround a cell which appears in every respect similar to the neighboring connective tissue cells. (b) Nerve (*n*) gives off branches which coil round each other or the parent stem forming a long narrow ending. ZEISS comp. oc. 4; obj. 2 mm.

FIG. 11. Cuticular layer of pars tensa of monkey, superior posterior quadrant. (*a*) Subepithelial plexus with endings in epidermis; (*b*) Nerve branching and interlacing with subepithelial plexus. ZEISS oc. 4; obj. 2 mm.

PLATE 1

1



2

6

9

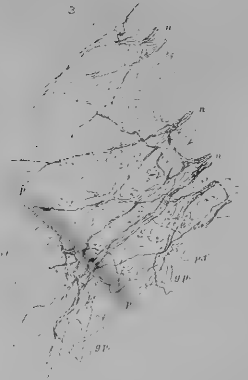
5

7

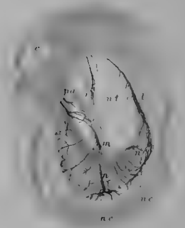
10 (a)

10 (b)

3



4



8

11

K. Hill del.

A. HOEN & CO., BALTIMORE.

# A STUDY OF THE DIAMETERS OF THE CELLS AND NUCLEI IN THE SECOND CERVICAL SPINAL GANGLION OF THE ADULT ALBINO RAT.

BY

SHINKISHI HATAI, Ph.D.

(*Associate in Neurology, The Wistar Institute.*)

From The Wistar Institute of Anatomy and Biology, Philadelphia.

WITH FOUR FIGURES.

## INTRODUCTION.

It is generally believed that the spinal ganglion contains several types of nerve cells which can be morphologically differentiated from one another. The varieties of cells whose existence in the ganglia have been repeatedly confirmed are: (1) cells with a T- or Y-shaped division of the processes. Such cells are considered to be most abundant and to be both large and small in size. (2) DOGIEL's cells of second type, multipolar cells, and (3) multipolar cells which resemble in shape and structure sympathetic ganglion cells. The most complete classification is based on the study of methylene blue preparations. In a general way the presence of the several varieties of cells in the ganglia may also be demonstrated in ordinary paraffine sections treated with any of the basic dyes followed by a counter-stain. In such preparations one can easily distinguish cells of different sizes as well as those exhibiting different arrangements of the stainable substance. These two characters, size and arrangement of stainable substance, have been used as a criterion by several investigators in order to classify these cells.

By this method LUGARO ('96) distinguishes in the dog five different varieties of the spinal ganglion cells, LENHOSSÉK ('96) in the human spinal ganglion distinguishes three varieties, COX ('98) in the spinal ganglion of the rabbit, two main varieties, and the author ('01) using the same criterion has distinguished three varieties in the spinal ganglion of the albino rat. It is my intention later to analyse in detail all these classifications and at the present moment it is merely necessary to call attention to the fact that in the spinal ganglion several varieties of cells have been distinguished from one another. Can all these cells of different varieties be considered as belonging to a single class or are there really several types of cells composing the spinal ganglion? In other words, a frequency of distribution of all these cells based on their sizes[1] should give us more than one mode if there were more than one type of cell involved. If but one mode appears we have good ground to conclude that all these cells, though differing in size as well as in structure, may be considered from the standpoint of size, as members of a homogeneous population. The differences in structure are for the moment neglected and must form the subject of a special study.

## MATERIAL AND TECHNIQUE.

For the present investigation the second cervical spinal ganglion of the adult albino rat was employed. The second cervical ganglion was purposely selected since through the investigation of Ranson ('06) we have already some numerical data in regard to this particular nerve.

The second nerve with ganglion was removed from right side of a healthy male having a body-weight of 194 grams and was fixed with osmic acid. Following the usual procedure the sections of the ganglion were cut 12 micra thick and mounted in series. Three sections from the middle of the entire series of 80 sections and three sections from midway between the middle and end on both sides, thus making altogether nine sections, were chosen. These nine sections were selected for the measurement of the cells and nuclei on the assumption that the cells of the different sizes were uniformly distributed and consequently that the nine sections would adequately represent the total cell "population" of the ganglion.

The measurements obtained from each cell and its nucleus were recorded on a separate card. In every case two maximum diameters at right angles to each other were determined for both cell-body and nucleus by means of the ocular micrometer. The

---

[1] Although this point could be tested also from the standpoint of the structure, nevertheless it is very difficult to obtain numerical data in terms of the structure, suitable for biometric treatment.

values of the two diameters thus obtained were multiplied together and the square root of the product was called "calculated diameter" of the cells and nuclei. Of course every section of a cell which possessed a distinct nucleus and nucleolus was measured from the nine sections and altogether 1108 such cells were found. The 1108 cells and nuclei thus measured were arranged according to the magnitude of the "calculated diameters" and the frequencies of the variates were determined as shown in the correlation table (see p. 490). For grouping the variates I have selected 2 micra as the unit for the cell-body and 0.65 of a micron for the nucleus. As will be seen later, small differences in the value of the unit do not produce any significant change in the final results, and therefore it is advisable to select some integral number for convenience in computation.

## ANALYTICAL CONSTANTS AND FREQUENCY DISTRIBUTION.

I shall first discuss the frequency distributions of the cell-bodies and nuclei. The fundamental analytical constants necessary for such discussion are given in the following table:

TABLE I.

| No. of measurement. | Cell-body. | Nucleus. | Skewness. | Cell-body. | Nucleus. |
|---|---|---|---|---|---|
| | 1108 | 1108 | | .4081± .024 | .1734± .024 |
| $\mu_3$ | 27.1627 | 9.5254 | Modal divergence | 1.3558± .006 | .4918± .002 |
| $\mu_4$ | 446.9891 | 233.3303 | Standard deviation | 6.6448± .952 | 1.8457± .026 |
| $\beta_1$ | .5486 | .1731 | Mean | 23.3356± 1.346 | 10.9523± .037 |
| $\beta_2$ | 3.6687± .099 | 3.5889± .099 | Mode | 21.9798 | 10.4605 |
| $\sqrt{\beta_1}$ | .7407± .052 | .4161± .028 | Coef. of variation | 28.4749±0.4398 | 16.8521±0.2482 |
| $\beta_2-3$ | .6687 | .5889 | Coef. of correlation | .8616± .006 | |
| $\kappa_1$ | −.3084 | .6585 | Lower and upper ends of ranges | 7.5844<br>60.9693 | |
| $\kappa_2$ | −1.5179 | .8248 | Type of curve | I | IV |

It has been shown by PEARSON ('05) that in order to fit a given distribution of frequency to a Gaussian probability curve the following conditions, within the limit of random sampling, must be fulfilled:

$$\sqrt{\beta_1}=0;\ \beta_2-3=0;\ \tfrac{1}{2}\,\frac{\sqrt{\beta_1}\,(\beta_2+3)}{5\,\beta_2-6\,\beta_1-9}=0;\ \text{and } d,\ \text{modal divergence}=0.$$

By examining the analytical constants given in Table I, it is seen that all those constants for both the cell-bodies and nuclei are considerably greater than zero even when their respective probable errors are considered. This at once leads to the conclusion that in both cases the frequency distribution can not be represented by the normal curve. Furthermore a considerable deviation of those constants from zero, *i. e.*, skewness, as well as modal divergence, indicates that they can never be represented by any other symmetrical curve since the deviation in excess and

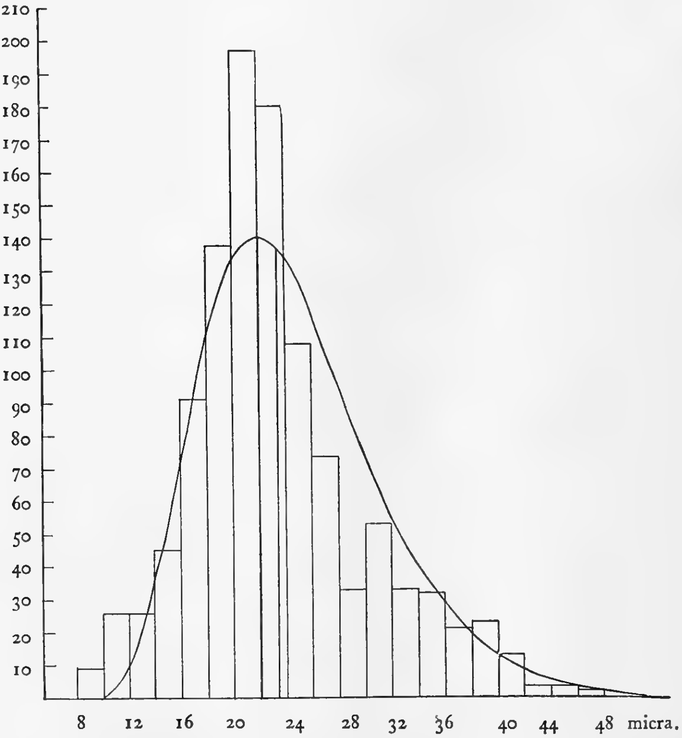


FIG. 1. Frequency polygon and fitted curve for variation in the diameters of the cell-bodies.

defect are not equally probable. It is therefore evident that n order to represent the data in hand we must find a curve which is able to represent the odds against any given deviation.

It has also been shown by PEARSON ('95, '01) that the assignment of a given distribution of frequency to any one of the six

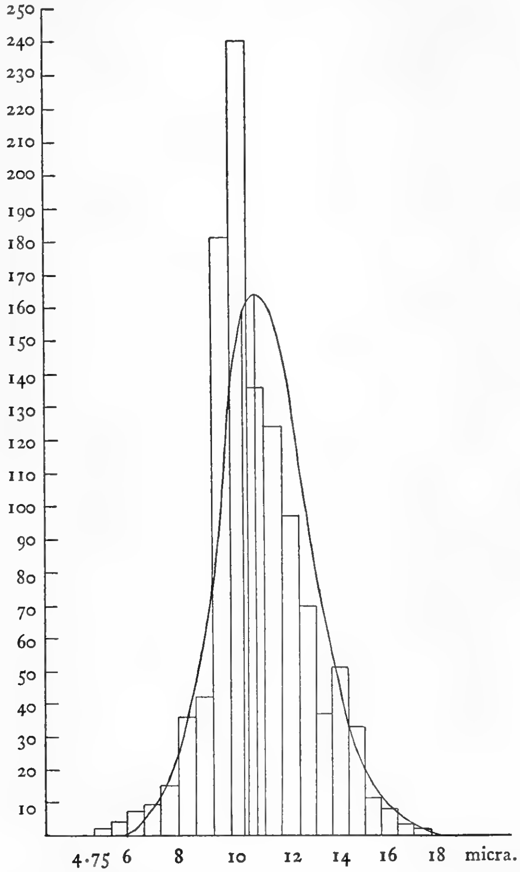


FIG. 2. Frequency polygon and fitted curve for variation in the diameters of the nuclei.

types of his skew curves depends on the value of the analytical constants $\kappa_1$; $\kappa_2$; $\beta_1$ and $\beta_2$. As is shown in Table I, in the case of the cell-body we have the following relations:

$$\kappa_1 < 0; \ \kappa_2 < 0 \text{ and } \beta_1 > 0$$

These three conditions satisfy PEARSON's skew frequency curve of Type 1, while for the nuclei we have

$$\kappa_1 > 0; \beta_1 > 0; \beta_2 > 3; \text{and } \kappa_2 > 0 \text{ and } < 1,$$

which calls for PEARSON's curve of Type 4.

The frequency distributions and their fitted curves are shown graphically in Figs. 1 and 2. The equations for the curves are:

For the cell-bodies (Type 1)[2]

$$y = 140.0657 \left(1 + \frac{x}{6.2286}\right)^{3.6107} \left(1 - \frac{x}{62.3049}\right)^{35.6365}$$

origin at mode.

For the nuclei (Type 4)

$$y = 13.0825 \left(Cos\,\theta\right)^{24.0118} \varepsilon^{11.20380}$$

origin at 7.4341 micra,

$$x = 11.6002 \quad tan\,\theta$$

Examining Figs. 1 and 2 we see at once that the theory and observation do not agree at all well. The theoretical curve in both cases considerably underestimates the observed ordinates for the smaller values of variates $x$, and overestimates the same for the larger values of $x$. The degree of deviation between the observed and theoretical curves is most pronounced at or in the neighborhood of the mode. This unexpected results forced the writer to reinvestigate the following points:

1. Since the spinal ganglion contains various sized cells it may be possible that these cells are not uniformly distributed from

---

[2] Original formula of Type 1 is given by

$$y = y_0 \left(1 + \frac{x}{a_1}\right)^{m_1} \left(1 - \frac{x}{a_2}\right)^{m_2}, \text{ where } y_0 = \frac{\alpha}{b} \cdot \frac{{m_1}^{m_1} {m_2}^{m_2}}{(m_1 + m_2)^{m_1 + m_2}} \cdot \frac{\Gamma(m_1 + m_2 + 2)}{\Gamma(m_1 + 1)\,\Gamma(m_2 + 1)}.$$

and for Type 4

$$y = y_0 (Cos\,\theta)^{2m} \varepsilon^{-\nu\theta}, \text{ where } y_0 = \frac{\alpha}{a} \cdot \frac{\varepsilon^{\frac{1}{2}\nu\pi}}{\int_0^{\pi} Sin^{r}\,\theta\, \varepsilon^{\nu\theta} .\, d\theta}.$$

section to section. In other words, some sections may contain relatively more cells having larger or smaller diameters, therefore the nine sections selected might not give a proper representation of the entire cell population and therefore the 1108 cells measured might not constitute a real random sampling of the entire population.

2. The disagreement between the theory and observation may be due to an improper selection of the unit for grouping the variates. If so, it may be improved by taking some other unit.

3. The two curves may agree more closely if the uncorrected or raw moments about the mean were used in determining various analytical constants.

4. The spinal ganglion cells may not represent a homogeneous population, but a mixture of various groups of elements. If so, dissection of the frequency curve into several components should give a better agreement.

The question contained in point 1 has been answered in the following way: the nine sections were divided into three series, each represented by three sections. For the series 1, one section was taken from the middle and one from the midway between the middle and the extremes on both sides, while for the series 2, the three sections which lie to the right of the three sections of the series 1 and for the series 3 those which lie toward left. The percentage values of these three series just mentioned were plotted separately, the same unit of course being used for each series. Comparison shows that these three curves agree with each other in every minor detail, and therefore with the original curve, too. This means that the cell-bodies of different sizes are uniformly distributed, otherwise the three curves should not agree so closely. Therefore the 1108 cells here measured can be regarded as giving a true representation of the entire cell-population. The disagreement found between the theoretical and observed curves is consequently not due to a lack of uniformity in distribution.

The question contained in point 2 was also answered by taking three different units for the cell-bodies; 1, 1.8, 2 micra; and one different unit for the nuclei, 1 micron, and comparing the new results with those already obtained. It was found that these variations in the units did not make any significant alteration in curve. This proves then the difficulty is not due to an improper choice of the unit.

As to point 3, I have treated the data for the cell-bodies, using the uncorrected moments, but without effecting any improvement on the results.

Finally I have tried to split the observed frequency curve (point 4) into two normal curves according to the method given by PEARSON ('94). After laborious calculations it was found that the present data can not be split. The reason for this conclusion is omitted since it needs an elaborate mathematical presentation. The result shows however that there is not the slightest indication of separate groups in the cell-population.

Therefore the cause of disagreement must depend on other conditions than those already enumerated.

After failing to obtain in this way a reasonable explanation for the considerable deviations between the observed and theoretical curves, it occurred to me that the explanation might be found in the method of sectioning and measurement. In order to make clear the relations existing within the ganglion let us suppose that 8000 spinal ganglion cells of various forms (from spherical to oblong) are thoroughly mixed in an ovoid receptacle. This is then cut into 80 slices of equal thickness. The entire series is sampled by taking three slices from the middle and three slices from the midway between the middle and extremes on both sides. Thus nine slices are selected for examination. The slices of the ganglion which we have examined in this way contained 1108 cells. Under these conditions the knife cuts the individual ganglion cell

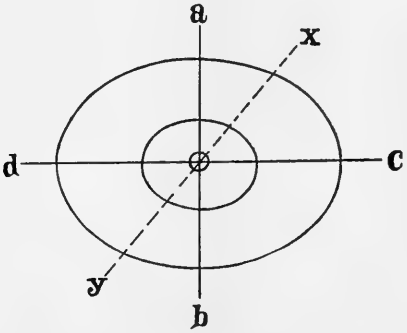


FIG. 3. Diagram of the spinal ganglion cell containing nucleus and nucleolus.

in various planes. In some cases the knife makes a right angle with the longest axis (*dc*, Fig. 3) of the cell-body and some cases with the shortest axis (*ab*). In the remaining cases the angles will always be less than 90°. It must be remembered that the 1108 cells counted are those which contain both nucleus and nucleolus, and therefore it is assumed that the knife always passed through the approximate center of the cell-body. The chance that the knife will make a right angle with shortest axis[3] must however be very small compared with a failure. Whichever plane we cut, as long as the knife passes through the center, the diameter (*ab*) is constant and therefore the product of the diameters varies directly with the changes in the longer. But (*cd*) is the maximum diameter and its length diminishes as the axis moves from the original position toward the axis (*ab*). As soon as it reaches (*ab*) it becomes minimum. As was stated already, there are more chances for the knife to pass through somewhere between the two points (*a*) and (*c*) than to cut through (*c*) itself. If therefore we determine the two diameters of the cell from the cut surface and the square root of their product is taken as the mean or "calculated diameter" of the given cell, the final value thus obtained will often be less than it should really be, because $\sqrt{ab \times dc}$ is always $> \sqrt{ab \times xy}$, where (*xy*) is any arbitrary line between (*a*) and (*c*). But as was stated already, the sections of the smaller cells are more nearly circular in outline. Therefore the mean diameters thus obtained may represent nearly the true value in the case of the smaller cells but less nearly, in the case of the larger cells which have become ovoid. From this it will be clearly seen that the frequency curve of the diameters of the ganglion cells based on the square roots of the product of the observed diameters can not represent the true frequency.

As to the range of the diameters, the maximum "calculated diameters" found may be considered to be the true value since there is at least one chance that the knife could pass through the longest axis while on the other hand the observed minimum diameter may be somewhat less than the true minimum diameter since there is a tendency for the diameter of those cells which are in any degree ovoid to be made smaller. Consequently if the values

---

[3] The maximum size of the cell is obtained only when the knife makes 90° with the axis (*ab*), provided it also passes through the center of the cell.

found for the small cells were nearly right but those found for the large cells were less nearly right it is evident that we should expect to find more cells showing smaller diameters than are actually present in the nine slices examined. This leads at once to the conclusion that the ordinates representing the cells of the small diameters must be compounded of two heterogenous elements; *the true small cells plus those cells which are artificially made smaller* by the method of section. In the same way the ordinates for the larger cells will be compounded of the measurements on *the larger cells minus those which were artificially made smaller.* Thus we shall find an excess of cases towards the smaller value of $x$ and a deficit towards the larger value of $x$. This is just what we have observed. It was found, when the observed polygon was compared with the theoretical curve that the latter considerably underestimated the observed ordinates which correspond to the smaller values of $x$ and overestimated the observed ordinates which correspond to the larger values of $x$. The facts mentioned above indicate that the deviations of the observed polygon from the theoretical curve are mainly, if not entirely, due to the method of section. The greater observed excess found in the neighborhood of the mean or mode is interesting, since it may be assumed that up to the neighborhood of the mean or mode the cells remain nearly spherical while beyond this region the increase in size is accompanied by a change in shape.

If my argument is correct, then we should expect the greater percentage deviation of the two diameters to appear more frequently towards the larger abscissal values. Although it would seem at first easy to test such hypothesis by taking the percentage deviation from the averages corresponding to the different abscissal values, nevertheless in practice we meet considerable difficulties. Any one who is familiar with the sections of the spinal ganglia prepared by the usual fixation methods, will recall that there are present a number of *small* cells with very unequal diameters. Such cells are most abundant along the periphery of the sections. The general outline of such cells is either rectangular, instead of curved, or the opposite boundaries are represented by nearly parallel lines. The cause of the deformation may be attributed to a shrinkage of the capsule of the spinal ganglion itself. On account of the presence of such deformed cells a mere comparison of the percentage deviations of the two diameters is unsatisfactory. Although it may not be a conclusive test, yet remembering that the spherical or nearly spherical cells should occur more frequently either towards the negative side or at the mode than towards the positive side, a determination of the relative frequency of such spherical cells, or the cells with nearly equal diameters, may be employed. Under the circumstances I think this is the only feasible method of testing this point. From an examination of original data, it has actually been found that such spherical or nearly spherical cells diminish with the increasing calculated diameter and increase with a diminishing calculated diameter. Even without any further test we cannot doubt from the theoretical standpoint that the method of section diminishes the diameter of the large cells, thus artificially increasing the frequencies of the small cells.

If this fact just mentioned is accepted, the conclusion follows that the theoretical curves may be considered as satisfactory representations under the circumstances and also may be considered much truer representations of the frequency distributions of the cell-bodies and nuclei than that shown by the actually observed data.

Since the curve of Type I has limited range in both directions, we find from the constants that

$$\begin{aligned}\text{lower limit of range} &= 7.5844\mu\\ \text{and upper limit of range} &= 60.9693\mu,\end{aligned}$$

while the observed limits are 7.8 micra and 47.4 micra, respectively. We see therefore that the theoretical lower limit agrees very closely with the observed, while the upper limit in the theory is considerably higher than that of the observed. But that this upper value may not be entirely improbable is indicated by my previous work ('02) on the spinal ganglion cells where I find cells in the fourth cervical spinal ganglion of the adult albino rat as large as 52.7 micra. This figure just given is the average for the three largest cells observed, therefore one or two individual cells must be still larger. Nevertheless it is not necessary to assume that these cells are the largest which could be found. This fact indicates that there is a tendency at least to approximate the values given by the theoretical curve.

## MEAN, STANDARD DEVIATION, AND COEFFICIENTS OF VARIATION.

In the equation $A = \frac{\Sigma\,(V.\,f)}{n.}$, where $A$ represents the mean, it will be clearly seen that the absolute value of mean ($A$) varies directly according to the greater or smaller number of frequencies associated with the smaller or greater values of $V$, as long as "$n$," the total number of variates, is constant. We have demonstrated above that the number of the observed frequencies of $V$ for both cells and their nuclei cannot be considered as the true frequency owing to the method of section. The true frequencies for the smaller values of $V$ should be the observed frequency minus those cells which have been transferred from the group of large cells, while for the larger values of $V$ it should be observed frequency plus those cells which have been thus transferred. Consequently the mean values actually found for the cell-bodies and nuclei must be considered as smaller than they should actually be. However we cannot determine at the present moment how large the true mean values should be, owing to the difficulty of determining the number of the cells and nuclei which are assumed to have been transferred. On the other hand, the values for the standard deviation and for the coefficients of variation in the present case should be smaller than those found, since following an increase in the frequencies towards the larger values of $V$ the resulting frequency distribution would become more regular than they are shown to be by the observed polygons and consequently the mean square deviation would become smaller. Diminution in the mean square deviation causes a reduction in the value of the standard deviation and consequently in the value of the coefficients of variation. As a matter of fact, we found the value for the standard deviation as well as the coefficients of variation decidedly larger when compared with apparently more variable characters. For example PEARL ('05) found the coefficient of variation in Paramecium from 8 to 9 per cent and in Arcella 10 per cent (PEARL and DUNBAR, '03) while in the present case that of the cell-body is as high as 28 per cent and that of the nucleus 17 per cent. Although we have not as yet any available data with which directly to compare our own, nevertheless our own values appear too great when they are compared with the coefficients of variation obtained from the measurement of highly variable organs like the weight of the liver (21 per cent, GREENWOOD, '04), weight of the body (10 per cent, PEARSON, '97), weight of the heart (18 per cent, GREENWOOD, '04), etc. I therefore corrected the values of the mean, standard deviation, and coefficients of variation, assuming that the theoretical curves represent more nearly the true distribution of frequencies. On employing the values of the theoretical ordinates there was found for cell-bodies, mean, 28.5948 micra, standard deviation, 14.8824 micra and coefficient of variation, 18.36 per cent; while for the nuclei, the mean was 13.0535 micra; and standard deviation, 1.7929 micra; the coefficient of variation being 13.73 per cent. When these corrected values are compared with uncorrected ones we find an increase of 3 micra for the mean in both the cells and the nuclei, and a reduction by 10 per cent in the coefficient of variation in the case of the cells and a reduction by 4 per cent in the case of nuclei. These corrected values appear to be the more probable, and are the best we can obtain until some further means of correcting the raw observations have been found.

## CLASSIFICATION OF THE SPINAL GANGLION CELLS.

The unavoidable modification in the size of the spinal ganglion cells due to the method of sectioning as here described suggests a revision of the classification of the cells so far as it depends on their observed sizes. It has been mentioned already that using the size of the cells and the arrangement of the stainable masses as criteria, several investigators have attempted to classify the cells composing the spinal ganglion. Three such classifications proposed by LUGARO, LENHOSSÉK and COX will be presented in detail.

LUGARO ('96) distinguishes in the dog five different varieties of the spinal ganglion cells:

1. Large cells with delicate, closely packed stainable masses which are distributed uniformly throughout the cell-body. Around the nucleus are large stainable masses closely packed. The nucleus is large and clear and is provided with a nucleolus. These cells appear to be numerous.

2. Clear, medium-sized cells with irregularly formed small and large stainable masses which are large at the periphery. Even here we see that individual masses are not isolated but are united

together by fine processes. The nucleus is clear and possesses a nucleolus. These cells are most numerous.

3. Small, dark cells with numerous small stainable masses lying in the region of the nucleus. The ground substance becomes diffusely stained. The nucleus also stains diffusely and contains two or more nucleoli. These cells rank third in point of number.

4. Small or medium sized clear cells with large stainable masses which are present in small numbers and connected with each other by processes. The nucleus frequently possesses more than one nucleolus. These cells are not numerous.

5. Large clear cells with long drawn out masses which are continuous with one another and which arrange themselves in concentric lines around the nucleus. These last cells present a laminated appearance like the cross section of an onion. These cells are least numerous.

LENHOSSÉK ('96) in the human spinal ganglion distinguishes three varieties.

1. The first variety consists of cells with a light staining ground substance only. These, which are the largest cells, have a pale ground substance and less numerous, loosely arranged stainable masses, which are most dense around the nucleus.

2. To the second variety belongs coarsely granular cells (grobscholligen Zellen), the appearance of which depends on the arrangement of the stainable substance, and most of the cells in the ganglion belong to this variety. These cells are of medium size, but sometimes small and rarely very large.

3. The third variety contains small cells which have a peculiar internal structure. These cells stain darkly because of the density of the ground substance.

COX ('96) distinguishes in the spinal ganglion of the rabbit two main varieties.

1. One variety contains larger or smaller irregular masses of stainable substance, which do not show a distinct concentric arrangement. The cells of this variety may be either large or small.

2. The other variety contains large, irregular masses of stainable substance arranged concentrically.

It will be clearly seen from the description given by these authors that there exist some structural characters common to both large and small cells. That is to say, some small cells have characters possessed by large cells and therefore size is the only means of distinguishing two forms. There is however another group of the small cells (third variety of both LUGARO and LENHOSSÉK) which exhibit still different structural characters. They are much darker in appearance owing to a strong affinity for staining reagents. The arrangement of the stainable substance is irregular and indistinct. The cell-outline is irregular. Thus there is no question as to the presence of the two kinds of the small cells which differ in both structure and shape from each other. The entire series of small cells which exhibit a resemblance to the large cells were considered by COX, LENHOSSÉK and LUGARO as early formed cell elements which persist in the spinal ganglion as such in small size. I have however just shown that a considerable number of the large cells are made smaller artificially by the method of sectioning. One would therefore expect to find a number of the small cells similar in structure to the large cells, except that the arrangement of the stainable substance may differ slightly according to plane of section. The cell-outline of the majority of the "artificial" small cells should be nearly spherical, unless they are distorted. Therefore the existence of small cells with the internal characters of the large cells can be explained readily on the assumption that they are in part if not entirely those large cells modified by the method of sectioning. I therefore conclude that a majority of these cells with the characters of the large cells do not preëxist as such and that consequently the conclusions of LUGARO, LENHOSSÉK and COX are to this extent misleading.

While the writer was engaged in the study of the structure of the spinal ganglion in the albino rat (HATAI '01) the following groups of cells were recognized and described. The one group is larger in size and stains lightly with eosin or erythrosin, while another group is smaller in size and stains deeply with eosin or erythrosin. Still a third group which, although it agrees in staining reaction as well as in an irregular outline with the small cells, nevertheless differs in the arrangement of the stainable substance and in size. The size is slightly larger on the average than that of the small deeply staining cells but much smaller than large cells. It now seems better to consider the group intermediate in size as a variety of the small cells rather than as a distinct type. The following are the reasons for this conclusion:

1. The intermediate sized cells agree with small cells in two important characters, the cell-body stains deeply with eosin or erythrosin and the cell-outline is irregular.

2. Since the arrangement of the stainable substance is rather unstable its difference has significance only when other characters also differ from any other given group under consideration. If the recently proposed hypothesis by SCOTT ('05) that the stainable substance is identical with the zymogen granules of the pancreas turns out to be true, then the size and form of the granules as well as their distribution may vary considerably according to the functional condition of the cell.

Consequently we have in the spinal ganglion two forms of cells; one which stains deeply and the cell-outline of which is irregular. Such cells are usually small in size. The other the cell-body of which stains lightly the cell-outline being regular. Such cells range from small to large in size. It must be remembered however that the entire cell-population when they are grouped according to their sizes grade from smallest to largest without showing any interruption. This means of course that there is no definite demarcation line to divide the large from the small cells or vice versa. As a matter of fact, the cells which stain lightly and which also exhibit regular outlines are by no means constant in size. This is also true for the group of the cells which stain deeply and which exhibit an irregular outline, although they are more uniformly small. For this reason, the size of the cell-body is not a proper criterion by which to classify them. The writer has adopted the staining reaction of the cell for classification because, as has been mentioned above, the ganglion cells fall readily into one of the two classes: that is (*a*) those with a deeply stained cell-body with irregular cell-outline and (*b*) lightly stained cell-body with regular cell-outline.

Although we should expect to find intermediate forms, which must always be present, nevertheless grouping by this method is more definite and practical than by the size and is much simpler than by those proposed by other investigators. In addition, these different histological characters are undoubtedly associated with different physiological states (HATAI '01).

I have chosen from NISSL's nomenclature two terms by which to designate the two groups of the ganglion cells with the idea that they may aid description.

1. Pycnomorphic cells, those cells which appear darker owing to a stronger affinity to the staining reagents. The cell-outlines are irregular. Such cells are usually small in size.

2. Apycnomorphic cells, those cells which appear pale owing to weaker affinity for the staining reagents. The cell-outlines are regular, being either spherical or oblong. Such cells range from small to large and include those which are made artificially smaller owing to the method of sectioning.

Attention is called to the fact that the above classification does not modify our views concerning the existence of three histological varieties of cells recognized in the spinal ganglion (see p. 1) but merely shows that these varieties do not distinguish themselves by their diameters in such a way as to form separate groups under this method of examination.

## ON THE CORRELATION BETWEEN CELL-BODY AND NUCLEUS.

The intimate physiological relations existing between the cell-body and the nucleus suggest that there may also exist a definite size or mass relation between these two structures. Generally speaking in the growing spinal ganglion cells (Hatai '01), the cell-body grows much faster than the nucleus. It was my object to determine this mass relation, between the cells and nuclei and if possible to find some mathematical expressions by which such relation could be concisely stated.

The correlation table (Table II, p. 490) furnishes us all the data necessary to determine such a relation. The table shows the range of variates in one character corresponding to that in the other. The coefficient of correlation would be then a numerical expression of the occurrence of the several values of $x$ in one character in association with the several values of $y$ in the other. Pearson gives the formula for obtaining the coefficient of correlation in the following form:

$$r = \frac{\Sigma\ (x.\ y.)}{n.\ \sigma_1\,\sigma_2}$$

Using the above formula, the value of $r$ (coefficient of correlation) was found to be 0.8616 ± 0.0055. This shows that the size of the cell-body is highly as well as positively correlated with the size of the nucleus. Therefore we infer that the larger cell-body is associated with larger nucleus, and vice versa. We can also find from the correlation table the diameter of the nucleus corresponding to the any given diameter of the cell-body. The value of the nucleus thus obtained is however affected by a variable probable error owing to insufficient number of observations combined with a random sampling. We therefore need to find the most probable values from the observed data, or the characteristic equation which can best represent the data with minimum error. We have two kinds of characteristic equations, linear and non-linear. Whether or not a given expression can be best represented by the linear or non-linear characteristic equation is of the utmost importance, and it is necessary to determine which equation applies to our present data. PEARSON ('04) has introduced a new constant, $\eta$, called the correlation ratio and this is used to test the linearity of the regression. The correlation ratio according to PEARSON is the ratio of the variability of the means of the arrays of one correlated character to the total variability of that character and is shown in the following formula:

$$\eta = \frac{\sigma_{my}}{\sigma_y}.$$

The constant $\eta$ has the same value as the coefficient of correlation when the regression is perfectly linear. If the regression is not linear $\eta$ will be greater than $r$. Then evidently $\eta \sim r$ is a measure of the approach of the regression to linearity. I have calculated the value of $\eta$ by the formula given above and found that when this value is compared with the coefficient of correlation the former is significantly greater than the latter as is shown in the following:

$$\eta - r = .9267 - .8616 = .0651$$

However, the difference between the value of these two constants will in practice deviate more or less from zero. It is therefore necessary to find whether or not the difference found between the two constants is significant. Recently BLAKEMAN ('05) has given methods of obtaining the probable error of various functions of $\eta \sim r$. If we let

$$\zeta = \eta^2 - r^2$$

an approximate formula for the probable error of $\zeta$, *i.e.*, $E_\zeta$, is

$$\frac{\zeta}{E_\zeta} = \frac{\sqrt{n}}{0.6745} \cdot \frac{1}{3} \sqrt{\zeta} \frac{1}{\sqrt{1 + (1 - \eta^2)^2 - (1 - r^2)^2}}$$

Applying this formula it was found that

$$\zeta = .1164 \pm .0135$$

Thus the difference is certainly significant and data demand a non-linear characteristic equation. I have applied PEARSON'S method of parabola ('04, '05) to the present data and obtained very satisfactory results as will be seen later. The general formula of parabolas of any order is as follows:

$$y = y_0 \left\{ \varepsilon_0 + \varepsilon_1 \left(\frac{x}{l}\right) + \varepsilon_2 \left(\frac{x}{l}\right)^2 + \varepsilon_3 \left(\frac{x}{l}\right)^3 + \dots\dots\dots \right\}$$

where $l$ is a half range of variates and $\varepsilon_s$ are the constants to be determined from the observed data. I found that for the present data the parabola of the second order makes a very close fit to the observed means of the arrays. The smooth curve in Fig. 4, where the observed and calculated results are graphically represented, was plotted from the following equation:

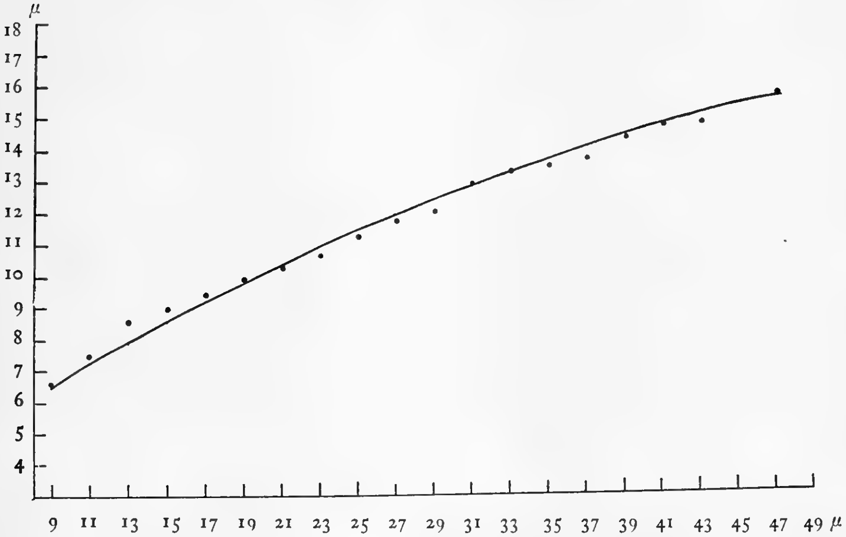


FIG. 4. Probable diameter of the nucleus for given diameter of the cell-body. ...... observed; ————, calculated.

$$y = 12.2939 \left\{ 1.0252 + .3564 \left(\frac{x}{l}\right) - .0758 \left(\frac{x}{l}\right)^2 \right\}$$

As will be seen from Fig. 4, the two curves agree very satisfactorily. It is therefore concluded that there certainly exists some definite mass relation between the cell-body and nucleus and its relation is mathematically expressed by the parabolic formula of the second order, as given. Since the regression is not linear but is best represented by parabola we may say that gain in the diameter of the nucleus following increase in the diameter of the cell-body varies in every stage and although the curvature is not pronounced from the nature of the parabola, the diameter of the nucleus is relatively greater in the small cells than in the large cells. For example, when the volume of the cell-body is compared with that of the corresponding nucleus, the following relation is found: In the cell-body whose diameter is 9 micra the volume of the same is 2.64 times that of the nucleus, while in the cell-body whose diameter is 47 micra its volume is 25.34 times that of the corresponding nucleus. This fact indicates, as was mentioned already, a predominant growth of the cell-body over that of the nucleus.

This gives us a method for comparing at some future time the relations in the small cells in the adult ganglion with that of the small cells having the same size in the immature ganglion.

## CONCLUSIONS.

We see from the preceding observations that: 1. The method of section modifies the true frequency distributions of the cells and nuclei when their diameters are considered. 2. Under the circumstances the skew curves of Type 1 for the cell-bodies and that of the Type 4 for the nuclei may be considered the best and most reasonable representation of the frequency distribution of the diameters. 3. The theory that the entire group of small cells with the structural characters of the large cells represents unchanged small cells is probably erroneous in view of the unavoidable modification of the large cells by the method of section. 4. The diameters of the nucleus and that of the cell-body are highly and positively correlated ($r = 0.8616$). 5. There exists a definite mass relation between cell-body and nucleus, and the diameter of the nucleus corresponding to any given diameter of the cell-body is best represented by a parabola of the second order. 6. The spinal ganglion cells in a given ganglion may be considered as a homogeneous group, so far as the size is concerned. 7. Spinal ganglion cells are classified into two groups according to their structural characters: (*a*) *Pycnomorphic cells*, those cells which appear dark owing to a stronger affinity to the staining reagents; and the cell-outline of the same is usually irregular. Such cells are usually small in size. (*b*) *Apycnomorphic cells*, those spherical or oblong cells which stain lightly and have cell-outlines which are regular. Such cells range from small to large in size. These two groups however grade into one another

## APPENDIX. TABLE II.

Correlation between cell-bodies and nuclei.

| Cell-bodies / Nuclei | 4.65– 5.30μ | 5.30– 5.95 | 5.95– 6.60 | 6.60– 7.25 | 7.25– 7.90 | 7.90– 8.55 | 8.55– 9.20 | 9.20– 9.85 | 9.85–10.50 | 10.50–11.15 | 11.15–11.80 | 11.80–12.45 | 12.45–13.10 | 13.10–13.75 | 13.75–14.40 | 14.40–15.05 | 15.05–15.70 | 15.70–16.35 | 16.35–17.00 | 17.00–17.65 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 8–10μ | 2 | 1 | 1 | 2 | 2 | | 1 | | | | | | | | | | | | | | 9 |
| 10–12 | | 3 | 2 | 6 | 6 | 4 | 3 | 2 | | | | | | | | | | | | | 26 |
| 12–14 | | | 2 | | 4 | 5 | 8 | 6 | 1 | | | | | | | | | | | | 26 |
| 14–16 | | | | 1 | 3 | 7 | 14 | 16 | 3 | 1 | | | | | | | | | | | 45 |
| 16–18 | | | 2 | | | 8 | 12 | 44 | 22 | 2 | | 1 | | | | | | | | | 91 |
| 18–20 | | | | | | 4 | 3 | 55 | 50 | 20 | 4 | 2 | | | | | | | | | 138 |
| 20–22 | | | | | | 6 | 1 | 37 | 76 | 36 | 25 | 11 | 2 | | 1 | | | | | | 195 |
| 22–24 | | | | | | 1 | 1 | 14 | 58 | 47 | 35 | 17 | 6 | 1 | | | | | | | 180 |
| 24–26 | | | | | | | | 7 | 20 | 22 | 25 | 14 | 14 | 4 | 1 | 1 | | | | | 108 |
| 26–28 | | | | | | | | | 8 | 7 | 14 | 26 | 14 | 3 | 2 | | | | | | 74 |
| 28–30 | | | | | | | | | 1 | | 11 | 10 | 7 | 3 | | 1 | | | | | 33 |
| 30–32 | | | | | | | | | | | 8 | 8 | 10 | 13 | 8 | 5 | | | | 1 | 53 |
| 32–34 | | | | | | | | | | 1 | | 5 | 5 | 5 | 11 | 6 | | | | | 33 |
| 34–36 | | | | | | | | | | | 1 | 2 | 9 | 4 | 9 | 4 | 1 | 2 | | | 32 |
| 36–38 | | | | | | | | | 1 | | | 1 | 3 | 1 | 6 | 6 | 3 | | | | 21 |
| 38–40 | | | | | | | | | | | 1 | | | 1 | 10 | 3 | 2 | 6 | | | 23 |
| 40–42 | | | | | | | | | | | | | | 1 | 2 | 4 | 4 | | 2 | | 13 |
| 42–44 | | | | | | | | | | | | | | | 1 | 1 | | | | 1 | 3 |
| 44–46 | | | | | | | | | | | | | | | 1 | 2 | | | | | 3 |
| 46–48 | | | | | | | | | | | | | | | | | 1 | | 1 | | 2 |
| Totals...... | 2 | 4 | 7 | 9 | 15 | 35 | 43 | 181 | 240 | 136 | 124 | 97 | 70 | 36 | 52 | 33 | 11 | 8 | 3 | 2 | 1108 |

## BIBLIOGRAPHY.

BLAKEMAN, J.
'05. On tests for linearity of regression in frequency distributions. *Biometrika*, vol. 4, pp. 332–350.

COX, W. H.
'98. Der feinere Bau der Spinalganglienzellen des Kaninchens. *Anatomische Hefte*, Abth. 1, Bd. 10 pp. 75–103.

GREENWOOD, M.
'04. A first study of the weight, variability and correlation of the human viscera, with special reference to the healthy and diseased heart. *Biometrika*, vol. 3, pp. 63–83.

HATAI, S.
'01. The finer structure of the spinal ganglion cells in the white rat. *Journ. Comp. Neurol.*, vol. 11, no. 1, pp. 1–24.
'02. Number and size of the spinal ganglion cells and dorsal root fibers in the white rat at different ages. *Ibid.*, vol. 12, no. 2, pp. 107–124.
'05. A note on the significance of the form and contents of the nucleus in the spinal ganglion cells of the fœtal rat. *Ibid.*, vol. 14, no. 1, pp. 27–48.

LENHOSSÉK, M. VON.
'96. Ueber den Bau der Spinalganglienzellen des Menschen. *Arch. f. Psychiat. u. Nerven'k., Berl.*, Bd. 29, pp. 346–380.

LUGARO, E.
'96. Sulle alterazioni delle nervosi dei ganglia spinali. *Rev. di. pathol. nerv. e ment., Firenze*, vol. 5, p. 457.

PEARL, R. AND DUNBAR, FRANCIS J.
'03. Variation and correlation in Arcella. *Ann. Report of Michigan Acad. Sci. for the year* 1903, pp. 202–204.

PEARL, R.
'07. A biometrical study of conjugation in Paramecium. *Biometrika*, vol. 5, pp. 2, 13–297.

PEARSON, K.
'94. Contributions to the mathematical theory of evolution. I. On the dissection of frequency curves. *Phil. Trans. Roy. Soc. London*, vol. 185, A, pp. 71–110.
'96. Mathematical contributions, etc. Skew variations in homogeneous material. *Phil. Trans.*, 186 A, pp. 343–414.
'97. The chance of death. *London.*
'01. Mathematical contributions, etc. Supplement to a memoir on skew variation. *Phil. Trans.*, 197 A, pp. 443–459.
'02. On the systematic fitting of curves to observations and measurements. *Biometrika*, vol. 1, pp. 265–303, and vol. 2, pp. 1–23.
'05. "Das Fehlergesetz und seine Verallgemeinenungen durch Fechner und Pearson." A rejoinder. *Biometrika*, vol. 4, pp. 169–212.
'05. Mathematical contributions, etc. On the general theory of skew correlations and non-linear regression. *Drapers' Comp. Research. Memoirs, Biometric series*, 2, pp. 1–54, *London.*

RANSON, S. W.
'06. Retrograde degeneration in the spinal nerves. *Jour. Comp. Neurol. and Psychol.*, vol. 16, no. 4, pp. 265–293.

SCOTT, F. H.
'05. On the metabolism and action of nerve cells. *Brain*, Part 111 and 112, pp. 506–526.

# ANOMALIES OF THE ENCEPHALIC ARTERIES AMONG THE INSANE.

## A STUDY OF THE ARTERIES AT THE BASE OF THE ENCEPHALON IN TWO HUNDRED AND TWENTY CONSECUTIVE CASES OF MENTAL DISEASE, WITH SPECIAL REFERENCE TO ANOMALIES OF THE CIRCLE OF WILLIS.

BY

I. W. BLACKBURN, M.D.

*Pathologist to Government Hospital for the Insane, Washington, D. C., Professor of Morbid Anatomy in the Medical Department Georgetown University, and in the Medical Department of the George Washington University.*

WITH ELEVEN FIGURES.

Minor anomalies of the encephalic arteries are so common that their study and observation have been mainly confined to modifications of the circle of WILLIS and the principal basal trunks. Slight deviation from the normal is very common in my autopsies and probably in most cases unimportant, though it is claimed that anomalies of the basal trunks are more common in the insane, to quote BERKLEY, indicating some defect in the "molding of the vital clay." BERKLEY admits, however, that comparative statistics are wanting, while he states that in four cases out of sixteen the arteries showed anomalies, a very large proportion. It would seem evident that developmental defects in the arteries would in most cases be compensated for by modifications of other trunks; and that under normal conditions functions would be preserved, but under diseased states and possibly unusual circulatory disturbances the abnormality might be of serious importance. The actual ætiological relationship of arterial anomalies to mental diseases other than to defective developmental states, in which it may be inferred, is hard to establish; but the relation they bear to gross cerebral disease, and to surgical operations upon the cervical arteries is easily demonstrated.

It must be borne in mind in the study of these anomalies that developmental defects should be considered apart from the changes produced by arterial disease. In most cases this is not difficult, and in many instances the acquired condition is clearly inadequate to produce the anomalies present.

In order better to comprehend the significance of the arterial anomalies of the circle of WILLIS and the great basal trunks it is necessary to refer to the normal condition of the circulation as indicated by the diagram, Fig. 1. Normally the carotid system and the vertebral system are separated by a balance, or meeting of the two currents, in the middle of the two posterior communicating arteries, while at the same time the circulation of the two cerebral hemispheres is virtually distinct on account of a normal balance which exists in the anterior communicating artery, and by the direction of the blood current in the first part of the posterior cerebral artery. Under normal conditions of current and pressure it must be extremely improbable for any part of the cerebrum to receive even temporarily any blood supply but from the proper vessels. The separation of the cerebellar circulation from that of the cerebrum under normal conditions is equally distinct, the current from the carotid system being opposed by that in the basilar artery. The pontine and upper cerebellar arteries have a more common blood supply, being in keeping with the fusion of the vertebrals into the basilar, though the two posterior inferior cerebellar vessels must normally receive their blood supply from the corresponding vertebrals. Anastomoses between the cerebellar arteries are also more common than in the cerebral trunks though usually the obstruction of a cerebellar artery results in softening of its proper area.

In abnormal developmental conditions this regulation of circulation is of course disturbed and the direction of the current in a vessel may be permanently reversed, while in disease of the vessels these anomalies may greatly add to the gravity of the situation.

As a basis for this study I have noted the conditions found in 220 consecutive cases of mental disease; and, as a matter of some additional interest I have given the age, sex, pathological condition of the vessels, and the form of mental affection in each case. I must claim, however, as the foundation of my opinion, the examination of over 2220 cases rather than the smaller number given as the basis for the statistics.

I have also given somewhat in detail three cases of anomalies of unusual interest, not included in the list, and have introduced a number of diagrams of associated anomalous conditions which are for the most part self-explanatory. I would, however, call attention to the number of these in which surgical ligation of the internal carotid, or obstruction of the vessel by thrombosis would endanger the whole hemisphere.

It will be noted in these diagrams, and in a number of the cases in the list, that anomalous conditions are frequently associated. In the sixteen cases diagramed this was strikingly manifested, and at the same time there is a certain correlation between some of the anomalies, notably in enlargement of the anterior cerebral of one side and small size of the opposite vessel; enlargement of a posterior communicating artery with underdevelopment of the corresponding posterior cerebral; and in increased size of the opposite vertebral when one of these is undeveloped.

In the list of cases, 227 were included—Nos. 1968–2194—but in some of these the brain was not examined, leaving 220 consecutive cases in which the vessels were studied. This number and order of cases I think may be taken as fairly representative of the relative frequency of arterial anomalies among the insane, and, though the number is too small for valuable statistics on this question, it may be taken as showing the frequency in the several forms of mental disease.

In the 220 cases studied, 65 showed no anomalies, slight disparity in size of the paired vessels being disregarded, and no anomalous conditions being noted unless presenting a deviation beyond the normal variation.

Professor WINDLE, who studied the vessels in 200 cases among those presumably sane, found 76 cases normal, and disregarding slight difference in the size of the paired vessels he found 119 cases normal in number and arrangement. As I have included the cerebellar arteries in my list, while WINDLE studied only those of the circle of WILLIS, this must be taken into consideration in comparing the two final results.

As I shall have to make frequent reference to the statistics of WINDLE, for comparison with my own, I would here acknowledge my indebtedness.

## SUMMARY.

*Internal Carotid Artery.*—The internal carotid artery has been quite constant in size and development in my cases. It is all the more remarkable that in several reported cases, a large anomalous branch has been found arising from the cavernous portion of the vessel and turning abruptly backward, joining the basilar. A case of this interesting anomaly is given somewhat in detail in Case No. 1926, Figs. 7 to 9. A case of direct union of the carotids without the intervention of an anterior communicating artery is given by MITCHELL and DERCUM; this I have not met with, though direct fusion of the anterior cerebrals, a closely allied condition, has been seen a number of times. Occasionally some disparity in size of the two vessels is seen, but it was deemed noteworthy in only one case.

*Middle Cerebral Arteries.*—The middle cerebral artery does not enter into the circle of WILLIS, though the circulation in it is markedly influenced by anomalies of its component vessels. A few abnormal branches were noted, and in one case the inferior external frontal branch was absent and its place was taken by a recurrent vessel from the anterior cerebral. As a result of this a large thrombotic softening of the Sylvian region did not affect the third frontal convolution and speech was preserved. Cases have been recorded of abnormal origin of the vessel itself, and of origin of the post communicating artery and the anterior choroid from this artery, but I have found no case which could not be otherwise explained.

*Anterior Cerebral Arteries.*—The most common anomaly of the anterior cerebral arteries is the enlargement of one artery and a corresponding small size of the opposite artery. As the result of this the main blood supply comes through the enlarged vessel, the anterior communicating artery is enlarged, and both anterior cerebrals appear to arise from one carotid. Sometimes the anterior communicating artery remains distinct, but it may be completely merged into the anterior cerebrals and the remnant of the small undeveloped anterior cerebral join it at an acute angle. Nos. 2057, 2063, 2066, 2099 and 2137 represent this type of anomaly. Another modification of these arteries is their fusion into a common trunk from the site of the anterior communicating artery onward to the vicinity of the genu callosi, where they commonly again form the two anterior cerebral trunks with a normal distribution. In this condition there is no proper anterior communicating artery. Sometimes the anterior cerebral of one side is very small, in some the vessels are about equal in size.

In a few instances the two arteries have fused anterior to the anterior communicating artery leaving a triangular opening between the vessels. Nos. 2073, 2077, 2139 and 2141 show this type of anomalous development.

Other anomalies of these arteries are occasionally met with. The vessels may both arise from one carotid as distinct trunks, one of which may be joined by an undeveloped vessel representing the opposite artery, or this vessel may be completely absent. Sometimes both vessels arise from one carotid by a single trunk which may or may not be joined by an abortive branch representing the opposite vessel. This condition must, however, be carefully analyzed as it is not essentially different from the conditions represented by Nos. 2004 and 2066; especially if the vessels divide at the situation of the anterior communicating artery.

The important surgical complications which would arise in these anomalous developments of the anterior cerebral arteries will be readily comprehended by reference to the accompanying diagrams of combined anomalies.

In my 220 cases the anterior cerebrals were fused into a common trunk in seven cases; see examples Nos. 2073, 2139 and 2141. This condition seemed at first sight to be more frequent as one of the vessels was not infrequently quite small and sometimes practically impervious, so that the vessels appeared as one trunk arising from the carotid. Nos. 2004, 2057, 2063, 2066, 2073, 2099 and 2137 show this type of anomaly.

In the list ten cases showed the right artery small and the blood supply coming from the opposite carotid; in six, the left was the defective vessel. In one case the right artery was unusually large while the left was normal; and in five instances a large recurrent branch originating commonly from the anterior cerebral at its junction with the anterior communicating turned backward and supplied the third frontal gyrus and the insula.

WINDLE found eight cases of fusion of the anterior cerebral arteries; and two instances of absence of one vessel, the place of the missing trunk being taken by a small branch from the opposite carotid. I have not regarded these cases as absence of the vessel in question, but as instances of underdevelopment with compensatory enlargement of the opposite trunk and the anterior communicating artery. See Nos. 2066, 2077, 2099.

*Anterior Communicating Artery.*—The anterior communicating artery may be absent, extremely small, double, or treble, or it may be formed of two vessels which join before junction with the anterior cerebral of the opposite side then forming a Y-shaped vessel. When double the anterior is usually the larger trunk. In a number of cases a median anterior cerebral artery arises from this vessel. This trunk is sometimes as large as or even larger than the true lateral trunks, and in some cases it curves around the genu, extends backward along the callosum, and finally divides into two branches which supply the two medial surfaces of the quadrate lobules. In such cases the true anterior cerebral arteries are distributed to the anterior portion of the medial surfaces, and to the orbital gyri.

In normal conditions and in cases of complete fusion of the anterior cerebrals, absence of the anterior communicating artery is of slight importance; in conditions of thrombosis of the carotid its absence may be of serious import.

In my list this vessel was absent in only two cases; it was unusually small in five; large in two; double in thirteen cases; formed a Y-shaped vessel in one; and gave off a large median anterior cerebral in two instances.[1] In quite a large number of cases this vessel was markedly modified by changes in the anterior cerebral trunks as mentioned above; it was also absent or greatly modified in cases of fusion of the anterior cerebrals, as in Nos. 2073, 2077, 2099, 2141 and 2169.

In WINDLE's cases this vessel was double in fourteen; triple in three; formed a Y in six cases; in six instances it was absent in fusion of the anterior cerebrals; in two it was present under like conditions, as in No. 2139; in two cases he found the vessel absent on account of there being but one anterior cerebral artery; and in one case in complete fusion of these arteries. There were nine instances of a median anterior cerebral artery.

*Posterior Communicating Arteries.*—The commonest anomalous condition of the posterior communicating arteries is enlargement of one or both of these vessels. In almost every case enlarge-

---

[1] It is probable that had a more careful search been made this artery would have been more frequently found. Since the above was written an excellent example of this vessel has been found. The artery took its origin from the anterior communicating, and proceeded as a single trunk with a few small branches to the callosum, to about the anterior border of the precuneus, when it divided into two equal sized trunks going to supply both of the quadrate lobules and adjoining portions of the paracentral lobules. The true anterior cerebral vessels were a little smaller than usual and were distributed to the lower and anterior medial surfaces of the hemispheres.

ment of the posterior communicating arteries is correlated with small size of the posterior cerebral trunks at their first part or origin from the basilar. When but one of these arteries is enlarged it is most commonly the right. QUAIN found the right artery enlarged in 5.5 per cent of the cases examined; the left in 4.5 per cent; both in 2 per cent.

In all these cases of enlargement of the posterior communicating arteries the main blood supply to the posterior cerebral territory comes from the internal carotid artery, but I think it a mistake to regard even high degrees of this anomaly as instances of origin of the posterior cerebrals from the carotid system. Often the posterior cerebral is represented by a mere thread, sometimes this may be impervious or even absent, but in none of my cases have I been convinced of the carotid origin of the posterior cerebral.

HYRTLE reports a case in which the middle cerebral was given off by the posterior cerebral a condition not so readily explained, but it must be extremely rare. The posterior communicating artery is not infrequently wanting, fails to join the posterior cerebral, or ends in a few filiform branches about the crus. QUAIN gives it as absent on the right side in 4.5 per cent; on the left in 6.5 per cent; and on both sides in 1.5 per cent.

The origin of the posterior communicating arteries from the middle cerebral rather than from the internal carotid I deem unimportant, as the former vessel is merely a continuation of the latter without definite dividing line, though the posterior communicating arteries arise inside of the origin of the anterior choroids, the latter arising from the terminal part of the internal carotid.

The posterior communicating artery of the left side was abnormally small in seven of my cases; that of the right side in three; both unusually small in four cases. The vessel was totally absent on the right side in one case. The right vessel was enlarged twenty-six times; the left sixteen times; and both were enlarged in twenty-three cases. In all of these cases the corresponding posterior cerebral arteries were below the normal in size. In several instances there were slight and inadequate anastomoses with the basilar through small and abnormal branches representing the posterior cerebral arteries. Nos. 2099, 2159 and 2177.

WINDLE found these arteries normal in 175 of his cases. In twenty-eight cases the right was the larger; in fifteen it was the left; both were abnormally small in seven cases. He gives these arteries as absent in twenty-five cases; thirteen times the left, the right nine times and both three times. The author states that a partial anastomosis with the basilar was secured in some of these by means of small twigs in the interpeduncular space. It seems possible that some of these may have represented undeveloped posterior cerebral and posterior communicating arteries, as in No. 2177.

*Posterior Cerebral Arteries.*—The most common abnormal condition of the posterior cerebral arteries is small size of the vessels at their first part before joining the posterior communicating arteries. This, as mentioned above, is the condition which leads to the conclusion that the vessels arise from the carotid. In some cases the vessel joins the posterior communicating artery by a fine practically impervious thread, it may join at an unusual place, or may fail to anastomose with the vessel at all. In case of undevelopment of this vessel it is almost invariably compensated for by enlargement of either the posterior communicating, or the anterior choroid, but in obstruction of the internal carotid of the same side the effects are disastrous. See Case No. 1909.

In my list the posterior cerebral of the right side was noted as smaller than normal in fifteen cases; the left in ten, and both in twenty-one cases. The right artery was absent in one case, and in two instances the main distribution was supplied by an enlarged anterior choroid artery. Nos. 2163 and 2177.

WINDLE claims that in twenty-four of his cases this vessel originated from the *carotid artery;* eleven on the right side; nine on the left; and four on both sides. I have not been able to satisfy myself that this was so in any of my cases, as it seems to me that all may be regarded as compensating enlargements of the posterior communicating and anterior choroid arteries.

In one of WINDLE'S cases and one of my own the third nerve was divided by this artery.

*Anterior and Posterior Choroid Arteries.*—The anterior choroid artery is fairly constant but may be represented by mere threads. In two instances among my cases I found this vessel in part taking the place of the posterior cerebral. Nos. 2163 and 2177. The posterior choroid arteries sometimes arise from the posterior cerebrals; sometimes from the superior cerebellar arteries. They are somewhat irregular in their development but were not carefully studied.

*The Basilar Artery.*—This artery, formed originally by coalescence of the two vertebrals, sometimes contains a septum in its interior, and occasionally shows an incomplete fusion, leaving an opening in the vessel as seen in Case 2009 and in Fig. 2. The vessel is sometimes joined by a large anastomotic branch from the carotid artery. See Case 1926. In my list of cases the basilar showed partial separation into its embryonic components in two cases. It was markedly curved in most cases of enlargement of one of the vertebral arteries, the convexity of the curve being opposite to the enlarged vessel. Nos. 2004, 2063 and 2066. Anomalies of origin of the cerebellar arteries arising from the basilar were common.

*Superior Cerebellar Arteries.*—The superior cerebellar arteries were quite constantly represented, sometimes being duplicated. This occurred on the right side four times; on the left twice; and on both sides in two cases. Occasionally this vessel sends branches to reinforce the anterior inferior cerebellar when it is ill developed.

*Anterior Inferior Cerebellar Arteries.*—This vessel is quite variable in its place of origin from the basilar. The vessel was duplicate in eight cases; one or the other was absent in seven; and in five instances it sent large branches to take the place of the posterior inferior cerebellar artery when this vessel was small or absent. There seemed to be a constant correlation between the two inferior cerebellar arteries, so that in eighteen cases the two had a common origin in a single trunk arising from the basilar.

*Posterior Inferior Cerebellar Arteries.*—This vessel was absent on the right side in ten cases; on the left in six. In these cases the place of the vessel was usually taken by branches from the anterior inferior cerebellar. In a few cases the artery took its origin from the basilar just above the junction of the vertebrals.

*Vertebral Arteries.*—One vertebral artery, according to QUAIN, more frequently the left, is sometimes much smaller than the other. The right vertebral was abnormally small in twenty-one cases; the left in twelve cases; both were small in two instances. An unusually large right vertebral with the left about normal in size was noted twice; the two vessels united by a transverse trunk in two cases. The posterior inferior cerebellar artery was large and received practically all of the blood from the cervical portion of the vertebral, in five cases; three times on the right; twice on the left. In these and a few other cases the vertebral was almost or quite inpervious, but in no instance was either vessel absent.

*The Anterior Spinal Artery.*—The anterior spinal artery usually shows slight variability in its trunks of origin, depending upon the size of the vertebrals. Occasionally the vessel takes its origin from a short transverse trunk joining the two vertebrals.

The *posterior spinal arteries* have not been studied.

*Associated Anomalies.*—In many cases the anomalous conditions were so associated that several were present in the same case. I have, therefore, introduced diagrams of a number of the most interesting cases, and have described three somewhat in detail.[2]

*Pathological Conditions of the Arteries.*—It was a matter of some surprise and interest to find that no less than 148 of the 220 cases showed some degree of arterio-sclerosis. However, as 138 of the patients were over sixty years of age this may be accounted for. In this connection it is well to bear in mind that arterial thrombosis, one of the most common accidents of arterio-sclerosis in the aged, is most apt to result seriously in these anomalous states of the arteries. BULLEN claims that arterial anomalies are most frequent in paresis; in thirteen cases of this disease in my list, six showed slight anomalous conditions, while some were normal in arrangement and not diseased.

Of the cases studied seventy were of senile dementia; forty, chronic dementia; fifteen, dementia precox; fifteen, epileptic dementia; nineteen, chronic melancholia; fourteen, chronic mania; thirteen, paresis; eight, manic depressive insanity; seven, organic dementia; four, terminal dementia; three, acute mania; three, imbecility; three, acute confusional insanity; two of toxic insanity; two, acute melancholia; and one each of acute confusional insanity and acute febrile delirium. It is perhaps well to state that under a more modern system of classification some of the above diagnoses of the mental diseases, made when the patients were admitted to the hospital, would be materially changed.

### *Case of Anomalous Circle of Willis.*

No. 1926. A. C.; white; male; aged 78; soldier; nativity, Ohio. Mental disease, senile dementia; duration uncertain.

Autopsy partial, only the brain being examined.

---

[2] Sixteen of these diagrams, Figs. 3–6, are included among the descriptions of the forty cases abstracted from the complete list of 220 cases. They are, however, sufficiently clear to be understood without reference to the descriptive list.

Skull thick and dense; symmetrical; sutures and bones normal. Over inner surface of dura of the convexity is a thin neo-membrane of internal pachymeningitis.

Brain. Weight, 1420 grams. Slight general shrinkage over the convexity; veins prominent; arterial branches tortuous. The arteries at the base are sclerotic and present the following anomalies.

1. Anterior communicating artery double.

2. At the junction of the upper and middle third of the basilar artery it is joined by a large vessel fully equal to the normal basilar in size, which comes from the left internal carotid just after its emergence from the carotid canal in the temporal bone. This abnormal artery has pierced the dura mater just outside of, and posterior to the posterior clinoid process, and dissection shows that it comes from the internal carotid at the junction of the intra-osseous portion with the cavernous portion of the vessel. The branch is not at all in the bony canal nor does it pierce the dorsum sellæ, though it lies at its origin quite close to the posterior clinoid process.

The aberrant vessel curves abruptly backward and inward joining the basilar, which is so altered as to appear a part of the anomalous trunk. The large size of the abnormal branch has diverted the basilar from its course and evidently the main blood supply to the posterior cerebral arteries, and the superior cerebellars, came through the anastomatic vessel from the left carotid, the other portions of the basilar and the whole vertebral system being small. The sixth nerve has the normal relation to the carotid artery and the anomalous branch pierces the dura at its anterior and inner side. The other cranial nerves are not in any way interfered with. Complete dissection of the carotid artery outside of the cranium is not permissible. Two or more minute arteries arise from the anomalous vessel and are distributed to the dura in the vicinity.

3. The vertebral system presents marked deviation from the normal. The left vertebral is unusually small and the main blood supply from below entered a large trunk which represents both the posterior inferior cerebellar artery and the anterior, no trace of the latter arising at the usual place from the basilar. This common trunk is distributed to the territory of both vessels represented. The right vertebral artery is about the usual size and passes without change of size but with marked curvature into the basilaris. There is no artery on this side corresponding to the posterior inferior cerebellar.

4. The basilar artery is so changed that the limits of the vessel can only be determined by the junction of the vertebrals and the division into the posterior cerebrals. At about the junction of the middle and lower thirds of the basilar a large trunk is given off which takes the place of the anterior inferior, and posterior inferior cerebellar arteries, the exact reverse of the condition on the left side. The middle portion of the basilaris is small and on the left side gives off the internal auditory artery and some pontine vessels. The upper part of the vessel, scarcely recognizable as such, gives off the superior cerebellar arteries, divides into the posterior cerebral arteries, and receives the anomalous carotid branch, as above described. The posterior cerebrals give off the posterior choroid arteries and both are distributed as usual.

5. The posterior communicating arteries are rather small but their origin and destination are normal. The anterior choroid arteries are normal in origin and distribution and so far as can be determined the other arterial trunks show no anomalies. (Figs. 7, 8 and 9.)

### *Thrombotic Softening of an Entire Hemicerebrum.*

No. 1909. O. B.; female; white; aged 69; nativity, U. S. Mental disease, chronic melancholia with secondary dementia.

Six days before the patient's death she had a general convulsion from which she did not fully regain consciousness, followed the next morning by another, with hemiplegia and loss of speech; after this she remained comatose until she died four days later.

*Synopsis of Autopsy.*—Arteries at base of brain sclerotic and tortuous; posterior communicating artery of left side unusually large; posterior cerebral of the same side small and impervious; anterior communicating artery small and impervious; On the right side the vessels were of normal caliber except the posterior communicating which was rather large. A clot had formed at the upper end of the left internal carotid artery, and as result of the above peculiarities of the circulation the whole left hemicerebrum had undergone acute softening.

The hemisphere was deeply reddened, extremely soft, and the cerebral veins were engorged even to their smallest visible branches. It was in fact, practically a hemorrhagic infraction of the whole hemisphere. The sinuses were not obstructed. The softened hemisphere was generally swollen, presenting a marked contrast with the right, which was moderately atrophied. (Fig. 10.)

### *Anomalous Condition of the Basal Arteries.*

No. 1954. M. J. B.; female; white; aged 64; nativity, U. S. Mental disease, chronic dementia.

The patient had a history of cerebral hemorrhage occurring about six years before her death. This resulted in partial paralysis of the right side, from which she suffered when admitted to the hospital. Her last illness was a sudden attack of left hemiplegia with evidences of disturbance or irritation of the motor region of the *left* side of the brain.

*Synopsis of Autopsy.*—The arteries at the base of the brain were extremely sclerotic, calcified and anomalous. The left anterior cerebral was large; the anterior communicating artery large; and the right anterior cerebral was small, thus the main blood supply to the anterior cerebral region came from the left carotid. Both posterior communicating arteries were unusually large; both posterior cerebral vessels small, especially the right. The left superior cerebellar artery double; left vertebral artery as large as the basilar; the right quite small, and the posterior inferior cerebellar, received nearly all of the blood brought by the vertebral.

A small aneurism had formed on the right middle cerebral artery at the point of origin of the principal branches, and a large intra-cerebral hemorrhage had occurred on this side from one of the lenticulo-striate arteries but the actual vessel could not be determined.

A horizontal section of the brain revealed an enormous hemorrhage of the right side which had completely destroyed the basal ganglia and capsules and torn its way into and filled the ventricles. On the left side there was a small brownish lesion in the internal capsule just posterior to the angle, which was supposed to be the remains of the former hemorrhage. The brain was œdematous and soft, and the perivascular spaces were greatly enlarged; some general atrophy of the convolutions of the surface. Other conditions found not important in this connection.

It would seem probable that in this case we had both the formation of the aneurism and the hemorrhage in part dependent upon arterial overstrain consequent to the lack of anastomoses between the right side and the left. The enlargement of the right posterior communicating artery seems to be a direct compensation for the small size of the posterior cerebral, but the small size of the right anterior cerebral and the current in the anterior communicating artery would effectually prevent relief to overstrain in this direction. Certainly the left carotid had a much freer outlet for its contents than the right, but at the same time owing to the compensation present the two hemispheres probably received a normal supply of blood until the complications due to arterio-sclerosis supervened. (Fig. 11.)

## CONDITION OF THE ENCEPHALIC ARTERIES IN FORTY OF THE TWO HUNDRED AND TWENTY CASES.

Case 1973. R. M.; colored; male; aged 61; paresis. Arterio-sclerosis. Right anterior cerebral artery small, and the larger portion of the blood came from the left side. From the anterior communicating artery onward, the left anterior cerebral artery forms a large trunk which afterwards divides opposite the genu callosi into two callosal arteries. Left posterior inferior cerebellar artery absent; right small.

Case 1974. E. N.; white; male; aged 76; chronic dementia. Arterio-sclerosis. Right posterior communicating artery very large; the corresponding posterior cerebral small; post choroid artery arises from the right posterior communicating artery. Left posterior communicating artery rather large; posterior cerebral of this side small. Anterior communicating artery small and practically impervious. Right vertebral artery very small and separates into two branches, one of which forms the posterior inferior cerebellar artery; one of which joins the basilar.

Case 1980. L. F.; colored; female; aged 40; manic-depressive insanity. The right posterior communicating artery large and furnishes the main blood supply to the posterior cerebral region, this artery being quite small. The left anterior cerebral artery is larger than normal and sends its blood supply to the opposite artery through an enlarged anterior communicating artery. The right anterior inferior cerebellar is double; the opposite artery comes off the basilar by a common trunk with the posterior inferior cerebellar, and supplies its region, the proper artery being very small.

Case 1985. W. E.; white; male; aged 65; senile dementia. Arterio-sclerosis. Left posterior communicating artery very large and is distributed to the inferior temporal regions. The posterior cerebral artery of this side does not join the former, but is distributed to the parts around the crus and the choroid plexuses. The left anterior cerebral artery rather small, the main blood supply coming from the opposite artery.

Case 1986. D. L.; colored; male; aged 95; senile dementia. Arterio-sclerosis. Both posterior communicating arteries very large; post cerebral arteries extend forward and join them at an acute angle. Anterior communicating artery absent. Right superior cerebellar artery double.

Case 2000. L. T.; colored; male; aged 82; senile dementia. Arterio-sclerosis. The right anterior cerebral artery extremely small both anterior cerebral arteries being supplied from the left side. Anterior communicating artery double. Right posterior communicating artery very large and the posterior cerebral joins it about its middle as a small vessel. (Fig. 3.)

Case 2004 W. L.; colored; male; aged 50; chronic dementia. Arterio-sclerosis. Right anterior cerebral very small at its origin, both anterior cerebral arteries appear to come from the left side. No true anterior communicating artery exists. After turning around the genu callosi the anterior cerebral arteries are distributed as usual. Right posterior communicating artery small; left larger than normal. Right vertebral artery very small; posterior inferior cerebellar artery of this side represented by a small thread and an impervious branch from the common trunk with the anterior inferior cerebellar artery. On the left side a double anterior inferior cerebellar artery is present, and a double superior cerebellar. (Fig. 3.)

Case 2009. S. W.; white; male; aged 66; chronic epileptic dementia. Senile arterio-sclerosis. Both vertebral arteries, about equal in size, join at the upper end of the medulla, and again separate, making a fenestra in the basilar about one-half an inch in length. The right posterior inferior cerebellar artery is normal in position, the left arises at the first point of junction of the vertebrals. The two anterior inferior cerebellar arteries arise from the right and left division of the basilar respectively.

Case 2011. J. W.; colored; female; aged 36; dementia from tumor of the brain. Slight arterio-sclerosis. The left anterior cerebral artery crossed mainly to the right through an enlarged anterior communicating artery, joining with the opposite artery in a common trunk as far as the genu callosi, after which this trunk sends branches to both hemispheres. From the anterior communicating artery onward the left vessel is represented by a small branched vessel.

Case 2014. E. B.; colored; female; aged 71; senile dementia. Slight arterio-sclerosis. The left vertebral artery is extremely small, the posterior inferior cerebellar artery taking nearly all the blood that comes through the vertebral artery. Right posterior inferior cerebellar artery very small and a large vessel from the basilar takes its place. Above this vessel is the proper anterior inferior cerebellar artery. Right superior cerebellar artery double.

Case 2016. J. C.; colored; female; aged 61; senile dementia. Arterio-sclerosis of the small-vessel type. The anterior communicating artery has a Y-shape. Both posterior communicating arteries are large and furnish the main blood supply to the posterior cerebral territory, these vessels being small. Right posterior inferior cerebellar artery absent, its place being taken by branches from the anterior inferior artery.

Case 2018. J. H.; white; male; aged 76; senile dementia. Arterio-sclerosis. Right anterior cerebral small; left large. On each side from the anterior cerebral artery a branch turns abruptly backward and is distributed to Broca's convolution in part. The right anterior inferior cerebellar artery large and supplies the posterior inferior cerebellar territory, this vessel being inadequate.

Case 2034. A. W.; colored; male; aged 76; senile dementia. Arterio-sclerosis. Left anterior cerebral artery small. Both posterior communicating arteries are very large and the corresponding posterior cerebral arteries are small at their origin. Both anterior inferior cerebellar arteries are large, and are sent in part to the posterior inferior cerebellar region, these vessels being rather small. Anterior inferior cerebellar of right side is duplicated.

Case 2037. M. G.; white; male; aged 74; chronic melancholia. Arterio-sclerosis. Anterior cerebral of left side small. Left posterior communicating artery very large and supplies the posterior cerebral region as this artery is very small. Anterior inferior cerebellar artery of right side extremely small and its territory is supplied by branches from the superior cerebellar which is unusually large.

Case 2039. J. W.; white; male; aged 50; chronic dementia. Arteries not diseased. The right anterior cerebral artery is small and the main blood supply comes from the opposite vessel. The anterior inferior cerebellar arteries are large and supply the posterior inferior cerebellar regions.

Case 2041. M. H.; white; female; aged 74; chronic dementia. Arterio-sclerosis. The vertebral arteries are joined by a transverse vessel about one-fourth inch from their junction with the basilar, and from this vessel arises the anterior spinal artery. Left posterior communicating artery rather large. Right anterior inferior cerebellar artery supplies the posterior inferior cerebellar region.

Case 2057. A. K.; white; male; aged 77; chronic melancholia. Arterio-sclerosis. Both posterior communicating arteries large; posterior cerebral arteries small. Right anterior cerebral artery large and sends the main blood supply to the opposite side through a large anterior communicating artery, the left anterior cerebral being very small. Anterior inferior cerebellar artery practically absent on left side. (Fig. 3.)

Case 2063. J. B. C.; white; male; aged 65; senile dementia. Arterio-sclerosis. Right anterior cerebral artery small at its origin; left, enlarged and sends the main blood current to the right side through a large anterior communicating artery. Left vertebral artery very small, right unusually large and enters without change of caliber into the basilar. (Fig. 3.)

Case 2066. L. D.; colored; male; aged 34; paresis. Slight arterio-sclerosis. Left anterior cerebral artery large and furnishes the opposite side with blood through a large anterior communicating artery, the right anterior cerebral being very small at its first part. Left vertebral artery small; right about the size of the basilar. (Fig. 4.)

Case 2070. C. J.; colored; female; aged 57; chronic dementia. Arterio-sclerosis. Anterior communicating artery double and from the anterior vessel arises a large artery which supplies the corpus callosum—a median anterior cerebral. Both posterior communicating arteries are very large, and the posterior cerebrals are very small.

Case 2073. A. S.; colored; male; aged 25; dementia præcox. No disease of arteries. Left anterior cerebral artery small and distributed mainly to the inferior surface of the frontal lobe; right artery forms a large trunk which divides an inch posterior to the genu of the callosum and is distributed as usual. Left posterior communicating artery rather large. (Fig. 4.)

Case 2077. A. M. M.; colored; female; aged 72; senile dementia. Arterio-sclerosis. Right anterior cerebral artery small; anterior communicating artery also small; left anterior cerebral artery forms a large trunk which extends as far as the genu callosi where it divides into two large branches, one of which supplies each median surface. Both posterior communicating arteries are large; posterior cerebral arteries small. (Fig. 4.)

Case 2092. H. F.; colored; female; aged 65; senile dementia. Slight arterio-sclerosis. Both posterior communicating arteries very large and supply the posterior cerebral region, the posterior cerebral of the right side being represented by a small thread which was impervious, and the left is a small trunk which curves around the crus but does not join the posterior communicating artery.

Case 2094. S. S. T.; white; male; aged 65; chronic mania. Arterio-sclerosis. The vertebral arteries are connected by a transverse trunk of considerable size, from which arises the anterior spinal artery. Right anterior inferior cerebellar artery absent, and branches from the posterior inferior cerebellar take its place.

Case 2097. P. McC.; white; male; aged 74; chronic dementia. Arterio-sclerosis. Posterior communicating artery of left side very large; the posterior cerebral very small; posterior communicating artery of opposite side very small, posterior cerebral very large. Anterior communicating artery double. Right posterior inferior cerebellar artery large; anterior inferior cerebellar small.

Case 2099. M. D.; white; female; aged 71; senile dementia. Arterio-sclerosis. Right anterior cerebral artery very small; the left is very large, divides into two trunks which correspond to the two anterior cerebral arteries, and there appears to be no true anterior communicating artery. The right posterior cerebral artery apparently arises from the carotid, and is only united to the basilar by a very small branch of a rudimentary vessel which is mainly distributed to the crus and interpeduncular space. (Fig. 4.)

Case 2137. C. N.; white; male; aged 66; senile dementia. Arterio-sclerosis. Right anterior cerebral artery very small, its place being taken by the opposite artery which supplies the two vessels through an enlarged anterior communicating artery. Right posterior communicating artery large, posterior cerebral small. Left posterior inferior cerebellar artery absent, its place being taken by a large branch from the anterior inferior cerebellar artery.

Case 2139. R. W. E.; white; male; aged 48; chronic epileptic dementia. Arterio-sclerosis. The two anterior cerebral arteries join into a common trunk just anterior to the anterior communicating artery leaving a triangular opening between the vessels. The two arteries then form a large vessel about one-half an inch in length after which they again divide and the upper vessel forms a callosal artery, while the other branch is mainly distributed to the medial surface anteriorly. On the left side, opposite the junction of the anterior communicating artery with the anterior cerebral a three branched trunk arises, the anterior branch taking the place of the anterior cerebral artery of this side, the middle branch distributed to the orbital surface, and the posterior branch goes backward to supply BROCA's convolution and the insula. The right posterior inferior cerebellar artery is absent, the anterior inferior being rather large. (Fig. 5.) No. 2139; all of the branches not represented.

Case 2141. J. C.; white; male; aged 80; senile dementia. Arterio-sclerosis. The two anterior cerebral arteries join directly into a single trunk without an anterior communicating artery. This trunk extends to the genu callosi where it again divides into two vessels which are distributed normally. A large branch which arises from the junction of the vessels supplies the orbital and medial regions of the left frontal lobe and is possibly the representative of the left anterior cerebral artery. The right posterior communicating artery is very large, corresponding posterior cerebral artery very small at its origin from the basilar. Left superior cerebellar artery is doubled. (Fig. 5.)

Case 2153. R. W.; white; female; aged 66; senile dementia. Arterio-sclerosis. Anterior communicating artery very small and impervious. Left anterior cerebral does not lie close to the genu of the callosum but is distributed to the orbital, and outer anterior medial surfaces of the left side; the opposite artery furnishes a single callosal artery, only one being present. Both posterior communicating arteries are large and supply the territory of the posterior cerebral arteries, these vessels being small at their origin. (Fig. 5.)

Case 2159. P. J.; white; male; aged 66; senile dementia. No disease of arteries. Right posterior communicating artery large; posterior cerebral artery of this side practically absent being joined to the former artery by a small impervious branch. Posterior communicating artery of left side enlarged and the posterior cerebral very small. The basilar, both vertebrals, and the posterior inferior cerebellar arteries are quite small. Anterior communicating artery absent. (Fig. 6.)

Case 2160. J. S. G.; white; male; aged 66; chronic mania. Slight arterio-sclerosis. Left vertebral as large as the basilar; right small and the posterior inferior cerebellar artery receives nearly all the blood brought by the lower part of the vertebral artery. Left posterior communicating artery unusually large. Small aneurism at origin of right anterior choroid artery.

Case 2163. A. H. T.; white; male; aged 68; senile dementia. Arterio-sclerosis. Posterior communicating artery of left side represented by an extremely small vessel. The left anterior choroid artery is unusually large; it lies at its first part deeply in the hippocampal fissure and branches supply the choroid plexus; it finally emerges and forms the parieto-occipital and the calcarine artery. The posterior cerebral of this side is distributed mainly to the inferior temporal region and the crus. On the right side a small aneurism is situated at the origin of the posterior communicating artery from the carotid, and one at the junction of the right anterior cerebral and anterior communicating artery. (Fig. 6.)

Case 2169. A. J. L.; white; male; aged 72; epileptic dementia. Arterio-sclerosis. Right anterior cerebral artery large, left small; and distributed mainly to the lower medial surface. A large median cerebral artery takes the place of the left anterior cerebral, and after it passes the genu it is distributed to the left upper medial surface and forms a callosal branch. Both posterior communicating arteries are enlarged; left posterior cerebral artery quite small. (Fig. 6.)

Case 2172. F. J. L.; white; male; aged 64; senile dementia. Arterio-sclerosis. Right anterior cerebral artery sends a large callosal branch which afterwards divides and supplies both quadrate lobules, while another branch of this artery forms the callosal branch of the left side. Right vertebral artery small; left continuous with the basilar and of the same size.

Case 2176. P. C.; white; male; aged 66; senile dementia. Marked arterio-sclerosis. Posterior communicating artery of left side large; posterior cerebral small, mainly distributed to velum interpositum, crus, and a small branch which joins the posterior communicating artery about one-half inch from its origin. The posterior communicating artery of this side, therefore, chiefly furnishes the posterior cerebral region.

Case 2177. D. P.; colored; male; aged 63; senile dementia. Arterio-sclerosis. Right posterior cerebral artery very small, and joins the posterior communicating artery by a small impervious branch. This artery is distributed mainly to the crus, and a large artery corresponding with the anterior choroid runs backward in the fissura hippocampi and after supplying the choroid plexus takes the place of the posterior cerebral artery being distributed in the same way. A small branch from this anomalous vessel anastomoses with the posterior choroid artery. The right posterior inferior cerebellar artery arises from the basilar; the opposite artery arises by a common trunk with the anterior inferior cerebellar, Fig. 6.

Case 2179. J. F.; white; male; aged 69; senile dementia. Advanced arterio-sclerosis. Both posterior communicating arteries are large and furnish the region of the posterior cerebral arteries. The left posterior communicating artery communicates with the basilar artery by a small impervious branch; the right anastomoses with the superior cerebellar by a small pervious branch; both posterior cerebral arteries being practically absent. The left anterior inferior cerebellar artery is very small.

Case 2184. W. T.; white; male; aged 57; chronic epileptic dementia. No arterial disease. Both posterior communicating arteries are small and are distributed mainly to parts around the crura. The left anastomoses with the posterior cerebral artery by a small branch, the right has no connection with the posterior cerebral artery. The nutrient arteries of the interpeduncular space are larger than usual, otherwise the posterior cerebrals are normal.

Case 2189. M. J.; colored; female; aged 65; senile dementia. Arterio-sclerosis. Both posterior communicating arteries small; both posterior inferior cerebellar arteries arise in common with the anterior from the basilar. Small impervious trunk connects the two anterior cerebral arteries posterior to the anterior communicating.

## LITERATURE CITED.

BERKLEY.
Mental Diseases. 1900.
BROWNING.
The Cerebral Circulation. Reference Hand-Book of the Medical Sciences, vol. 2. 1901.
BULLEN.
Post-Mortem Examination of the Brain, etc. *Journal of Mental Science*, vol. 36. 1890.
DERCUM.
A Collection of Anomalies of the Circle of Willis. *Journal of Nervous and Mental Disease*, vol. 14. 1889.
LUCAS, E.
Essai historique, critique et expérimental, sur la circulation, arterielle du cerveau. Thése de Paris. 1879.
WILDER.
Encephalic Nomenclature. Arteria Termatica. *New York Medical Journal*, vol. 41, 1885, and *Journal of Nervous and Mental Disease*, vol. 12, 1885.
WINDLE.
On the Circle of Willis. Reports of the British Medical Association for 1887, *New York Medical Journal*, vol. 2, 1888, and *Journal of Anatomy and Physiology*, 1887–1888.

Fig. 1. Diagram showing the normal direction of the blood current in the basal arteries, and how completely separated are the carotid and the vertebral system by the balance in the middle of the posterior communicating arteries. At the same time in normal conditions the two hemispheres are almost as distinctly supplied, owing to the balance in the anterior communicating artery, and the direction of the current in the posterior cerebral arteries. The cerebellar circulation is not so distinctly separated on the two sides and the anastomoses between the cerebellar arteries are more complete than those of the cerebrum.

Fig. 2. Diagram showing the most common variations in the circle of Willis, etc. (*A*) Enlargement of one anterior cerebral artery with corresponding small size of the opposite artery; (*B*) double anterior communicating artery; (*C*) common trunk made by junction of the two anterior cerebral arteries, with division at the genu callosi; (*D*) enlargement of one, or both posterior communicating arteries which then go to supply the region of the posterior cerebral arteries which are abnormally small; (*E*) doubling of the superior cerebellar artery; (*F*) partial doubling of the basilar artery; (*G*) common trunk giving off the anterior, and posterior inferior cerebellar arteries from the basilar; (*H*) common trunk giving off these two arteries from a vertebral artery; (*I*) small size of one vertebral artery with corresponding large size of the opposite artery; (*K*) large size of a vertebral artery before giving off the posterior inferior cerebellar artery.

Fig. 3. Anomalous arrangements of arteries shown by Cases 2000, 2004, 2057 and 2063.

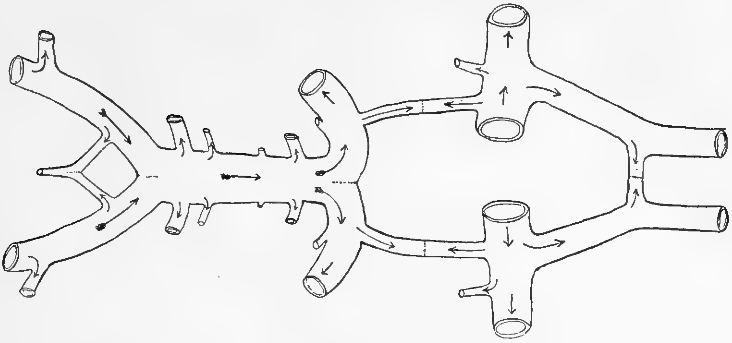


Fig. 1.

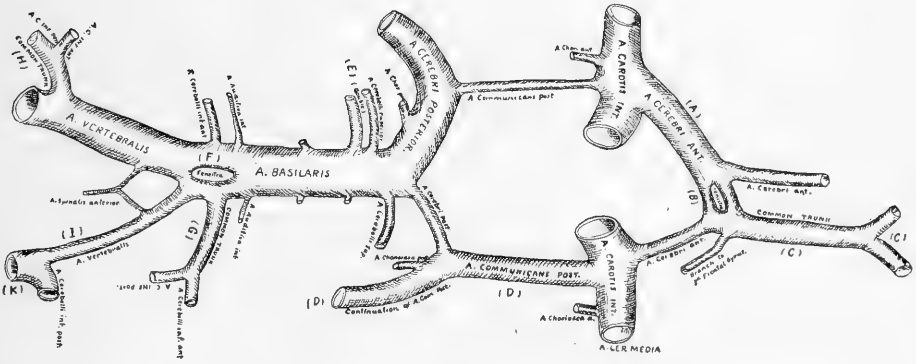
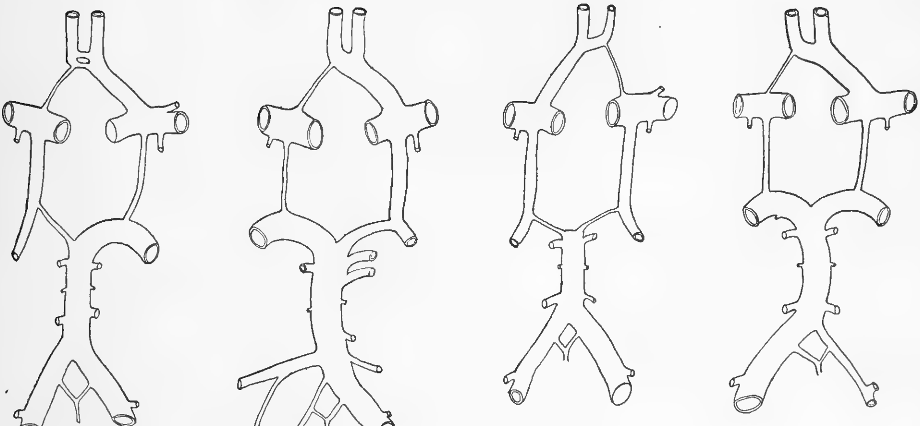


Fig. 2.



No. 2000.

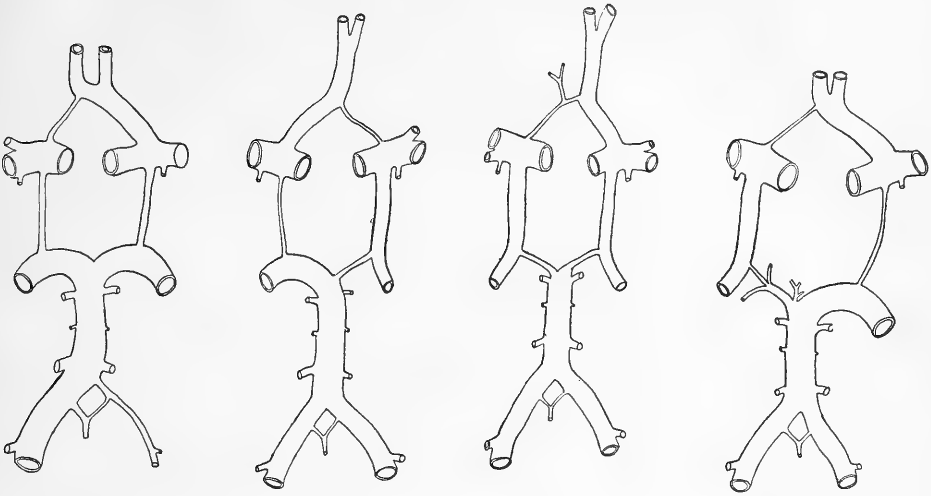
No. 2004.

No. 2057.

No. 2063.

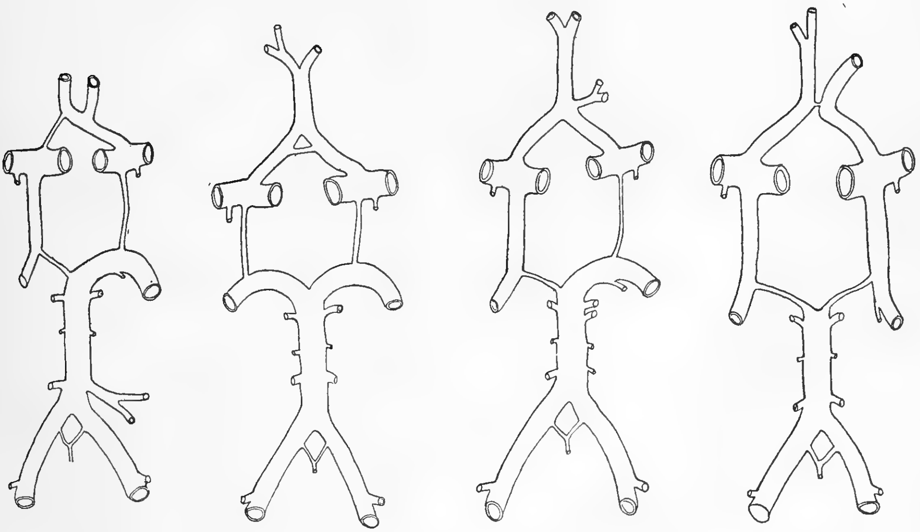
Fig. 3.

Fig. 4. Anomalous arrangements of arteries shown by Cases 2066, 2073, 2077 and 2099.
Fig. 5. Anomalous arrangements of arteries shown by Cases 2137, 2139, 2141 and 2153.



No. 2066. No. 2073. No. 2077. No. 2099.

Fig. 4.

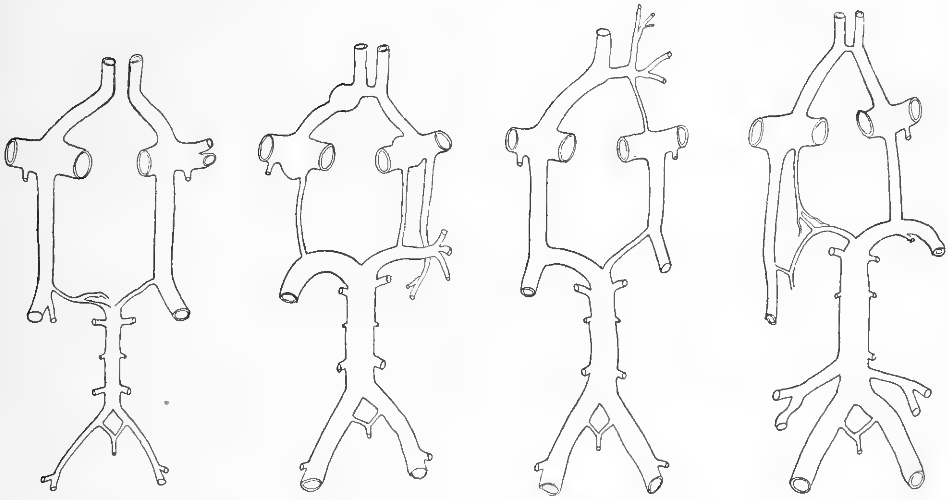


No. 2137. No. 2139. No. 2141. No. 2153.

Fig. 5.

Fig. 6. Anomalous arrangements of arteries shown by Cases 2159, 2163, 2169 and 2177.

Fig. 7. Case 1926. Semidiagrammatic sketch of the circle of Willis viewed from the left, partly in profile, showing the point of origin of the anomalous branch from the internal carotid artery and its junction with the basilar. By the origin of the basilar branches it will be seen that the basilar artery is represented by three portions which have been designated upper, middle, and lower portions, and that the vessel is very irregular in caliber owing to the junction with the abnormal branch, and the unusual origin of the cerebellar arteries.



No. 2159. No. 2163. No. 2169. No. 2177.

FIG. 6.

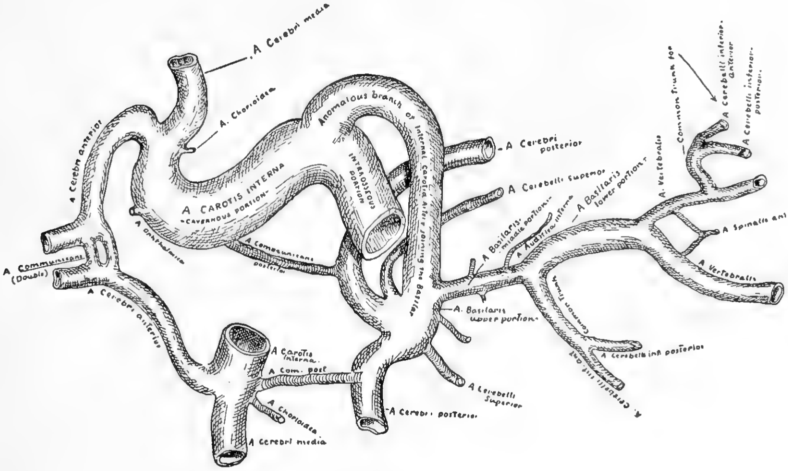


FIG. 7.

Fig. 8. No. 1926. Diagram of the cerebral arteries viewed from above, as they lie at the base of the skull. The cavernous portions of the carotid arteries are exposed, and the dotted line shows the position of the anomalous carotid branch.

Fig. 9. No. 1926. Diagram of the arrangement of the arteries of the base of the brain in Case 1926, viewed from below as they lie on the brain. The point of origin of the anomalous branch and its junction with the basilar artery are shown.

Fig. 10. Case 1909. Thrombotic softening of the left hemicerebrum from a thrombus, situated in the intracranial portion of the left carotid artery; the anterior communicating artery and the posterior cerebral artery of the same side being small, partly obstructed by arterio-sclerosis, and insufficient to maintain the circulation. Thrombosis of the right carotid would not have so resulted on account of the large size of the posterior cerebral and the normal size of the posterior communicating artery.

Fig. 11. Case 1954. Set of cerebral arteries showing almost all of the common anomalies, with their compensatory relationships. 1, The anterior communicating is large and modified by enlargement of the left anterior cerebral; 2, left anterior cerebral large, right small; 3, both posterior communicating large, corresponding post cerebral arteries small, especially the right; 4, left superior cerebellar artery double; 5, right vertebral artery small, and the posterior inferior cerebellar receives nearly all of the blood brought by the vertebral; 6, left vertebral artery as large as the basilar. An aneurism on the right middle cerebral artery at the origin of its principal branches.

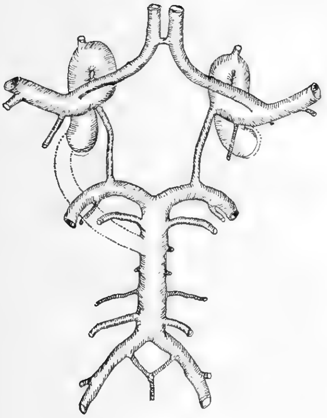


FIG. 8

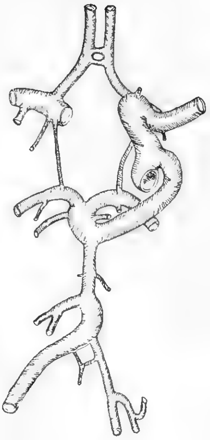


FIG. 9.

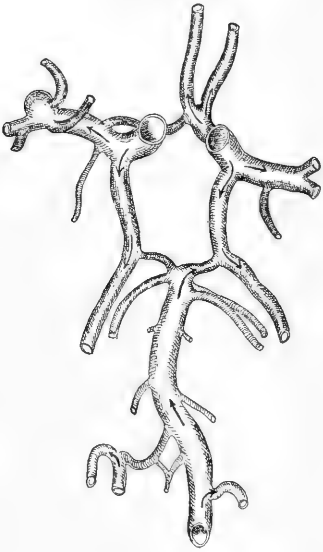


FIG. 11.

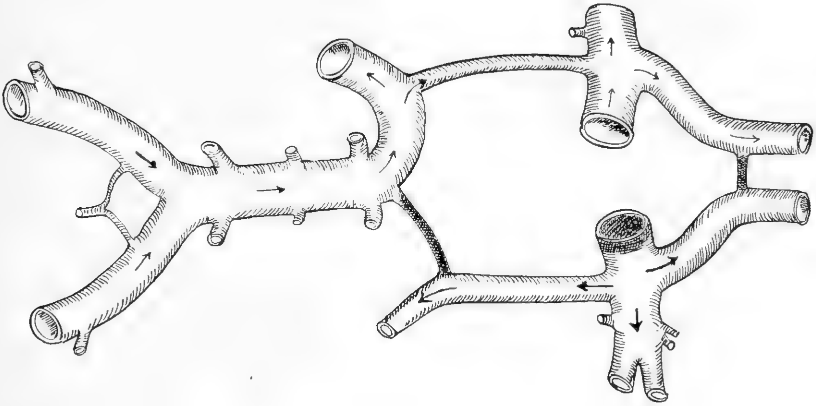


FIG. 10.

# EDITORIAL.

## PROFESSOR GOLGI ON THE DOCTRINE OF THE NEURONE.

The address delivered by Professor GOLGI on the occasion of his reception of the NOBEL prize, which was printed in full in *Archivio di Fisiologia* for March of this year, is of more than passing interest to neurologists, physiologists and psychologists. As is well known, the discoverer of the method of silver impregnation of nervous tissue was led to conclusions regarding the structure of the nervous elements which are widely at variance from those reached by the majority of the able students who have followed him in the use of his own methods.

The neurone theory, as built up by the labors of HIS, FOREL, CAJAL, VAN GEHUCHTEN and others and formulated by WALDEYER, has dominated all recent work in neurology, both in morphology and in physiology. And now we are again inquiring how far this dogma was accepted uncritically because of its illuminating simplicity and how far it is adequate as a basal concept. With still newer methods we are reaching still different points of view. We therefore welcome this review by Professor GOLGI of the whole problem of the neurone doctrine, containing the fully matured opinions of his ripest years.

Professor GOLGI insists first that if the word *neurone* is used at all, it should be applied in the sense proposed by its inventor, WALDEYER, the concept implying, (1) the embryological, (2) the anatomical, and (3) the physiological, independence of the nerve unit. He brings out evidence in vertebrates for a continuous network of nervous processes, as opposed to their anatomical independence and also opposed to the doctrine of polarization of the neurone. The existence of the *rete nervosa diffusa* is in fact, as it has been from the beginning, the chief point in Professor GOLGI's consistent opposition to the widely prevalent views based on the neurone theory.

Taking up first the alleged independence of the nerve elements in embryological origin, attention is called to the fact that the classical results of His upon which this teaching is so largely based were reached by the use of ordinary histological methods and that the application of the silver methods reveals a much more complex structure. Besides evidences brought out by the Golgi method of intercellular connections in very early stages, we have the accounts of the pluricellular origin of nerve cells, and of the origin of nerve fibers by cellular concatenation, both of which, if confirmed, would be contrary to the doctrine of the neurone. The results of the most recent studies on nerve regeneration are also interpreted by Professor Golgi in harmony with the conclusion that the embryological independence of neurones is unproved.

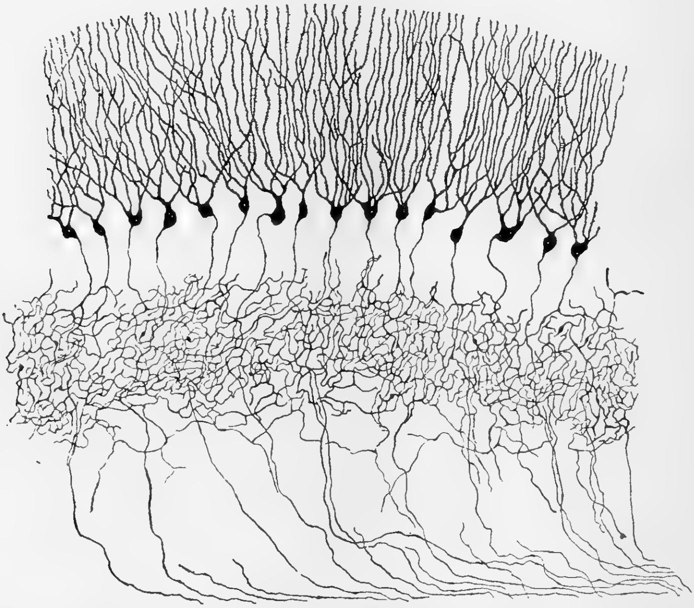


Fig. 1. Structure of the fascia dentata of the hippocampus, as figured by Professor Golgi. From *Archivio di Fisiologia*, vol. 4, fasc. 3, March, 1907, p. 202, by permission of the publishers.

On the question of the cellular independence of the adult neurone the well known views of the author are reaffirmed and reference is again made to the overshadowing importance of the *rete nervosa diffusa* as a morphological and physiological entity, the full import of which other neurologists have been slow to appreciate. This *rete*, which is the most important structure in putting the various elements of the nervous system into functional relationship, GOLGI insists must be regarded as a network whose elements are in protoplasmic continuity. And this, he maintains, is at variance with the fundamental postulate of the neurone doctrine. This matter of terminology is in our opinion of minor significance, but the question of fact involved is of the greatest importance; for the truth of GOLGI's contention is now generally recognized, in so far at least as the recognition of the great importance of the neuropil, or *rete nervosa diffusa.*

Whatever may prove to be the truth regarding the anatomical structure of the neuropil, or *Punktsubstanz*, neurologists are giving more and more attention to it as the medium of interneuronic communication. Indeed it is probable that by far the most important nervous functions take place here rather than in the cell bodies. SHERRINGTON's doctrine of the synapse illustrates the extreme fruitfulness of this conception when applied in concrete physiological problems.

GOLGI maintains that all of our physiological knowledge is opposed to the idea of *physiological independence* of neurones within this reticulum, but that a given *rete* must function more or less as a whole. Such a *rete* is found in the granular layer of the cerebellum and in the deeper layers of the cerebral cortex. In the fascia dentata of the hippocampus we have the mechanism in question in diagrammatic form (see the accompanying figure). Between the cortical cells and the fimbria the fibers break up into a reticulum. "Everything in this relation speaks in favor of the cumulative action of the cells of the whole stratum of the fascia dentata and against any individual action whatever of the cells themselves."

The evidence in favor of the existence and functional importance of such a *rete nervosa diffusa* as Professor GOLGI describes, at least in some parts of the central and peripheral nervous system, is growing. At the same time, whether or not we call the elements which compose this *rete* neurones, it remains true that the conceptions comprised under the term "neurone doctrine" are by no means valueless. The doctrine itself in its original form has been of the greatest assistance in the solution of knotty problems of nervous structure and its usefulness is by no means outgrown, even though the form of the concept may ultimately be greatly modified. Making the best use of all of these aids to research, let us strive to keep an open mind and avoid a slavish devotion to dogma, whether new or old.

## NEUROLOGICAL TERMINOLOGY.

The appearance of Dr. LEWELLYS F. BARKER's manual of Anatomical Terminology[1] suggests some reflections upon a subject which was formerly actively debated, but which has by common consent apparently been left to one side in recent years. A decade ago the editors of this *Journal* remarked (vol. 7, p. 168), "The unification of our nomenclature is to be accomplished, if at all, by a process of survival of the fittest among competing terms at the hands of our working anatomists rather than by legislative enactment. Yet the international discussions now in progress may do much to further this end." In the interval which has elapsed since those words were written anatomists have devoted themselves to the prosecution of research, in America at least, with unparalleled vigor, and, though for the most part silent on questions of anatomical terminology, it is evident that they have not been heedless of them. The American usage has evidently tended more and more to take its departure from the BASLE terms of the Nomenclature Commission of the German Anatomical Society (commonly referred to as the BNA terms), and we are therefore indebted to Dr. BARKER for the publication of their list with vernacular English equivalents in parallel columns. This little manual is almost a necessity on the desk of every anatomist who has not the original German list at hand for ready reference.

To many neurologists the selection of the terms of this list does not seem to have been always happy; but the adoption of the terms in their entirety is not binding on any one and nothing but practical use in the manifold complexity of actual research and didactic conditions can demonstrate which of the terms have actual survival value and which ones will ultimately give way to better ones. It is gratifying to remember, in this connection, that the Basle system is not designed as a finality, but as one stage merely

---

[1] BARKER, LEWELLYS F. Anatomical Terminology, with Special Reference to the [BNA]. With Vocabularies in Latin and English and Illustrations. *Philadelphia, P. Blakiston's Son & Co.* 1907. $1.

in the development of a more uniform nomenclature. Much remains for future revisions, even in the case of the parts enumerated in these tables, to say nothing of future additions to the list. Already a few minor changes have been widely adopted, such as the substitution of dorsal and ventral for posterior and anterior.

The naming of encephalic nuclei and fiber tracts opens new problems in nomenclature, which are assuming large proportions. The tracts should without doubt be named from their termini, the nucleus of origin preceding the terminal nucleus, much as muscles are named; but to make this plan practicable we must have shorter names for many cerebral structures. Thus by common consent the word bulb has supplanted rhombencephalon and medula oblongata as a component of names of fiber tracts connected with this part of the brain.

The most distinctive feature of the BNA neurological terms is the consistent way in which they have been built up on the embryological foundation laid by the researches of Professor HIS upon the development of the human brain. While this is an element of great strength, it is also an element of weakness, even from the standpoint of human neurology. For the natural subdivision of the human brain must be based quite as much on phylogeny as upon its ontogenetic development. And when the application of the terms chosen by Professor HIS to the lower vertebrates is attempted the system breaks down in many parts. The path of the comparative neurologist is peculiarly difficult and it is hoped that at the next revision of the Basle terms the neurological list may be very carefully worked over with this standpoint in mind.

# THE INTERNATIONAL ZOÖLOGICAL CONGRESS.

The seventh International Zoölogical Congress held its meetings in Boston, August 19 to 24. The Congress, as judged by the papers which were offered and the attendance at the meetings, was eminently successful. The program clearly indicates that the interest of biologists at present centers about the problems of heredity and animal behavior.

We present below a list of the neurological papers which were announced on the programs of the various sections, and a report of the meetings of the section of Animal Behavior, which the organizing secretary of the section, Professor H. S. Jennings, has prepared for this *Journal.*

F. E. Botezat Epicelluläre Nervenscheiben in Tastkörperchen.

A. Meyer The Homologies of the Mesial Wall of the Cerebral Hemisphere of Vertebrates.

J. B. Johnston The Phylogenetic History of the Somatic Sensory Column of the Vertebrate Brain.

B. G. Wilder Provisional Phyletic Schema of the Selachian Prosencephal (forebrain).

H. H. Donaldson The Nervous System of the American Leopard Frog, Rana pipiens, Compared with that of the European Frogs, Rana esculenta and Rana temporaria (fusca).

E. H. Dunn Some Neurometric Findings from the Peripheral System of Rana virescens.

R. J. Terry The Morphology of the Pineal Region in Teleosts.

S. P. Gage Changes in Form of the Forebrain of Human Embryos during the First Eight Weeks.

H. W. Norris The Cranial Nerve Components of Amphiuma.

H. F. Nachtrieb Lateral Line System of Polyodon.

F. E. Botezat Localization und Arten der Geschmacksorgane bei Vögeln. Microscopic preparations.

Y. F. Gudernatsch Ueber Geschmacksorgane bei Wassersäugern. Microscopic preparations.

S. Apàthy New Facts and Critical Notes about Neurofibrillæ.

H. V. Neal The Development of the Ventral Nerves in Squalus. Part II. Ventral Cranial Nerves.

C. Van Bambeke Considérations sur la genèse du névraxe, spécielment sur celle observée chez le Pélobate brun (Pelobatis fuscus Wagl.).

R. G. Harrison Outgrowth *versus* Primary Continuity: A Study of the Development of the Nerve Fiber in Living Specimens.

W. M. Smallwood and C. G. Rogers Physiological Studies on Molluscan Nerve Cells.

W. M. Smallwood and C. G. Rogers A Cytological Study of Invertebrate Nerve Cells.

O. Zur Strassen Animal Behavior and Development.

L. Roule L'origine de la notochorde et du neuraxe chez les larves.

B. G. Wilder The Taxonomic Value of the Brain in the Sharks.

B. G. Wilder The Educational Uses of Certain Vertebrates and of Vertebrate Brains.

A. Petrunkevitch Sense of Sight in Spiders.

E. Yung Le sens de l'humide chez les Mollusques.

### THE FOLLOWING DEMONSTRATIONS WERE ANNOUNCED.

R. J. Terry Neuroglia syncytium in a Teleost.

J. F. Gudernatsch (for F. E. Botezat) Epicellular Nerve Disks in Touch Corpuscles.

J. F. Gudernatsch (for F. E. Botezat) Taste-buds in Birds.

J. F. Gudernatsch Organs of Taste in Aquatic Mammals.

W. A. Locy The Nerve Terminals in Selachians.

R. J. Terry Model of Brain of Opsanus (pineal region).

A. Petrunkevitch Images in the Spider's Eyes.
H. F. Nachtrieb Lateral Line System and other Features of Polyodon.
J. Warren Paraphysis and Pineal Region in Necturus maculatus, Lacerta muralis, and Chrysemys marginata.
B. G. Wilder Photographs of Brains.
R. M. Yerkes Apparatus for the Study of Animal Behavior.
R. G. Harrison Preparations Illustrating the Development of the Nerve Fiber.

### ANIMAL BEHAVIOR.

The International Zoölogical Congress had for the first time at its seventh session in Boston a section of Animal Behavior. That the recognition of this subject was justified is shown by the fact that this section was one of those having the fullest program and the best attendance among those of the Congress, as well as by the character of the communications made. The section was in session throughout the entire time set apart for sectional meetings, though this was by no means the case with all of the sections of the Congress. The program, given below, contained many papers which marked real and important advances in our knowledge in this field. Animal behavior is a subject of such popular interest that there is of course danger of its degenerating into dilettantism; of its reverting to the anecdotal and generally unsystematic condition which characterized it some years ago. It is therefore gratifying to note the thorough experimental and analytical character of most of the papers presented. There is nothing in biology which lends itself better to studies of the origin, development, and essential nature of the characteristics of living things than the activities with which the subject of behavior deals; but nowhere else is a thoroughly scientific method more indispensable.

The section of Animal Behavior united with the section of Comparative Physiology for its sectional address, which was given by Professor Jacques Loeb, on the Chemical Character of the Process of Fertilization.

A peculiar feature of the program is the absence from it of any papers by foreign members of the Congress, save in the case of two papers whose authors were not present. This of course shows the prominent part taken by America in developing in a scientific way the field of animal behavior; but the real reason for it is doubtless mainly the fact that the students of animal behavior abroad are largely drawn from among the physiologists and psychologists. It was perhaps too much to hope that these would come so far for a Zoölogical Congress.

The program as presented was as follows:

L. T. Hobhouse The Importance of Animal Psychology for the Theory of Evolution.
E. G. Spaulding Postulates and Results in Treating the Problem of Conduct.
S. J. Holmes The Relation of Behavior to Formative Processes.
T. B. Robertson The Genesis of Protoplasmic Motion.
S. Smith The Educability of Paramœcium.
S. O. Mast Light Reactions in Volvox.
L. J. Cole The Influence of Intensity *versus* Direction of Light in Determining the Direction of Movement of Bipalium and Allolobophora.
C. W. Hargitt Behavior of Tubicolous Organisms.
A. G. Mayer The Annual Swarming of the Atlantic Palolo.
H. S. Jennings Feeding and Defensive Reactions in the Starfish.
H. S. Jennings Features in the Behavior of the Starfish, illustrating the Basis for the Attribution by Older Authors of Intelligence to Lower Animals.
A. L. Herrera On the Comparative Behavior of Insects and Winged Fruits.

V. E. Shelford The Behavior of the Tiger Beetles and its Relation to their Variation and Distribution.
B. G. Wilder Two Contrasted Modes of Feigning Death Adopted by the Same Beetle.
W. B. Herms The Reaction of Sarcophagid Fly Larvæ to Light.
C. H. Turner Do Ants Form "Practical Judgments"?
J. E. Reighard Color Vision, Association, and Warning Color in Coral-Reef Fishes.
J. P. Porter A Comparative Study of Birds with Respect to Intelligence and Imitation.
F. H. Herrick Organization of the Gull Community: a Study of the Communal Life of Birds.
C. S. Berry An Experimental Study of Imitation.
R. M. Yerkes Visual Reactions of the Dancing Mouse.
L. W. Cole Behavior of Raccoons under Experimental Conditions.
B. G. Wilder The Habits of the Coati. Living Animal.
B. G. Wilder Habits of the Domestic Cat not Commonly Recognized or Interpreted.
B. G. Wilder Examples of the Power of Association with the Cat and Dog.
G. V. Hamilton An Experimental Study of an Unusual Type of Reaction in a Dog. Diagrams.

# LITERARY NOTICES.

**Bose, Jagadis Chunder.** Plant Response as a Means of Physiological Investigation. *London, Longmans, Green and Company.* xxxviii + 781 pp. and 287 text figures. 1906.

In an important sense this volume is a continuation of the work which the author presented in 1902 in a book entitled "Response in the Living and the Non-living."[1] As the title of the book which we are now to examine suggests, the writer is interested primarily in physiological research, and the plant serves him merely as a means of approaching certain problems of general physiology which he wishes to investigate. "Plant Response" deals with a large range of facts the greater part of which its author presents as the results of his own researches. It is a book for the general physiologist rather than for the botanist, the zoölogist, the plant or animal physiologist, or the student of behavior. But all of these specialists will find an abundance of interesting material in most of its chapters.

The volume consists of nine parts, which bear the following headings: Part I, Simple Response; Part II, Modification of Response under Various Conditions; Part III, Excitability and Conductivity; Part IV, Multiple and Autonomous Response; Part V, Ascent of Sap; Part VI, Growth; Part VII, Geotropism, Chemotropism, and Galvanotropism; Part VIII, Heliotropism; Part IX, General Survey and Conclusion. Each of the fifty-two chapters, except the last three, which are résumés of the contents of the preceding forty-nine chapters, ends with a brief summary. The reader is thus enabled to get the gist of the author's results, if he so desires, without reading all of the eight hundred pages of the book.

Bose believes in the continuity of response from the inorganic to the organic and he further believes that the responses of plants do not differ in any fundamental way from those of animals. In fact, his book, "Plant Response" is devoted primarily to a defense of the thesis that plant response and animal response are essentially the same.

By the employment of a number of ingeniously contrived instruments, to which unfortunately hybrid Sanskrit-Greek names have been applied, Bose succeeded in demonstrating that plants give definite and immediate motor responses to all forms of stimulation which influence animal tissues. The so-called sensitive plants differ from other plants merely in degree of responsiveness. All plants react to stimuli, but some react more obviously than do others.

As an illustration of the type of method by which Bose was enabled to get graphic records of the form of plant responses I shall briefly describe what he calls the "Optical Pulse-recorder" (p. 7). To the end of a lever of aluminum wire, the fulcrum of which rests on frictionless supports of glass, is attached a thread of cotton silk which is fastened to a motile leaflet by a drop of shellac varnish. The other arm of the lever carries a sliding counterpoise. The fulcrum rod carries a small mirror. A movement of the leaflet causes the lever to move and there is a

---

[1] Longmans, Green and Company. xix + 199 pp. 1902.

rotation of the fulcrum rod and of the mirror. A spot of light which is reflected from the mirror is thereby caused to move. At a distance from the mirror which is determined by the amount of magnification of the plant's movement which he desires to obtain, the experimenter places a revolving drum on which he has arranged a record sheet. As the spot of light moves over this sheet he traces its course with a pen, or if he desires an automatic record he so arranges the mechanism that a photographic record is made by the spot of light. This device in a highly perfected and far more complex form than I have attempted to describe enabled the author to obtain graphic records of extremely slight movements.

In what he calls the "kunchangraph" (from the Sanskrit kunchan = contraction) BOSE has a device which records the contractile response of the plant as the myograph records that of the animal. The optical lever, for so the essential part of the optical pluse-recorder is named, is employed in the kunchangraph.

Largely through the use of the kunchangraph the author obtained the measurements of the responses of a number of plants which constitute the basis for the following conclusions.

"The principal types of response seen in animal tissues are found also in the responses of plants and of inorganic substances.

"Three types of response are possible: (1) that in which response is proportionate to stimulus; (2) that in which response is disproportionately greater than stimulus; and (3) that in which all or part of the stimulus is, for a longer or shorter time, absorbed by the tissue and held latent.

"The subsequent effect of stimulus which is held latent may sometimes be seen in singly ineffective stimulus which becomes effective on repetition; or in the staircase response, consequent on the enhancing of molecular mobility by the partial absorption of previous stimulus.

"The fact that stimulus may be held latent for a time, and subsequently find expression, is strikingly shown in the occurrence of multiple response, in answer to a single strong stimulus.

"It is also possible for the incident stimulus to become divided in its expression, part of it finding an outlet directly in mechanical response, and part becoming latent, and causing accelerated growth. . . ." (p. 128).

I have quoted thus, from the summary of chapter nine, in order to exhibit the kind of conclusions which BOSE formulates in "Plant Response."

Measurements of the velocity of transmission of excitatory waves in plants indicate that the rate varies between .5 and 14 mm. per second in different plants; that the rate is not the same centripetally as centrifugally; that it increases with increasing intensity of stimulus; that fibro-vascular bundles are the best channels of conduction; and that a refractory period is exhibited by plants.

The author presents the results of a study of the effects of anæsthetics, poisons, heat, cold, etc., on the various forms of plant response. Even to summarize his results, as he has stated them, would lead us far beyond the limits of this review notice.

For his investigation of the ascent of sap, BOSE invented the "shoshungraph" (from the Sanskrit, shoshun = suction). It is a mechanism by means of which changes in the amount of suction can be recorded on a revolving drum. As the author states "It consists of (1) an arrangement by which the specimen may be rapidly subjected to the action of different excitatory or depressing agents; (2)

a potometric tube, by which the constant changes of suctional activity are measured; (3) a contrivance by means of which the movements of the water-index with their time relations, are recorded" (p. 364).

In the light of a variety of observations concerning the changes in suctional response which are exhibited by plants under stimulation the author concludes that the ascent of sap is an excitatory phenomenon due to the stimulation of the root by contact with the soil, friction of the growing organ, excessive turgidity, and chemical action.

Similarly, growth is described as a phenomenon of multiple response. All growth movements are the indirect effects of stimulation of the organism.

A microscope recorder was employed by the author in his work on the tropisms of plants. He was thus enabled to obtain graphic records of extremely slight movements. By means of the response-curves which this instrument gave him Bose describes the various tropisms of plants. He states that plants exhibit phototropism, chemotropism, galvanotropism, etc., as do animals, and, further, he insists that the phenomena in the two cases are the same in principle. Again I may quote at length from the text. "Though at first sight it would appear as if there were no connection between the simple responsive curvatures of radial organs and the apparently complicated responsive movements of swimming, yet on closer analysis we shall find that there is little essential difference between the two; for we have seen that growth itself, or growth-curvature, is simply a phenomenon of multiple responsive movements, which, owing to the rapidity of the individual responses, appears continuous. Hence, when, under moderate stimulation, the organ moves toward the light, or exhibits a positive response, this means that the resultant of its multiple movements is towards the stimulus, like the resultant movement of the ciliated organism towards light. Similarly, under strong photic stimulation, the negative heliotropic movement of the organ corresponds to the swimming of the ciliated organism away from the light. In the intermediate case, again, where the stimulated organ shows no resultant curvature, but oscillates about a mean position, we have an instance which is paralleled in the case of the ciliated organism, by alternate swimming backwards and forwards" (p. 695–96).

Critical comments are now in order. I find it extremely difficult to judge of the value of Bose's work. What I most feel the need of is a few hours with him in his laboratory, and the opportunity to observe some of his experiments. His methods certainly are most ingenious, and they appear to have given him very valuable results. However, the reader is impressed with the fact that unless the experimenter was extremely careful at every point in his work serious errors must have appeared in the records. The methods are so delicate that a very slight change in the adjustment of the apparatus must inevitably produce a great change in the record.

The author has worked to prove that plants respond essentially as do animals. At every point he attempts to show that one or another of his conjectures is supported by experimental results. After reading for a time one begins to wonder whether the theory and conjecture and conclusion portion of the book does not weigh too heavily for the demonstrated facts. "One gets such wholesale returns of conjecture out of such a trifling investment of fact" that the experiments come to take a secondary place. It is quite possible that Bose has fully established his points and that the weakness which I have mentioned results from his method of presentation, and not from the nature of his materials. He constantly annoys his reader by making statements which rest upon facts that are presented further on in the discussion. This tends to weaken the work, for it makes the reader feel that after all the book is too largely an attempt to verify surmises.

Whether BOSE's researches are to prove to be important contributions to general physiology further investigation should soon decide. At present they should serve the excellent purposes of stimulating interest in the reactions of plants, and of emphasizing the fact that the range of vital responses is far larger than is usually supposed. If the author's books are accepted immediately as authoritative statements of fact, general physiology may lose more than it gains by them. I am confident that there are few experimentalists in biology who might not profit by the study of BOSE's method of investigation; and it is to be hoped that his books may stir other investigators to attempts to test the truth of his statements.

R. M. Y.

**Watson, John B.** Kinæsthetic and Organic Sensations: Their Rôle in the Reactions of the White Rat to the Maze. *Psychol. Rev., Monogr. Suppl.*, vol. 8, no. 2, May, 1907, 100 pp.

Dr. WATSON's study is an attempt to apply what he calls an "adaptation of an established method to meet new conditions." The established method is the method of extirpating a sense-organ; the new conditions are those involved in the study of the effect of such extirpation upon the learning processes of animals. Briefly, the experiments investigated the consequences of removing the eyes, the middle ears, the olfactory bulbs or the vibrissæ of white rats, or of making their paws anæsthetic, upon their reactions to the Hampton Court maze. As a preliminary to the tests upon operated rats, it was found that rats which had learned the maze in the light could go through it in darkness without error, that untrained rats could learn the maze as readily in the dark as in the light and that emphasizing the tactual and kinæsthetic sensations by making the rats squeeze through holes in wooden blocks at "the entrance to the true pathway at every point where the maze offers a choice of turns" rather delayed than facilitated the learning process. One rat, indeed, made a complete failure of the darkness tests. When the maze was equipped with miniature electric lights so placed as to illuminate the proper openings, this rat did well when the lights were turned on, but could not learn the maze in the dark. Rather than to suppose that he was guided by brightness discrimination, the author prefers to adopt a suggestion of Professor ANGELL's, that the clue was the eye muscle pull established by the tendency to look at the light.

Rats with the eyes removed showed no disturbance in traversing the maze which they had already learned in the normal condition. Nor did untrained rats, similarly operated on, have any difficulty in learning the maze. Rats with the olfactory lobes removed and those with the middle ear removed were likewise normal in their behavior to the maze. Removal of the vibrissæ did disturb the first few performances of rats that had previously learned the maze when normal, but rats without vibrissæ learned it for the first time without difficulty—a curious fact to which we shall refer later. No effect upon either trained or untrained rats was observed from making the paws or the nose anæsthetic. The theory that the rat utilizes "the possible differences in the temperature values to be found at the correct turns versus the incorrect" it was attempted to test by placing at a certain point in the maze a copper plate, which was in some experiments cooled to the freezing point, in others heated to 75° C. In no case did it disturb the rats. Changing the direction of air currents sent through the maze with an electric fan was also without effect. Tests of the rat's sense of taste indicated that it is not delicate enough to be a factor in maze reactions. Very suggestive are the experiments where the rat was put down not at the beginning of the maze but at some point along its course, the results showing that sometimes immediately, sometimes after a certain amount of movement, the rat would get the proper orientation, even if put down with the wrong one, and traverse the remainder of the path without error. The most remarkable results are those obtained when the maze was rotated through an angle of 90°. Both blind and normal rats were decidedly confused by this proceeding, although not a single turn required of them was in any way altered thereby. Dr. WATSON suggests the possibility "either that static sensations have a rôle or else that the rat has some non-human modality of sensation which, whatever it may be, is thrown out of gear temporarily by altering the customary relations to the cardinal points of the compass." When the maze was rotated through 180°, however, blind rats were not disturbed, and there still seems some possibility that further experiments will furnish an explanation involving retinal factors.

Such are the facts resulting from this careful and painstaking investigation. A few considerations in the way of criticism may be briefly appended. The first of these concerns the value of the method. Without sympathizing with any accusations of cruelty, which Dr WATSON's account of the condition of the animals after operation shows to have been unfounded, one has still a certain prejudice against turning a normal animal into an abnormal one, even though the abnormality may seem to be restrained within desired limits. This prejudice might be overcome if the conditions could be altered in no other way. But that such is the fact remains to be proved. The rôle of vision in learning and traversing the maze cannot, Dr. WATSON maintains, be investigated by experiments in darkness because adaptation to darkness may be much more rapid and complete in rats than in human beings. Surely this is merely a question of securing a sufficiently dark room. There is no such thing as adaptation to darkness; there is only adaptation to faint light; and it ought not to be insurmountably difficult to assure oneself of a degree of darkness in which even the rat cannot make *visual* discriminations. Similarly with the tactile and olfactory senses; the experimental conditions can be varied so as to exclude them without operating on the animal.

Again, a certain caution must be observed in making inferences from any experiments thus far designed to study the conditions that influence learning a labyrinth. In the first place, it must be recognized, as Dr. WATSON does recognize, that experiments on an animal that has *previously learned* the labyrinth prove nothing. You do not show, when you show that an animal having learned a maze perfectly is not disturbed by the removal of (say) visual landmarks in its path, that it took no account of the landmarks during the learning process. After it has acquired the habit perfectly, it has become an automaton, and the stimuli originally used as clues have become unnecessary to it. Yet, although Dr. WATSON realizes the force of this consideration, he neglects it in his experiments on the temperature sense. The rats that ignored the hot or cold metal plate were *practiced* rats. Secondly, even if you show that an animal can learn the maze as well in the absence of a given set of stimuli as in their presence, you have not proved that it did not use them while they were operative. Certain of Dr. WATSON's results suggest this possibility. Rats deprived of their vibrissæ learned the maze as well as normal rats. But rats that had previously learned the maze in the normal condition showed some disturbance when the vibrissæ were removed. One might have expected that their reactions would have become too nearly automatic to be affected; but the facts certainly indicate that, although the rats could learn the maze without vibrissæ, they would have used those appendages if they had possessed them.

The author's interpretation of the psychic aspect of the rat's behavior, while sound in its contention that no images or ideas are involved, might, it seems to the present reviewer, go further than it does in pointing out the automatic character of the movements of a practiced animal. Even kinæsthetic sensations and "feelings" are likely to play little or no part when an animal has thoroughly learned a labyrinth, though they may indeed occur when a mistake is made.

A final comment concerns the nature of the records. These are wholly of times, not of paths or of errors. "The time record, carefully controlled, is the only safe guide in estimating the learning process of a maze constructed along the lines of the present one," says Dr. WATSON. It is to be hoped that this statement will not influence other investigators, particularly of animals less active than the rat. Such animals often vary widely in the times they require to traverse a maze that has been perfectly learned and in the course of which no errors are made.

MARGARET FLOY WASHBURN.

**Judd, Charles Hubbard.** Psychology: General Introduction. *New York, Scribner's Sons.* xii + 389 Pp. $1.50. 1907.

This book, as the author states on his title page, is the first volume of "a series of text-books designed to introduce the student to the methods and principles of scientific psychology." The second volume of the series, *A Laboratory Manual of Psychology*, has already appeared; and a third, which is to deal with the equipment of a psychological laboratory, is in preparation.

I shall now present a review of Professor JUDD's *General Introduction to Psychology* which I have based upon the results yielded by the book in connection with a course in psychology which I offered in the Harvard Summer School during the past summer. I am indebted to the twenty-five students who took part in the work of the course for brief and candid statements of opinion concerning the value of the text-book for them.

About eighty per cent of the members of the class felt that the book had given them an eminently satisfactory and profitable introduction to psychology. The remaining members of the class were disappointed, and gave predominantly adverse criticisms.

My own impression, gained from the written exercises and the examinations of the course as well as from the critical statements of the students and my own reading, is that the book gave very satisfactory results with this rather mature and decidedly serious-minded body of students. I feel that I can unhesitatingly and without qualification recommend it for the use of similar classes. Whether it would prove as satisfactory with beginning college students I do not know, and I refuse to make any predictions, for experience has taught me that I have no safe ground for predicting the reaction that a text-book may evoke.

It is especially to be noted that the author devotes one chapter to the evolution of the nervous system (22 pp.), and another to the human nervous system (28 pp.). Both of these chapters will give the neurologist the feeling that their writer was not at home with his materials, for they lack the touch of the master. Nevertheless there can be no doubt that under existing conditions they will prove valuable to the average student. The pity is that the beginner in psychology is not expected to get his neurology from the specialist previous to his study of psychology, instead of being permitted to get a meager, vague, and confused knowledge of the structure and functions of the nervous system from the psychologist. It is not Professor JUDD's fault, however, that psychology is generally taught to students who lack adequate preparation in neurology. In his way, he has undertaken to remedy the evil.

The chapter on the evolution of the nervous system is excellent in plan and defective in form. It needs to be worked over carefully, rearranged, and rewritten. Several statements whose truth is extremely doubtful are to be found. For example on p. 25 we read of the bee, "Individual experience does not modify its modes of behavior, for there is no part of its nervous structure which is left undeveloped at the beginning of its life, to be mapped out in the course of individual contact with the world." And again, on p. 25, the reader may be permitted to doubt whether it was worth while for the author to guess at the kind of consciousness which may be associated with a certain type of nervous system.

The chapter on the human nervous system is devoted largely to a discussion of functions, and the influence of SHERRINGTON's views is everywhere apparent. Fortunately it is a good influence. There is an inexcusable lack of a general description of the chief structural divisions of the nervous system, and of illustrations to make clear the structural relations of those portions of it whose functional significance is considered.

Sensation is dealt with effectively, but affective consciousness receives far less convincing treatment. That the author, like many others of us, is at the beginning of his thinking concerning modes of expression ("experience and expression") is clearly shown by the chapters which he devotes to the subject.

In concluding this fragmentary and inadequate discussion of the book, I wish to say that it appeals to me as an admirable text-book, the work of a teacher whose personality should do much to inspire his students, and whose enthusiasm and good judgment should go a long way toward making psychologists of them.

R. M. Y.

**Herter, Christian A., and Clark, L. Pierce.** Diagnosis of Organic Nervous Diseases. With 109 illustrations. *G. P. Putnam's Sons, New York and London.* 1907.

It always appears to me like a rebuke to the methods of teaching that the student should need a special book summing up the propædeutic knowledge of neurology. Either the introduction of anatomy and physiology or the discussion of the principles of analyses of the facts of observation in the examination of the patient or of autopsy material must be at fault to account for the difficulty of many students in this relatively well differentiated field. The feeling that such a gap exists between the teaching of anatomy and physiology and the teaching of the clinical and post-mortem study of neuropathology was no doubt the origin of the excellent little volume which Doctor HERTER wrote in 1892. Before and since that time a number of similar books have appeared, and many of the text-books of clinical neuropathology have full chapters on this field, and still it is difficult to find just what one would like to put into the hands of a student as a real addition and supplement to the existing works.

Dr. L. P. CLARK has undertaken the task of bringing the second edition up to date. The many excellent features of the first edition are preserved. Indeed the larger part of the work could simply be reprinted. The chief alterations consist in the addition of 49 illustrations, especially in the first chapter on the structure and function of the nervous system, the chapter on the diagnoses of the clinical types, and the wholly rewritten chapter on the examination of the patient.

The anatomical chapter has lost much of its simplicity and is not altogether free of objectionable features. In too many places one feels that the mere translation of nerve-cell into "neuron" is untimely and a decided disadvantage, as in "the neuron exercises a nutritional influence over every portion of its structure," or "groups of neurons . . . . are commonly called centers." Figs. 9, 11 and 12 might have been changed to advantage. Further, the lenticular nucleus is put with the optic thalamus as "of great importance as primary terminals of the great sensory system from the periphery." "All the fibers connecting the periphery with the brain hemispheres pass through the crura cerebri (the olfactory and optic tracts excepted)." The cross section of the cervical cord, Fig. 23, is in two ways a poor substitute of Fig. 19 of the first edition rendering three levels, viz: because thus the very different pictures of the dorsal and lumbar cord are suppressed and because the section is turned so as to be no longer in harmony with the Fig. 28 and several others which follow the better usage of presenting the cord without that sudden turn at the anyhow rather difficult transition into the hind brain. The anatomy of the cerebral segments of the brain stem is much more fully treated than in the former edition. But it is not very happily done and not sufficiently harmonious. For instance, the auditory apparatus is represented in Fig. 47 in a very schematic manner. This correct but not sufficiently explained figure is supplemented in Fig. 48 by a second sketch attributed to STARR, which represents the auditory fibers as forming the mesial fillet. From the first edition Fig. 55 is taken over giving quite a wrong idea of the domain of the posterior cerebral artery. All in all the first chapter, which has grown from 68 to 83 pages, should rather have gained in simplicity or might have been given so that it would facilitate the later parts and invite cross-reference. It is too difficult for the student and not sufficiently correct.

The chapter on the diagnoses of clinical types has received a number of illustrations, and as mentioned above, the chapter on examination of the patients is treated especially fully. But after Fig. 79 (p. 590) a renumbering of the figures begins from "Fig. 48" to "Fig. 78," an oversight which the proofreader should not have allowed to pass.

In a third edition somewhat more attention might be given to facilitation of survey of contents. The book contains many excellent helps, but it is too compact for continued reading and not quite easily subdivided for quick reference. The recent book of STEWART, while not as good and full in many special topics, gives the student a greater feeling of ease.

A. M.