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THE STRUCTURE OF THE TELEOSTEAN AND SELACHIAN BRAIN

BY

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With Sixteen Plates

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HISTORICAL NOTE.

Even the earliest researches on the brains of fishes, as done by Willis, Collins, Camper, von Haller, Monro and Vicq d'Azyr, treated of the homologies of the different parts of these brains with the brains of mammals, especially man. These investigators, working with the teleosts as a rule on account of their greater accessibility, found great difficulty in interpreting the fore-brain centers, the ependymal parts of which were not yet known, until after RABL RÜCKHARD's discovery. Some of the authors considered the solid lobes or hemispheres as corpus striatum, and TIEDEMANN and ARSAKY correctly considered the lobi optici as homologous with the corpora quadrigemina of mammals.

The majority of the others, however, struck by the resemblance of the roof of the optic lobes to the hemispheres of young mammals, considered them to be the hemispheres, interpreting the lobi anteriores as the olfactory lobes. It was especially CUVIER who several times expressed this opinion, which after him was accepted by WEBER, KUHL, TREVIRANUS (in his first publication), FENNER and VALENCIENNES. SERRES, however, studying the embryology of the brain accepted ARSAKY's and TIEDEMANN's interpretation and so did MAGENDIE and DESMOULINS. The other interpretation, however, was not overcome by their work, and the injury done by CUVIER's errors is clearly shown by GÖTTSCHE's work, who agreed in considering the optic lobes as the hemispheres, and consequently the torus longitudinalis as fornix and the valvula cerebelli as the corpora quadrigemina.

VON BAER, again reviewing GÖTTSCHE's statements, declared the torus longitudinalis to be a structure peculiar to the mid-brain roof of fishes and made a general division of the brain into fore-brain, 'tween-brain, mid-brain, hind-brain and after-brain, which is still current. He, JOHANNES MÜLLER, WAGNER and STANNIUS contributed very much to the exact knowledge of the central and peripheral nervous system in different groups of fishes.

A great technical impetus was given by HANNOVER, who in 1844 introduced chromic acid for staining purposes, and by HEINRICH MÜLLER, who in 1859 introduced the chrome salts, especially the bichromate of potash, which afterward, combined with WEIGERT's staining method, created a new era in neurological work.

Almost all workers, however, in the first years after HANNOVER dealt with the macroscopic aspect of the brain and peripheral nerves. The work of BUSCH, KLAATSCH, CARUS and MAYER conformed to the opinions of ARSAKY, SERRES and VON BAER.

On the other hand, HOLLARD defended the interpretations of CUVIER and GÖTTSCHE. So, comparing the lemniscus fibers which came from the optic tectum with the corona radiata in the fore-brain of man, he accordingly called the lobi inferiores, corpora striata, thus consummating the earlier errors, which, however, were surpassed by MIKLUCHO-MACLAY, who not only doubted the homology of the fore-brain, but even considered the cerebellum of fishes to be the homologue of the mid-brain of higher vertebrates, considering a dorsal enlargement of the oblongata to be the cerebellum.

Happily his opinion was only defended by GEGENBAUR; neither HUXLEY, BALFOUR nor SANDERS in England, nor WILDER in America, accepting this interpretation, which was also rejected by VIAULT and ROHON, to whom we owe good descriptions of the brain of the selachians. Now, while BELLONCI's work on the course of the optic tracts and those by EHLERS and CATTIE on the pineal gland settled forever the identification of the mid-brain roof, our knowledge of the fiber tracts was greatly enlarged by FRITSCH and MAYSER, whose excellent works are even yet studied by every one who investigates this subject.

They, however, did not give a good explanation of the fore-brain of fishes, which we owe to RABL-RÜCKHARD. As already stated, the great difficulty until now had been the solid structure of the anterior lobes, in which no pallium could be distinguished from a striatum. Although STIEDA had already regarded the median fissure between the anterior lobes as a ventriculus communis whose lateral walls he found covered with ependyma, even he did not find the dorsal covering of this ventricle, which was discovered by RABL-RÜCKHARD who applied the principle already given by REICHERT that a mere ependymal membrane can be the pro-stadium of a thickened nervous wall; and he found that the pallium of the teleosts is such a membrane which does not contain nervous substances in these fishes but in other animals becomes the center for important fiber tracts.

This discovery of RABL-RÜCKHARD gave rise to the question whether the whole pallium is here represented by membrane as EDINGER and JOHNSTON believe, or whether the basal lobes themselves contain parts which in other animals are situated in the mantle, as C. L. HERRICK maintained. This author, although granting that the pallium itself is only represented as an ependymal membrane, maintains that the basal lobes contain regions which physiologically have the same functions as certain pallial regions of mammals. So he speaks of a hippocampal lobe, a cuneus, a corpus callosum and other parts.

HALLER does not go as far as HERRICK did and only declared that he had been convinced by his researches that in the basal lobes of the teleosts there is included a region which in the selachians is situated in the pallium itself.

Besides these authors, who wholly or partly drew their conclusions from the microscopic structure of the gray substance and the course of the fiber tracts, there were BURCKHARDT and STUDNICKA, who worked out the question from a morphological standpoint. BURCKHARDT'S considerations originate in KUPFFER'S discovery of the so-called lobus olfactorius impar, a recess which was considered by this author as the anterior neuroporus. Now, BURCKHARDT calls that part of the fore-brain roof which extends from the anterior neuropore to the paraphysis and laterally from one nervous mass to the other the "lamina supraneuroporica." The extent of this ependymal membrane is the criterion for the degree in which the pallium has become a nervous mass. Now, according to the degree in which the lamina supraneuroporica persists, he classifies the fishes in this order: Teleosts; Ganoids; among the selachians, Notidanidæ, Holocephali, Spinacidæ, Carchariidæ, and finally the group to which belong Myliobates, Zygæna and Trygon, where almost the whole lamina supraneuroporica has become a thickened nervous mass. Among these fishes, the teleosts and ganoids should have no thickened nervous pallium, while in the ascending series of the selachians, a nervous pallium already occurs in the Notidanidæ and becomes larger in the other forms.

STUDNICKA, in contrast with the other authors, does not consider the ependymal roof of the fore-brain as a real pallium but rather as a tela choroidea, a continuation of the roof of the third ventricle, which, accordingly, in the ganoids would extend to the olfactory bulb, because the roof of the olfactory bulb, as appears from the investigations of RABL-RÜCKHARD and others, is ependymal. The real pallium of the cyclostomes and ganoids would be represented in these fishes by the lateral parts of the anterior lobes in a more or less degree.

In his further publications on this subject STUDNICKA confirms his original opinion that the lateral parts of the anterior lobes of the fishes just mentioned are to be reckoned with the pallium, and even speaking of the teleosts he says (1896), "Ich selbst bin der Meinung, dass da keine Gründe bestehen, um eine vollständige Homologie leugnen zu müssen: Wie die Hemisphaeren (Lobi post. derselben) der Ganoiden, sind auch die der Teleostier nach aussen umgestülpt." He asserts that what EDINGER calls the epistriatum in these fishes contains a pallial region, and so, morphologically and embryologically, he comes to the same results to which HERRICK and HALLER came by their histological researches and to which STUDNICKA also refers in his last publication on this subject.

I have thought it necessary to point out this question here because it has dominated and still dominates the whole fore-brain problem and is of fundamental interest. From this historical sketch it appears that almost all the problems have arisen from the different interpretations of the fore-brain, which for many centuries before RABL-RÜCKHARD's discovery of the pallium was misunderstood, and which in turn caused all kinds of misinterpretations of the more caudal parts of the brain.

The new question now current regarding the anterior lobes which has been raised by RABL-RÜCKHARD, BURCKHARDT and STUDNICKA morphologically, and by EDINGER, HALLER, C. L. HERRICK and JOHNSTON histologically, will be treated again after I have communicated my own results. It will be unnecessary to review here the history of the microscopical structure. The opinions of my predecessors will be mentioned in connection with each part.

TECHNICAL NOTE.

Before I started my researches upon the brains of fishes I examined a human oblongata and mid-brain to get some first-hand knowledge of the structure of that part of our own brain. The serial sections of this material, after fixation in MÜLLER's fluid, were stained by VAN GIESON's method, an excellent method for general purposes, especially for the study of heavily medullated tracts and the structure of the gray substance.

For my researches on the brains of the different fishes examined I made use of PAL's modification of WEIGERT's method, which I prefer to WEIGERT's original method as it enables us to use a good contrast coloring. I tried all kinds of contrast stains, of which Mayer's paracarmin appears to me to be preferable to other cell stains as it takes less time than other carmins and the stain is stronger. The paracarmin coloring is preferable to that by any anilin stain on account of its permanence.

Finally some supplemenatry preparations have been made of the brains of teleosts and selachians by Bielchowsky's method and Ramón y Cajal's new alcohol-ammonia-silver method, which are great acquisitions for the investigation of fiber tracts. Bielchowsky's method was applied, among others, to a brain which had been for more than a year in formalin of 10 per cent. and gave the most beautiful results for the unmedullated tracts, while the medullated are pretty clear for orientation by reason of their brown color. I made celloidin sections of it and even applied it to a series of celloidin sections fixed to the slide by means of a celloidin film. This goes very well provided the whole section is everywhere fixed to the slide with no free edges or wrinkles, for the silver precipitates in the wrinkles and between the glass and the celloidin where it is not fast to the slide to such a degree sometimes that the neighboring sections wholly fail of impregnation. This is a beautiful illustration of the behavior of silver in histological technic—that it precipitates in small spaces, either natural or artificial. Another thing to remember when applying Bielchowsky's method in celloidin is to extract as little formalin as possible from the embedded piece before and after embedding. Accordingly, it is impossible to keep a celloidin-embedded block in alcohol in the customary way. The formalin is extracted from it in a few days and the preparations do not succeed well. For keeping the celloidin block Apathy's method of enveloping the whole block in gelatin to prevent its becoming too hard is good. I preferred, however, to keep the block in 80 per cent. alcohol with 10 per cent. formalin. I made no paraffin sections by this method, but after my celloidin experience I fully trust Bielchowsky's statement that this is quite possible.

In studying the following pages the reader is recommended to make frequent reference to the figures—not only the sections figured on Plates I to VII, but also the diagrams on Plates VIII to XVI, which are designed to summarize the several chapters.

CHAPTER I.

THE FORE-BRAIN, PROSENCEPHALON OR TELENCEPHALON.

1. The Fore-brain of the Teleosts.

The structure of the secondary fore-brain of the teleosts is characterized by its simplicity as compared with that of the selachians. Indeed, as we know from RABL-RÜCKHARD'S investigations, the pallium merely consists of a thin ependymal membrane, from which it follows that we do not find here the complications appearing in the selachians from the development of tracts and centers in the mantle itself.

If, however, in the lateral parts of the anterior lobes covered by the pallium, there are hidden none of the nervous parts which in higher vertebrates are situated in the pallium, as STUDNICKA and MAYER maintain for the cyclostomes (but recently contested by JOHNSTON), a second question arises which may be treated quite differently. HALLER and HERRICK consider these parts to contain cortical areas, while EDINGER is of the opposite opinion. I shall have to recur to this matter after having described the fore-brain and 'tween-brain of the fishes which I have examined and compared them with the selachians.

If for the study of the external structure we consider the telencephalon of Lophius as it appears in a series of transverse sections, we find far in front (Fig. i, Plate I) immediately over the NN. optici the lobi olfactorii, which in Lophius are short and compact but in Gadus (Fig. vii, Plate I) are very long. These lobi olfactorii anteriores consist dorsally of an ependymal membrane and over them part of the lobi cerebrales projects, as EDINGER states for Barbus fluviatilis and as is also mentioned by C. L. HERRICK: "the cerebrum overlaps the olfactory dorsally."

Farther back the aspect alters in such a way that against these masses first described a new mass appears, in Lophius (Fig. ii) dorso-laterally; in Gadus (Fig. vii) more ventro-laterally, with the pallium attached along the exact line of union between the two masses. This line, as described by others, is always obvious (Figs. iii, iv, v, vi, viii, ix, x), on account of the presence of a sinus and of the attachment of the pallium, which is always visible here (BELLONCI, Macropodus viridiauratus; C. L. HERRICK, Haploidonotus grunniens). It may be termed the *sinus rhinalis*, or probably better, the *fovea limbica*. The lateral mass will be called the *lobus olfactorius posterior*, or *area olfactoria posterior lateralis*. Still farther back the striatum itself exhibits a more important dorso-median enlargement and accordingly occupies a higher position than the lateral mass, which in consequence is depressed in a lateral direction in such a way that the configuration in Lophius becomes exactly the same as in Gadus (*cf.* Figs. iv, v and vi with Figs. viii and ix). The morphologic distinction between these two parts will be demonstrated later by the description of the different tracts with which they are in connection.

These parts may be distinguished more clearly than in the smaller fishes in Gadus morrhua, where the difference in the courses of the various olfactory fibers is very apparent (Fig. vii). BELLONCI has sharply distinguished them as *lateral* and *medial tracts*, and they were also carefully examined by C. L. HERRICK, EDINGER and HAMILTON and GOLDSTEIN.

While the medial tractus olfactorius runs caudad nearly in the original direction, the lateral one deviates more and more to the side and, situated in the sinus rhinalis, or fovea limbica, runs to the *area olfactoria posterior lateralis*, as Professor EDINGER, Dr. GOLDSTEIN and I in conference have decided to call this part of the fore-brain in the future. BELLONCI called the place where the outer thinner olfactory tract ends, "corteccia del emisfero," and C. L. HERRICK characteristically called it "hippocampal lobe" because it seemed to be the physiological homologue of the lobus hippocampi of higher vertebrates. Since, however, the latter names suggest a more developed cerebrum than this area exhibits, we choose the name first mentioned and likewise prefer to call the tract just described the *lateral olfactory radix* instead of *tractus bulbo-corticalis*.

The way by which the lateral fibers reach this point is not always so short as it has been described for Gadus. Dr. GOLDSTEIN showed in his paper on the fore-brain and 'tween-brain that in the fishes which he examined these lateral fibers cross through the commissura anterior and then end in the area olfactoria posterior lateralis of the opposite side, which I am able to confirm for the greater part of these fibers in Salmo salar, preparations of which have been given to me by Professor RUDOLF BURCKHARDT, to whom I am greatly indebted for his kindness. In an adult

Thynnus and some other adult Lophius, however, I again found the uncrossed tract, so that we must assume that both occur and that probably the uncrossed course of the lateral fibers is the more general one, as it has been described by BELLONCI, EDINGER and C. L. HERRICK. It would be interesting to find out the conditions which determined this different behavior.

In following the course of the medial olfactory fibers we see that they soon divide into two parts (Lophius, Gadus, Salmo, Thynnus). The part farthest medial in Gadus is the smaller and more heavily medullated; the other farther lateral is somewhat larger, but less medullated. They are but slightly separated when they enter the cerebrum and both run parallel to the median fissure, the medial somewhat lower than the lateral. Before they reach the commissura anterior (Fig. ix) they are farther separated and from this point pursue quite different courses.

The larger less heavily medullated fasciculus of the medial olfactory tract decussates—at least partly—earlier than the smaller more heavily medullated fasciculus. The decussation of the latter fibers, moreover, takes place at a somewhat higher level, though originally they lay lower. The greater part of these last fibers terminate after the decussation more laterally and in many fishes seem to end in the area olfactoria posterior lateralis, as GOLDSTEIN describes, which again I can confirm for Salmo, but not for the other fishes which I have examined. In the others the fibers do not reach so far as the lateral area but end in the medial part of the fore-brain, directly adjacent to the terminus of the less heavily medullated fasciculus which crosses before and under this decussation. The region where these medial olfactory fibers end will be termed the *area olfactoria posterior medialis*, or *epistriatum*, as it is designated on the plates, a name, however, which Professor EDINGER, GOLDSTEIN and I have thought better to give up.

Accordingly, the secondary olfactory connections in the forebrain of teleosts can assume two forms which are represented in the diagrams on Plates VIII and IX. The two secondary olfactory centers form probably one region that lies on the lateral and caudo-dorsal side of the striatum and of which in some fishes, like Salmo, the lateral connections are better developed and in others the medio-caudal. Together they cover a part of the striatum, whose highest part, accordingly, overhangs the olfactory lobes.

From the medio-caudal secondary olfactory center a median tract of fibers arises, chiefly medullated, and goes backward along the median fissure of the thalamus to end without decussation (Gadus, Lophius, Salmo and Thynnus) in the hypothalamus directly in front of the nucleus rotundus. Some of its fibers may go into this nucleus, as BELLONCI describes, which I could not make out, since no GOLGI preparations have been made. At first I got the impression that this tract contains also a great many secondary olfactory fibers and thus constitutes a direct connection between the lobus olfactorius anterior and the lobi inferiores, an opinion, however, which I no longer hold so firmly since my investigations have been extended to a larger number of teleosts. But still it may be possible that this tract, which according to JOHNSTON, is present in Petromyzon (tr. lobo-epistriaticus, JOHNSTON), in the teleosts contains some direct connections with the anterior olfactory lobe, as BELLONCI and after him EDINGER described. This tract for which I choose the name *tr. olfacto-lobaris medialis*, or *tr. olfacto-hypothalamicus medialis*, has been well known for many years having first been described by BELLONCI in Anguilla as a direct connection between the nuclei rotundi and the olfactory bulbs.

In EDINGER'S work of 1887 he stated that in Corvina the only medullated tract of the commissura anterior extends in the direction of the 'tween-brain, and in his "Vorlesungen" he says, "Es ist wahrscheinlich dass bei den Fischen Fasern von der Olfactorius-schenkel der Commissura anterior rückwärts in den Hypothalamus ziehen." And OSBORN, C. L. HERRICK (fornix) HALLER and CATOIS all treat of this connection; however, there is no certainty about its secondary or tertiary character. On further examination of more material I get the same impression as GOLDSTEIN, that this tract begins chiefly if not wholly without decussation in the area olfactoria medialis, or epistriatum, and that the decussating fibers of the region where it begins do not belong to this tract but to those secondary medial olfactory fibers that end where the tractus olfacto-hypothalamicus begins.

There are two other tertiary olfactory tracts connecting the lateral part of the area olfactoria posterior with the thalamencephalon. The first of these is the *tractus olfacto-lobaris lateralis*, or *tractus olfacto-hypothalamicus lateralis*, a compact large tract of unmedullated fibers that gather from the area olfactoria posterior lateralis and extend backward, always lying at a higher level than the tractus strio-thalamicus, of which I shall have occasion to treat later. This bundle ends after decussation in the post-infundibular region of the diencephalon in the neighborhood of the ventriculus lobi inferioris partly under the ventricle, and has never before been described in the teleostean brain, unless perhaps by C. L. HERRICK as the "dorsal peduncle." JOHNSTON observed a similar connection in the ganoids, as mentioned in 1898 in his first publication on the brain of Acipenser, where it is present as two bundles, a more medial and a more lateral one, of which one has a more ventral and the other a more dorsal course. He did not, however, observe a decussation of the fibers. That such a tertiary lateral olfactory connection is present in all fishes appears, moreover, from the fact that this author describes it in Petromyzon also as "gathering from the lateral expansions of the fore-brain and ending in all parts of the inferior lobes." Its exact course in the 'tween-brain I shall take up in the second chapter.

The third tertiary olfactory connection originates in almost the same region but more ventrally and in a smaller group of cells which lie in the area posterior lateralis and have been designated *nucleus tæniæ.* The neurones of this nucleus have medullated fibers which run mingled with the tr. olfacto-hypothalamicus lateralis, but separate from it where they pass under the ganglia habenulæ of the thalamus. The medullated fibers go into the ganglia habenulæ, where they end in the opposite ganglion for the most part, constituting in this way a part of the habenular commissure, while the olfacto-hypothalamicus fibers run farther backward without giving off fibers to these ganglia. This tract is the *tractus olfacto-habenularis,* first described by EDINGER in fishes and afterward recognized in all lower vertebrates (Acipenser, JOHNSTON).

The *commissura anterior* (Fig. x) too, must be regarded as belonging to the olfactory system. The greater part of its fibers I have already mentioned in the description of the medial olfactory tract, whose feebly medullated decussating fibers form its foremost part, while the decussating fibers of the more heavily medullated medial olfactory bundle (some of whose fibers perhaps run backward with the tr. olfacto-hypothalamicus medialis while the greater part end more laterally) form the more medullated part of the commissure in Gadus just as it has been described by

Belloncı for Macropodus and Anguilla. Regarding the relations of the last-mentioned part of the commissure, which he calls the "chiasma olfattoria," this author says that it is situated "subito sopra ed indietro la commissura trasversa olfattoria"; by which name he denotes the foremost part which I described above.

It should be added here that in some fishes the structure of the commissure differs from that of Gadus, Lophius and Thynnus. Thus it has been stated by Goldstein that fibers of the lateral olfactory tract form a part of it, as I can confirm for Salmo salar, as stated above. These, however, are not all the component parts of this commissure. In Gadus and Lophius there are between and under these two parts unmedullated fibers originating from the area where the medial olfactory fibers end and the medial hypothalamus bundle begins, and in Salmo there are a great many fibers that connect the back parts of the medial secondary olfactory lobe, as was first described by C. L. Herrick under the name of hippocampal commissure and as Dr. Goldstein confirms for many fresh water fishes. I have seen the same in Salmo.

Finally I have to mention some fibers of which it is difficult to say whether they originate from the medial olfactory area (epistriatum) or from the striatum. These fibers also form a bilateral connection and do not enter one of the longitudinal tracts. The difficulty in establishing the real origin of the last-mentioned fibers does not lie in the fibers themselves, which are very distinct, but in the determination of the boundaries of the different regions of the fore-brain, which must be distinguished mainly by their connections, since in most of the fishes examined the shape of the cells, though varying greatly, is scarcely typical for the different parts, for different types of cells occur in almost every region.

We have now defined two important parts of the lobi anteriores, the *area olfactoria posterior lateralis* and the *area olfactoria medialis*, or *epistriatum*, terminal centers of secondary olfactory tracts and centers of origin for the caudal attachments. Another not less important part of the anterior lobe, however, is formed by the *striatum* mentioned above. This cell mass is bounded latero-ventrally by the area olfactoria posterior lateralis and latero-caudo-dorsally by the area olfactoria medialis. From this relation it appears that the striatum itself is for the most part free on the upper side and constitutes the highest point of the lobi anteriores.

Now, from the striatum there originates the important bundle of the teleostean fore-brain, the *tractus basalis*, also called *tractus strio-thalamicus* or *pedunculus cerebri* (Figs. vii, viii, ix, x and xi, Plate I). The origin of this large tract extends as far forward as the striatum itself, *i. e.*, the beginning of it is visible in cross sections in that part of the lobi anteriores which projects dorsally over the tracti olfactorii before they have yet entered the cerebrum (Fig. vii).

Besides the areas mentioned above which are situated outward and backward from the striatum, the striatum is enveloped medially by a large layer (*area parolfactoria*) of a tissue which seems to contain no ganglion-cells and through which the medial olfactory fibers take their course. Thus the striatum itself remains clearly recognizable both by its richness in ganglion cells and by its large masses of fibers. The latter originate (or terminate) dorsally both before and behind and, converging medio-basi-caudad, run without decussation backward into the lateral portion of the 'tween-brain, where they terminate in the lobi inferiores under and probably in the nucleus rotundus. The great extent of the striatum and the tract which originates from it at its widest part appears in Figs. viii and ix, in which we also see quite clearly the line of union between its area and that of the area parolfactoria and the area olfactoria posterior lateralis.

I cannot decide whether we are to consider the tractus strio-thalamicus as a single or a double tract. The latter opinion might be confirmed by the fact that in the codfish one part of this tract is rather strongly medullated and another part unmedullated. With the methods which I have employed I cannot arrive at a complete certainty on this question, which of late has been generally answered in favor of a centripetal and a centrifugal tract.

Caudad, all the fibers of the tractus strio-thalamicus unite, in part entering between the lateral and medial olfactory centers, and form a compact bundle that runs along the median fissure of the præthalamus and thalamus below the level of the tertiary olfactory connections with the hypothalamus. Its connections in the lobi inferiores will be described in the second chapter.

2. *The Fore-brain of the Selachians.*

The fore-brain of the selachians is distinguished from that of the teleosts especially by the development of nervous elements in the pallium. The degree of this development, however, varies with the species examined. While the Rajidæ, as well as Pristiurus and Lamna, have a pallium so extremely developed as even to obliterate completely the ventricles which are so enormously spacious in the teleosts, the Holocephali and Notidanidæ have large fore-brain cavities, whose pallial covering remains for quite considerable part still membranous, as appears from the description given by WILDER of Chimæra monstrosa, and especially from the excellent comparative investigations made by BURCKHARDT. The fore-brain of the Notidanids (Heptanchus, for instance) is nearly the same as far as this point is concerned as that of Chimæra, in whose pallium it is the lateral parts chiefly which have developed such nervous masses. The selachians, Galeus canis and Angelus squatina, whose fiber tracts I have examined, present a pallium whose thickness surpasses the breadth of the ventricles. This is especially the case with Angelus squatina, in which respect I quite agree with BOTAZZI.

In this selachian the relations of the lateral ventricles are very simple as shown by Fig. xii, *a* to *f*, and there is no ventricle in the lobi olfactorii. This is not the case with Galeus canis (Fig. xiii, *a* to *l*), as also described by HOUSER (who names this species Mustelus canis). HOUSER has already mentioned that, although the lateral ventricles are small here, they show, in addition to their olfactory evaginations, also a small dorsal evagination which he calls the *diverticulum dorsale*, an unobjectionable name which I adopt. The presence of this ventricle brings it about that the lateral ventricle of Galeus, midway of its length, presents at the same place two evaginations (Fig. xiii, *h*), one rather large extending into the lobi olfactorii, and the other smaller going dorsad only a short way, the diverticulum dorsale. The lateral ventricle continues as a narrow fissure and terminates far forward, after having (between *f* and *c*) expanded, due to the fact that here (Figs. xiii, *d;* and xvii) there terminates a medial protrusion of its wall, about which I shall speak later.

Since it is impossible to distinguish the different areas of the fore-brain of Galeus morphologically, as in the teleosts, I proceed at once to treat of the tracts and groups of cells, whose description I shall illustrate with the pictures which Galeus canis gives, which are a great deal clearer and more easy to control than those of Angelus squatina.

Starting with the olfactory fibers, which have been studied by BOTAZZI, in Mustelus, I can confirm his assertion that these tracts, which in the lobus olfactorius itself lie directly adjacent to the ventricle, spread out in the fore-brain, both dorsad and ventrad. The greater part of them, however, go in a more dorsal direction. They end on the same side in that part of the brain which is situated in the direct continuation of the olfactory lobes—*area olfactoria posterior.* A decussation of these fiber tracts, however general in other animals, is scarcely important in the selachians. The highly developed decussatio inter-hemispherica seems to contain no direct olfactory fibers, in which I quite agree with BOTAZZI, ROMANO, HOUSER and CATOIS, and the commissura anterior is in Galeus comparatively poorly developed, and gets its fibers from other secondary regions. I even doubt whether in Galeus it contains any direct ventral olfactory tracts, which in Mustelus also, according to BOTAZZI, are only few.

The region where the olfactory fibers end forms a large part of the fore-brain situated dorso-laterally, characterized by rather large cells (Fig. xvii, Plate I), which are continued farther forward (*nucleus olfactorius dorsalis*) than the insertion of the lobi olfactorii, thus forming an elongated layer in the whole anterior half of the prosencephalon (see Plate X).

From this extensive region a tract arises broadly and runs to the dorsal median line, where it finally decussates with the corresponding tract of the opposite side, and then terminates in two places. The smaller part remains after the decussation medial to the ventricle, where it terminates in a group of small disperse cells (Fig. xviii) by which the ventricle is here compressed to a fissure (*cf.* Fig. xvii with the following figures). I consider this region equivalent to the *regio uncinata* described by BOTAZZI in Mustelus, with which it agrees in situation and which he also observed to be connected at least partially with the above-mentioned decussation.

However, as I have said, by far the smaller part of these fibers terminate in this region. The greater part, after the decussation, incline over the roof of the lateral ventricle and end much farther distally in small bundles in a group of cells situated laterally of the ventricle. Figs. xx and xxi clearly show this termination of the decussatio inter-hemispherica, which may also be called *tractus olfacto-epistriaticus cruciatus*. We find, moreover, in the latter region the termination of uncrossed fibers which likewise originate from the area olfactoria posterior, the *tractus olfacto-epistriaticus homolateralis*. For this part of the fore-brain, which surely belongs to the olfactorium but cannot be reckoned with the area olfactoria posterior itself, I choose the name *epistriatum*, in connection with which I will say no more, however, than that it has an olfactory character and is situated in the immediate neighborhood of the striatum. The precise character of this region depends on the nature of the crossed and uncrossed tracts described. The uncrossed tract originates, as I have said, in the same nucleus where the decussating tract begins and about the latter there is some difference of opinion.

ROMANO, who described this decussation in Scyllium, considered it as a commissure between cortical olfactory centers, which in my type could be the case only if we ascribe cortical functions also to what I call the epistriatum. BOTAZZI also, who described the decussation before ROMANO and justly called it a decussation and not a commissure, does not believe that it presents direct olfactory tracts, whose decussation he observed only in the commissura anterior. Both consider the decussation as a functional analogue of the corpus callosum, which, however, cannot be under any circumstances, if, as EDINGER maintains, we are to consider the callosum as connecting non-olfactory cortical layers with each other. CATOIS describes them as, "fibres affectées à la voie olfactive," as to which there can be no doubt, and he justly considers them as psalterium rather than as callosum, as they are decidedly connections of the olfactory parts of the pallium. As for me, I think they must be considered as decussated connections between the area olfactoria posterior and another olfactory center which is probably a more distal continuation of the more frontal center. As was first described in the teleosts by C. L. HERRICK and since confirmed by Dr. GOLDSTEIN for many fresh water fishes and by me for Salmo salar, we find here a bilateral connection of the area olfactoria posterior lateralis, an area which in these fishes has not so enormous a fronto-distal extent as in selachians.

If the teleosts have a vestige of a nervous pallium, this certainly is to be found in the place where C. L. HERRICK sought it and STUDNICKA supposed it to be, and in the selachians the bilateral connection of that part might have come to lie in a more dorsal position with the enormous development of the pallium. This interpretation of the decussation is the more probable, as the commissura anterior itself, which in teleosts includes this commissure, is poorly developed in Galeus and in Angelus squatina in comparison with their large olfactory centers; and it will appear still more probable after I have described the caudal connections of the secondary olfactory region of the sharks in comparison with the tractus olfacto-hypothalamicus medialis and lateralis of the teleosts.

In the same dorso-lateral region in which the decussatio inter-hemispherica originates there also arises a large medullated bundle which BOTAZZI in his first publication calls fasciculus cortico-medialis. This name he afterward altered to that which EDINGER had already given to the same tract, viz., *median bundle*, and then applied the name fasc. cortico-medialis to a tract which he had originally described as fasc. cortico-medialis centralis. As I also prefer to retain the usual nomenclature, I name this bundle as EDINGER did.

The median bundle has a fan-shaped origin of large extent in the lateral sub-cortical layer and runs toward the median line over that portion of the decussatio inter-hemispherica which has already crossed and under the part of this decussation which has not yet crossed, as clearly appears in Figs. xviii and xix, Plate I. Then it runs obliquely downward between the two lateral ventricles to the brain floor, where a portion of it again bends laterally, thus constituting a connection between the superior and inferior parts of the fore-brain, as BOTAZZI supposed, while another part of the fibers joins the tractus strio-thalamicus with which they go to the hypothalamus. This bundle does not decussate, either in the decussatio inter-hemispherica or in the commissura anterior. This can be stated positively; and, moreover, BOTAZZI himself, who did not consider a decussation of some of its fibers impossible, writes that he found it impossible to adduce much evidence for this.

Parallel with this bundle there is a second one, first described by BOTAZZI, who called it, *tractus cortico-medialis*, or tractus sagittalis, the first of these names being the one which I shall adopt. This unmedullated tract is not very compact, but large, as shown in Fig. xxii, which shows that it constitutes a connection between the dorsal and ventral layers of the fore-brain, running medially through its posterior part.

The dorsal group of cells where this tract originates is, however, merely a median local enlargement of an important dorsal mass of rather large cells, which, more distally, lies in the upper layers of the lateral part of the pallium. In this region there originates an important tract, *the tractus pallii*, which EDINGER has already described. It lies immediately under the dorsal surface of the brain and is gradually made up of short groups of fibers which come perpendicularly from the depths, as shown by Figs. xxi and xxii. This flat but large bundle then goes on the outer surface of the fore-brain toward its base, where, however, it always remains lateral to the tractus strio-thalamicus, which is still to be described. A decussation of the pallial bundle takes place in the 'tween-brain and will be treated in the next chapter.

So, then, we have become acquainted with the following groups of cells in the dorsal and lateral regions of the fore-brain:

1. The *area olfactoria posterior*, which lies in the lateral part of the fore-brain and must be regarded as the terminus of the secondary olfactory tracts. As a special enlargement of this region there lies dorsally:

2. The *nucleus olfactorius dorsalis*, from which originate the decussatio inter-hemispherica and the tractus medianus.

3. More ventro-laterally situated we found the ending of the decussatio inter-hemispherica in a group of cells which also receives an uncrossed bundle from the same region where the decussatio inter-hemispherica originates. The terminal nucleus of these tracts I have called the *epistriatum*, by which is indicated its situation directly adjacent to the striatum and the fact that it belongs to the olfactory centers.

4. The region where a part of the decussatio inter-hemispherica terminates has already been described by BOTAZZI in Mustelus; it forms the fourth dorsal group of cells, the *regio uncinata*, by which the ventricle is partially obliterated.

5. A more important dorsal center is the place where there originate medially the tractus cortico-medialis and laterally the tractus pallii and which may be called the *nucleus dorsalis pallii.*

Passing now to the basal region of the fore-brain, two groups of cells and their attachments remain to be described.

6. One group of cells, the *striatum*, lies behind and under the epistriatum. From this group the fibers of the tr. strio-thalamicus arise (Fig. xxii), at first a large mass of fibers with many cells between and becoming more compact behind and medially and then uniting with a part of the fasc. medianus in a single extensive bundle. Where they unite (Figs. xxiii and xxiv) fibers of one side pass to the other (commissura anterior), which, however, I do not regard as a decussation of the fibers of the tr. strio-thalamicus. The latter ends wholly uncrossed in the hypothalamus, as will be described in the second chapter.

7. Finally, there is a group of cells which is really the only one very accurately known. It lies in the medio-basal part of the distal fore-brain. It is the nucleus post-olfactorius, or *nucleus tæniæ*, which HOUSER has so accurately described. From it there originates a bundle of medullated fibers (Fig. xxii), which runs over the basal tract (Figs. xxiii, xxiv, xxv) and afterward terminates in the most anterior nuclei of the ganglia habenulæ. I prefer to retain the name, nucleus tæniæ, given by EDINGER, who has pointed out that this nucleus has a constant position in all vertebrates; moreover the giving of new names can only cause confusion.

BOTAZZI does not mention this *tractus olfacto-habenularis*, but it is obvious that he describes this bundle as a root of the tr. strio-thalamicus. I think that he likewise described the tr. olfacto-epistriaticus homolateralis as a part of the basal bundle.[1]

Now, a few words more about the commissura anterior, whose constituent parts are far less easily examined than in the teleosts, and a part of which, called by HERRICK the hippocampal commissure, I think, is represented in the decussatio inter-hemispherica of the selachians. The commissura anterior itself is, as I have already stated, for this reason not so strongly developed in the selachians. It is possible, but not probable, that it contains a part of the ventral olfactory fibers, though certainly this part is very small, especially as compared with the strong development of

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[1] As the insertion of the lobi olfactorii is so much more basal in the selachians which BOTAZZI figures than in Galeus canis, it can be easily understood that because of the basal situation of the basal bundle in BOTAZZI's specimens he failed to recognize it and described it as a part of the tr. strio-thalamicus.

the olfactory lobes. Surely most fibers of the commissura anterior arise from the epistriatum and the striatum. Further investigations are necessary to clear up this important question.

In regard to the peripheral nerve fibers connected with the fore-brain of the selachians, I should mention that I did not succeed in finding the cerebral center of LOCY's nerve, which nerve Professor JOHNSTON kindly demonstrated to me in some selachians during my last stay in Naples, and which has been regarded by ERNST DE VRIES as the analogue of the nervus vomeronasalis in man.

CHAPTER II.

'TWEEN-BRAIN, DIENCEPHALON OR THALAMENCEPHALON.

1. The 'Tween-brain of the Teleosts.

The 'tween-brain is considered to extend from the hind part of the lobi anteriores, which have been described, to what is generally called the tectum opticum, or more properly, to the commissure which lies immediately before it, the so-called commissura posterior, as the dorsal caudal limit, and ventrally to and including the lobi inferiores, which lie much farther caudad. Accordingly, the base of the 'tween-brain has a much greater fronto-caudal extent than the roof. Besides this difference in length there is another more important difference in the development of the nervous mass, in that, while the base and lateral walls of the 'tween-brain are rich in tracts and nuclei, the roof is formed almost exclusively of ependymal tissue folded in various ways.

The fronto-caudal sequence of these evaginations and invaginations in Lophius is as follows: First, there is an important invagination with many secondary inward projections, the plexus choroideus of the third ventricle, from which originates in higher vertebrates the choroidal plexus of the lateral ventricles of the fore-brain. Then follows a part whose lateral walls extend higher and whose roof also contains nervous elements called the *epithalamus*, consisting of the *ganglia habenulæ* with their commissura habenularis. (In this species neither paraphysis nor velum transversum were clearly to be found.) Behind this part the dorsal wall becomes thinner and terminates in the foot of the *epiphysis cerebri*, which passes over by means of a thin roof plate into the region of the commissura posterior. This roof plate, which is for only a small part nervous, is in front somewhat overlapped by the back part of the lobi anteriores, and latero-dorso-caudally by the roof of the mid-brain, the tectum opticum, which is so strongly developed in fishes and especially the bony fishes.

The highly developed tractus opticus, which has already decussated, extends ventro-laterally along almost the entire length of the walls of the 'tween-brain (Figs. xxvi, xxvii, xxviii, Plate II). The ventral wall with its excrescences, the lobi inferiores, extends a great deal farther backward, as appears in Figs. xxix to xxxiii, which show these excrescences still present under the mid-brain at the level of the oculomotorius and trochlearis. This enormous development of the thalamus base, or *hypothalamus*, is to be attributed to the numerous tracts and nuclei situated within it, among which there are some in the back part of the lobi inferiores which are probably to be considered as homologous with nuclei of the mid-brain of the higher vertebrates.

Now, proceeding to the description of these tracts and nuclei, I shall demonstrate them from preparations of Gadus morrhua (*cf.* Figs. 4 and 5, on Plates XI and XII).

In the first place I shall take up that part of the thalamus which immediately follows the fore-brain, the *præthalamus* of C. L. HERRICK. Before describing the attachments between the fore-brain and the parts caudad of it I must mention a flat, high, medially situated nucleus of large cells found in Lophius (Fig. xxvi) and Gadus (Fig. xxxiv), which was known to MAYSER and VAN GEHUCHTEN, but extensively treated and figured by C. L. HERRICK as the *nucleus præopticus*, a name which I propose to retain. As it is exactly at the border of the fore-brain and 'tween-brain, it was called nucleus posterior of the fore-brain (thalamic part) by HALLER who, as well as MAYSER, was of the opinion that some optic fibers ended there. C. L. HERRICK describes its cells as very large, which agrees with what I found. Further, he mentions that probably the nucleus forms one whole with a similar post-optic nucleus and that from there some fibers originate going latero-ventrally; but then he says, "The function and nature of these highly specialized cells is unknown." These cells have likewise been described for the ganoids, both by GORONOWITSCH, who gives several pictures of them, and by JOHNSTON who describes their situation in the recessus præopticus but reckons them to the nucleus tæniæ because he saw fibers going from them to the ganglia habenulæ. I call especial attention to the literary notices upon this point because I wonder that so eminent an investigator as EDINGER does not mention this nucleus in the fishes, where its existence and situation are so evident.[1]

As for the fibers which pass out from this nucleus obliquely downward and laterally (Figs. xxxiv to xxxviii) as C. L. HERRICK has described them, I can confirm in the teleosts JOHNSTON'S observation for Acipenser, that, curving backward at the brain floor, they run down parallel to the tr. strio-thalamicus and reach the anterior part of the infundibulum, the *tuber cinereum*[2] (Fig. xxxviii). I think that I could name this bundle, which JOHNSTON does not designate by a special name, most simply as *tractus præthalamo-cinereus.*

Now, having described this præthalamic nucleus and the tract belonging to it, I may take up the bundles coming from the fore-brain, of which I have already described in a broad way the *tr. olfacto-lobaris* (*or hypothalamicus*) *medialis*, when treating of the fore-brain, and mentioned the literature on the subject. It is seen again in Fig. xxxiv *et seq.* and in Fig. xliv we see it reach its terminus in and under the nucleus rotundus while turning mesad around it.

Along with this tertiary olfactory tract I must take up the second olfacto-hypothalamic attachment mentioned in the first chapter as the *tractus olfacto-lobaris* (*or olfacto-hypothalamicus*) *lateralis.* Though so much has been written about the course of fibers in this region, especially about the tractus strio-thalamicus, in the teleosts, I have never found this tract mentioned except perhaps by C. L. HERRICK, who divides the "peduncles," as he calls the tracts in this part of the thalamus, into two parts, a dorsal and a ventral peduncle. The ventral peduncle is the tractus strio-thalamicus, while the dorsal originates from the caudo-lateral

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[1] He may have described it as "nucleus magnocellularis strati grisei" in the reptiles; also as "high small nucleus of large cells lying by the side of the wall of the ventricle," though somewhat more caudad.

After I had already written these pages EDINGER told me that my supposition was right. GOLDSTEIN mentions the same nucleus in his work on the fore-brain and 'tween-brain of the teleosts and gives it the same name which EDINGER used for the reptiles.

[2] C. L. HERRICK may have described this attachment with the tuber cinereum as tract. tub. cin. ad com. ventralis.

part of the brain and ends in the hypothalamus, a course similar to that of the *tractus olfacto-lobaris lateralis*. This tract is collected from almost the same region where the tractus olfacto-habenularis originates, but from a more extensive area. Its unmedullated fibers go into the most dorsal part of the lateral wall of the præthalamus. That it should then give off fibers for the anterior part of the corpus geniculatam laterale, as HERRICK supposes, I think not probable for Gadus. Thereupon it runs with little inclination ventrad so that after a short distance it meets the *tr. olfacto-lobaris medialis*, which it almost entirely enwraps (Fig. xl). Since, however, the latter terminates in the lobi inferiores before the former, this afterward passes on alone and ends (Figs. xlv, xlvi) after decussation in the posterior part of those lobes partially under their ventricles. This might be the same tract which HALLER describes as a pallial part of the tractus strio-thalamicus which also decussates in the hypothalamus.

Among the olfactory connections I have still to treat of the *tractus olfacto-habenularis* which was also mentioned in the first chapter. This bundle consists of medullated fibers of much smaller caliber than those of the tr. olfacto-lobaris lateralis, in company with which it originates, though in a somewhat more ventral area. It runs along the dorso-lateral side of the latter tract and at once upon reaching the epithalamus, where it is situated immediately adjacent to the tectum opticum which here covers the epithalamus dorso-laterally, it enters the most anterior and dorsal ganglion of the ganglia habenulæ, joining the commissura habenularis (Figs. xxvii and xlii) which connects the ganglia. The area olfactoria posterior lateralis, being situated at about the same height as these ganglia and being quite near to them on account of its inclination backward, this tract is very short, which perhaps is the reason that some authors meet with great difficulty in finding it.

Thus the olfactory areas of the fore-brain are connected by one tract with the epithalamus and by two with the lobi inferiores.

The most ventral part of the præthalamus contains the fibers originating from the striatum and going to the lobi inferiores, the *tractus strio-thalamicus*, known now for many years. This large feebly medullated bundle passes backward laterally from the tractus præthalamo-cinereus and under the tracts last described almost in a straight line under the corpus geniculatum laterale.

In this neighborhood, according to GOLDSTEIN, it gives some fibers to the nucleus thalami anterior; this, however, I cannot confirm in the material which I have examined. The tractus then more and more assumes a circular outline on transverse section, a point which also struck HERRICK. Directly laterally of it there is a group of cells that can be followed backward up to a point a little before the nucleus rotundus (nucleus prærotundus, see below). Here, however, no fibers end, though perhaps they give off collaterals (Figs. xliii, xliv), since the thickness of the tract remains the same during this part of its course. Medially and at first a little above it there are here the two tractus olfacto-lobares, which now soon turn ventrally to their endings. Then the tractus strio-thalamicus of each side bends at a sharp angle in a lateral direction and ends (Figs. xlviii, il, Plate III) in the back part of the lobi inferiores laterally under and probably in the nucleus rotundus proprius (see below). In Gadus, where these points are very clear, one can easily be convinced that the fibers end here. VAN GEHUCHTEN writes that he has observed in GOLGI preparations that its fibers extend farther backward through the midbrain into the medulla oblongata, which, however, I must decidedly contradict as far as Gadus is concerned.

Having now treated of the tracts which at least in part run through the præthalamus, I can pass to one of the more difficult parts of the 'tween-brain: the *post-optic commissures.* There is a great variety of opinion regarding the commissures and decussations of the 'tween-brain, differences, which are partly caused by the confusion of nomenclature, partly undoubtedly by differences in the animals described. For the moment passing over the commissura horizontalis, I shall give a condensed account of the literature of the other commissures, after which I shall describe these as they are found in the fishes which I have examined, together with the course of the nervi optici.

Following the example of his predecessors FRITSCH called the most ventral commissure of the præinfundibular part of the 'tween-brain com. transversa or com. of GUDDEN, and he thought he saw in it a direct opticus decussation, an opinion which was rectified some years later by MAYSER. Both of them described as its end-nucleus the so-called stratum zonale (antero-lateral part) of the tori semicirculares. BELLONCI called this commissure, com. of GUDDEN or com. inferior and he, too, found its end-nucleus in the medial bilateral elevations in the floor of the optic ventricle (in this case the more caudal part of it). He also denied that optic fibers are contained within it. Moreover BELLONCI described as fibræ ansulatæ a crossing of disperse heavily medullated fibers situated above his com. inferior, which he saw to end under the roof of the lobi optici. EDINGER, who does not describe the teleosts in his "Zwischenhirn," mentions in his "Vorlesungen" a decussatio supra-optica ventralis and dorsalis and a commissura ansulata and further mentions for the teleosts also a decussatio tuberis, the latter as a connection between the ganglia anteriora thalami of both sides. Of the first decussation he says that it extends between the end of the caudal mid-brain and thalamus ganglia, while the second would have a similar course (at least in reptiles and birds) and the third (mentioned by him only for the reptiles) perhaps is connected with the fasc. longitudinalis dorsalis.

C. L. HERRICK, who, as I have seen by my own investigations, describes the 'tween-brain excellently, divides the com. transversa of authors (com. inf., dec. supra-optica ventralis) into two fiber groups, the lower one of which he calls com. ventralis, the upper com. transversa. He considers them to be morphologically one, as shown by their relation to the opticus system, and by the fact that he finds that both end partly in the corpus geniculatum laterale and partly farther backward in his colliculus (the torus semicircularis of most investigators). Now, I agree in considering his first two commissures as one and add that he mentions a second commissure of this præinfundibular region, the commissura minor, a small compact system of fibers crossing directly under the ventriculus tertius and ending where the opticus passes into the tectum (as EDINGER also represents the decussatio supra-optica dorsalis of Gobio fluviatilis).

In this area CATOIS also distinguishes two commissural systems, of which, however, according to his opinion, the first connects the corpora ecto-mammillaria as com. post-chiasmatica (which GOLDSTEIN confirms) and the other is the com. transversa of authors of whose fibers a small part ends in a separate group of cells (probably my nucleus prærotundus) situated before and lateral to the nucleus rotundus, while the greater part ends in the tectum opticum itself. Finally I must mention that KRAUSE finds the com. transversa ending in the stratum zonale of the tori semicirculares and that by experimental investigation he definitely proved the opinion, already generally accepted, that this commissure does not contain opticus fibers.

Since I am to describe the nervus opticus of Gadus morrhua, I shall describe the commissures also as they are in the cod. It was, of course, impossible to represent on the drawings the total decussation of the *nervi optici* (typical for all teleosts—RAMÓN Y CAJAL) which, in Gadus, takes place about 0.75 cm. in front of the lobi anteriores. As will be noticed from the drawings of the opticus where it runs under the fore-brain, the two optici are different in my subject. The right nervus opticus is smaller and evidently degenerated and somewhat atrophied and did not take so good a WEIGERT stain as the left one. This enabled me to examine the relations of the opticus more accurately than under normal conditions, thus controlling and confirming in most respects the experimental investigations of KRAUSE.

As many figures of serial sections greatly facilitate the description and comprehension of the subject, I shall make free use of the figures in treating of the præinfundibular region. In Fig. xi (Plate I) we see the formation of a part of the commissura transversa, viz., the most ventral part, probably the part designated by C. L. HERRICK as com. ventralis. A little more caudad (Fig. xxxiv, Plate II) the number of these commissural fibers is considerably increased and we see fibers situated higher up directed toward the median line.

While the lower fibers of the com. transversa do not in any way touch the bundles of opticus fibers, either proximally or caudally, the upper commissural fibers are seen to be applied to the inner side of the opticus next to the fibræ tectales optici, and to keep that place for some distance, which no doubt led the older investigators to consider them as decussating opticus fibers. That this is not the case I, like KRAUSE, could easily determine by the difference in color of the two optic tracts. The decussating fibers all have the same color and never penetrate more deeply between the opticus bundles. In sections of this region taken somewhat farther caudad (Fig. xxxvi) this is seen clearly. Moreover by this means it is easy to be more sure that there is no difference whatever either in color or in development of the fibers in the commissura transversa. This commissure does not contain any direct optic decussation, on which I can confirm the opinion of MAYSER, BELLONCI, HERRICK, EDINGER, KRAUSE and CATOIS. In the section taken somewhat farther caudad (Fig. xxxvii) we observe the ascending and descending loops of the commissura transversa, the lower loop as a compact whole, the other higher up as a few distinct bundles of which the most lateral are quite near to the n. opticus.

Here at the left, directly frontal to the corpus geniculatum laterale, the optic nerve begins to divide into two parts, one more lateral, the other more medial. (HERRICK calls them the cephalic and caudal; KRAUSE the ventral and the medial; MAYSER and BELLONCI the foremost and the hindmost or the upper and the lower roots.)

These, however, do not contain all of the opticus fibers. Immediately under the fissure of the ventricle in the median line a small bundle of opticus fibers has separated from the rest (Figs. x, xi, xxxiv, xxxv). In Fig. xxv they are situated over the uppermost decussating fibers of the commissura transversa. (Shown only on the left of the figure. The tract on the right side escaped the notice of the artist from the fact that it is colorless in the preparation.) In Fig. xxxvi they (together with a few fibræ ansulatæ to be mentioned later) join without decussation the commissura minor HERRICK, to be described later, and disappear at the outer side of the tectum opticum (Fig. xxxviii). MAYSER has already observed this small medial bundle, but does not say anything about its destination, nor could KRAUSE reach any certainty as to the character of these fibers. However, I can quite confirm BELLONCI's statement that ultimately they join the other opticus fibers. In Rhodeus amarus, where as I suppose EDINGER illustrates without naming them, they seem to advance far less deeply into the thalamus.

Proceeding caudad and observing chiefly the right half of the 'tween-brain and mid-brain roof, we see (Figs. xl, xli) far dorsad and lying obliquely in the middle of the scarcely colored optic tracts the highly developed strongly medullated *brachium laterale tecti.* This tract originates from the tectum opticum and terminates in the corpus geniculatum laterale (Fig. xlii), and not being degenerated contrasts clearly in the field of the degenerated opticus fibers, while on the left side it cannot be distinguished. On the left side, however, where the fibers are not so compact (Fig. xxxix) the much smaller *brachium mediale tecti* is much better seen as a distinct attachment between the corpus geniculatum laterale and the medial wall.

Meanwhile the fibers of a small but compact and rather heavily medullated commissure which lies close under the wall of the ventricle (Fig. xxxvi) pass upward and laterally where they enter the tectum near the corpus geniculatum laterale. This is HERRICK's commissura minor, which, as already observed, is accompanied by the medial opticus fibers and some fibræ ansulatæ. This commissure EDINGER, GOLDSTEIN and I have agreed to name in honor of the excellent American neurologist, HERRICK's commissure. It may be that it terminates in small part in the ganglion into which a few of the opticus fibers seem to enter, but by far the greater part passes under the brachium laterale through the upper layer of the tectum opticum. Accordingly, there is no doubt whatever that this commissure terminates for the greater part, if not wholly, in the tectum opticum. Moreover HERRICK, who first gave a description of this connection, observes that he lost sight of it at the point where the lateral optic radix enters the tectum.

The reason for the much greater size of the brachium laterale tecti as compared with the brachium mediale appears in the sections farther caudad. The brachium laterale extends in two branches over the whole dorso-lateral tectum; the dorsal branch is the one that first becomes visible in frontal sections, and from the same stem a latero-ventral branch is given off which may be seen along the right half of the tectum far posterior. Presently it disappears under the faintly colored fibers of the ventral opticus bundle which passes laterally over the tectum and with which it runs into the most caudo-lateral part of the mid-brain roof (Figs. xliii to xlvi). In these last sections we see the loops of the commissura transversa, now completely united, which end partly in the accumulation of cells under the optic ventricle (*nucleus corticalis = nucleus dorsalis thalami* of GOLDSTEIN), partly in the *nucleus prærotundus*, of which we spoke before.

In many authors whose works I have read for my investigations I have often wished to have a more systematic reproduction of the sections themselves rather than a very extended text. I have preferred giving many illustrations of this complicated region instead of presenting a description which, of course, would have to be very complicated and which could not present what the section itself gives. However, I will not neglect giving a short survey of the course of the different systems of the præinfundibular part of the thalamus, beginning with the nervus opticus.

After the total decussation of the nervi optici (which takes place in Gadus about three-quarters of a centimeter before the lobi anteriores, but in Lophius, Thynnus, Salmo and most bony fishes under the caudal part of the fore-brain and the anterior part of the 'tween-brain) they send a small bundle mesad immediately under the fissure-like ventricle and over the commissura transversa. For a short distance these medial bundles maintain this relation and then (without decussating again) join the commissure of HERRICK and so enter the most superficial layer of the tectum opticum, possibly having in the meantime given off collaterals to the ganglion geniculatum, in which, however, no fibers end directly. The chief group of the optic fibers runs laterally and upward from the thalamus and divides just in front of the corpus geniculatum into two paths.

I must mention here a very small group of strongly medullated fibers which persist diffusely scattered among the degenerated opticus fibers. Where the opticus first touches the hypothalamus it forms a small but compact bundle (Fig. xi) which then comes to lie entirely on the inner aspect of the tractus opticus (Fig. xxxv) and afterward can with difficulty be distinguished from that part of the upper loop of the commissura transversa, which is likewise heavily medullated and lies along the inner border of the opticus. While, however, this commissura transversa bundle very soon becomes closely joined with the other com. transversa bundles (Fig. xxxvi) the outer part of the fibers (Figs. xxxviii, xxxix, xl) turns upward where it ends in the medial wall of the tectum almost in the same place as the brachium mediale, running mesad of the corpus geniculatum. It is evident that these are the *fibræ tectales n. optici*, which KRAUSE has also described as the innermost fibers of the optic nerve and which, having their trophic center in the tectum itself, are not degenerated here.

A part of the centripetal opticus fibers seems to be connected directly or indirectly by means of collaterals with the anterior part of the *corpus geniculatum laterale.* The great enlargement of this nucleus farther caudad, however, must be attributed to its connection with the two *brachia*, of which the medial is much smaller than the lateral which divides again into dorsal and ventral branches, which together supply the whole dorso-lateral part of the tectum with fibers, situated immediately under the opticus fibers themselves.

The lower and upper loops of the *commissura transversa* differ in that the upper loop always consists of several distinct bundles which farther caudad unite into a compact cap over the lower loop. They may then be seen running on together into the subventricular cell layer the lateral part of which has already been described by FRITSCH as the *nucleus corticalis* (nucleus dorsalis thalami of GOLDSTEIN). The group of cells situated under the one just mentioned in which also fibers of this commissure end a little farther mesad, was mentioned by CATOIS without any special name as the homologue of RAMÓN Y CAJAL'S "ganglion of the commissura transversa" in the reptiles. As the latter layer of cells may be seen extending almost to the nucleus rotundus (at a somewhat higher level as it approaches the nucleus corticalis), I have thought best to call this group of cells simply *nucleus prærotundus*.

The method of the decussation of the commissura transversa is rather complicated. A careful reconstruction convinces me that the decussation takes place in three places. Several fibers decussate far forward (Figs. xi, Plate I, and xxxiv, Plate II) and probably it is this part which C. L. HERRICK treats separately from the rest as commissura ventralis. Another decussation of the same significance occurs at a higher level (Fig. xxxvi). This is the part which that author must have described as com. transversa. Finally there are still other decussations between these two chief parts of the commissure which relate parts of the second decussation with the contralateral parts of the first (Fig. xxxv). Afterward all the fibers run caudad together and terminate as I have just described. This is the reason why I do not consider this kind of a decussation as a commissure, and I am bound to declare that they have nothing to do either with the tectum opticum or with the corpus geniculatum laterale or even with the torus semicircularis, a name which KRAUSE and many others have improperly extended to include the whole region situated under the optic ventricle, about which I shall state my opinion more fully later.

There remain to be treated the *fibræ ansulatæ* of BELLONCI, the *commissura tuberis* and the *commissura horizontalis* or commissure of FRITSCH.

1. *Fibræ ansulatæ.* I have already called attention to the fact that these fibers have been described by BELLONCI as thick, not very compact, but strongly medullated fibers, as they also appear in my own preparations (Figs. xxxvi, xxxvii, Plate II). He is of the opinion that they join the com. transversa and he was able to follow their course as far as under the lobus opticus. As it is very difficult to follow the course of these diffuse fibers between which the median opticus bundle is also placed, I have nothing to add about them save that they either end in the corpus geniculatum or running through this enter the anterior part of the nucleus corticalis. In front they disappear in the commissura transversa, from which perhaps they originate. That they should have anything to do with the fasc. longitudinalis posterior, as EDINGER supposes for the reptiles, I can positively contradict as far as the teleosts are concerned.

2. *The commissura tuberis* is a thin bundle of fibers, very poor in myelin (Fig. xxxviii) which unites the two halves of the tuber cinereum and begins at the same place where the tractus præthalamo-cinereus (which was treated of in connection with the præthalamus) terminates.

3. Over the commissura tuberis we find the *commissura horizontalis* of FRITSCH strongly developed and easily followed. Its point of decussation, is placed at the same place by all authors (FRITSCH, MAYSER, BELLONCI, EDINGER, HERRICK and CATOIS), dorsad of the com. tuberis, caudad of the com. transversa. BELLONCI and CATOIS confirm the original description of FRITSCH that this commissure ends in the nuclei rotundi thalami, but MAYSER supposed that it only passed through these nuclei. EDINGER also says that the fibers which he marks as traversing the nuclei rotundi in Gobio fluviatilis originate from the tectum, while HERRICK remarks, that they appear again as a compact bundle above this nucleus, which he calls nucleus ruber, and terminate in the nucleus corticalis, just as DAVID describes.

I can almost entirely confirm the statement of the last four authors that the bundle comes out of the upper side of the nucleus rotundus proprius as compact as it entered it at the lower side (Fig. xlviii, Plate III). Then it runs dorsad and joins two other tracts, with which it then runs frontad under the optic ventricle and in the same region with which it ends. This is the region of the nucleus lentiformis, situated mesad of the nucleus corticalis directly behind the commissura posterior in the most anterior part of the eminentia medialis. The two tracts which it joins are the tr. rotundo-lentiformis and the tr. mesencephalo-cerebellaris superior, which will be discussed later. GOLDSTEIN called my attention to this cerebellar tract, of which I had recognized before only the most frontal part. He regards the com. horizontalis as a prolongation of this tr. mesencephalo-cerebellaris superior, which, however, I cannot confirm. That in this course between the nucleus rotundus and the nucleus lentiformis mesencephali there are two tracts is not so easily demonstrable in Gadus as in Lophius, for in the latter fish the two bundles are different in color and are not so close together.

Having now discussed the relations amongst the fore-brain and the diencephalon, the optic connections and the præinfundibular commissures, I shall now proceed with the description of the tracts which originate in the diencephalon, beginning with the ganglia habenulæ.

The *ganglia habenulæ* form on either side two groups of cells, an anterior group, more lateral, and a posterior group, more medial. Both are relatively better developed in Lophius than in Thynnus, Salmo and Gadus, where I have already described under the fore-brain the connection of the *tractus olfacto-habenularis* with the antero-lateral ganglion and where I also mentioned that its fibers decussate for the greater part in the commissura habenularis.

In Fig. xlii (Plate II) we see coming from the postero-medial ganglion the so-called *fasciculus retroflexus* or MEYNERT's bundle or tr. habenulo-peduncularis, a thin compact unmedullated tract on both sides, which in Figs. xliii to xlvi passes under the com. posterior. In the more caudal sections it may be followed to the beginning of the mid-brain basis and after decussation to its entrance into the so-called *ganglion interpedunculare* (Figs. il, l). The detailed description of this ganglion will be found in the chapter on the mid-brain.

As the third habenular relation, I have to mention the *commissura habenularis* (com. superior or com. tenuissima), more distinct in Lophius (Fig. xxvii, Plate II) than in Gadus (Fig. xlii). This commissure, the medullated fibers of which originate from the *tr. olfacto-habenularis*, contains also fibers connecting the anterior habenular ganglia which are unmedullated. The posterior ganglia with the fasciculus retroflexus do not receive any of it, though the somewhat horseshoe-shaped commissure curves backward along the posterior ganglia. Neither in Thynnus, Salmo, Lophius or Gadus was I able to find any asymmetry whatever of these ganglia, as so distinctly seen in the selachians.

Under and somewhat caudad from the ganglia habenulæ there is a group of small cells extending between the corpus geniculatum and the wall of the third ventricle, which is somewhat protruded there (Fig. xli), the *nucleus thalami anterius*, from which a diffuse partly unmedullated tract takes its course, first bending inward, along the lateral wall of the third ventricle, then downward to disappear somewhat before the nucleus rotundus in the same part of the lobi anteriores (pars anterior, Fig. xliv) where the tractus olfacto-lobaris lateralis et medialis terminate. This is the *tractus thalamo-lobaris*, also named tr. thalamo-mammillaris and compared with the tract of VICQ D'AZYR. GOLDSTEIN remarks that the origin of this tract is especially in the lateral parts of this cell mass, which I confirm, and this explains the inward curve which these fibers take.

In almost the same region the fibers gather which compose the *tractus thalamo-spinalis* (Figs. xlii, xliii). This passes under the fasc. longitudinalis dorsalis to the medulla. It is evident that it is these fibers which have been described as the thalamic origin of the fasc. long. dorsalis. But they are distinguished from the fibers of the fasciculus by the lighter color which they assume after the WEIGERT method, so that they cannot properly be said to belong to the thalamic fibers of that fascicle. Moreover, they get their medullary sheaths later than the true fasciculus. There is, however, no objection in principle to reckoning them with the fasc. long. dorsalis, as this is properly a collective term for longer or shorter longitudinal association fibers.

It is desirable before proceeding further to give a minute description of the so-called hypothalamus, especially of the lobi inferiores and of the various names which other investigators have given to this region and its constituent parts.

When following in serial sections the ventral wall of the thalamus caudad behind the decussatio transversa, we may easily convince ourselves that the hypophysis, which both in Lophius (Figs. xxvi to xxix) and in Gadus (Figs. ix to xi, xxxiv to xxxviii) is turned rather strongly forward, is attached to that part of the hypothalamus which can unmistakably be considered as infundibulum, while the lobi inferiores have not yet, or scarcely yet, come into view. Through the infundibulum the hypophysis communicates with the third ventricle and also backward with a second projection of the basis thalami, the *saccus vasculosus* (Lophius, Fig. xxx; Gadus, Figs. xliii to l).

Hypophysis and saccus vasculosus, though in connection with one another and inserted upon the hypothalamus at nearly the same place, are, however, genetically in no relation whatever with one another. The saccus vasculosus begins as a projection from this region of the hypothalamus (EDINGER), while the hypophysis begins, according to some investigators, as an ectodermal projection inward; according to others from ectodermal and entodermal tissue, which is secondarily connected with the infundibular region. BOEKE even maintains that in Murena the ectoderm does not participate in its definitive construction and claims that it originates from a meso- (ento-) dermal tissue.

At the place of the insertion of the saccus the lateral walls of the original infundibulum show an important lateral thickening, the *lobi inferiores* of FRITSCH, MAYSER, BELLONCI, CHATIN, USSOW, EDINGER, CATOIS; the hypoaria of SANDERS and HERRICK. Even among the earlier authors there was a difference of opinion about the functions of these lobes, which VICQ D'AZYR and TREVIRANUS considered as corpora mammillaria; A. v. HALLER as connected with the olfactorium; CUVIER as optic lobes; CARUS as a continuation of the tuber cinereum, the latter opinion being shared by CATOIS. FRITSCH homologized them with the corpora mammillaria of the higher animals, a view which SANDERS was inclined to accept. With good reason C. L. HERRICK points out that the relations of the tracts in this region which, like EDINGER, I call lobus inferior, make it impossible to consider it the homologue of the corpus mammillare, which, however, is not now accepted anywhere, for the whole lobe at least.[1]

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[1] C. L. HERRICK was the first to describe as corpora mammillaria two bilateral projections of the infundibulum which regularly appear and are provided with their own ventricle corresponding with the ventric. lobi inf. along which run fibers of the saccus vasculosus. They are seen in Lophius and Gadus in Figs. xxx, xliv and xlv, of Plate II. After HERRICK they were mentioned by DAVID, who, however, did not consider them as homologues of the corpora mammillaria and called them "lobi mediani." JOHNSTON, who described them in Acipenser, considers that they, together with the "mid-ventral part" of the lobi inferiores, constitute the corpora mammillaria.

Before proceeding to describe the tracts of the lobi inferiores it should be stated that they have a small ventricle, corresponding to the inferior part of the third ventricle. This *ventriculus lobi inferiores* is indented from below by a cell mass which gives it a falcate form in Gadus (Figs. xlvi, xlvii). The free caudal ends of these lobes extend caudad under the midbrain beyond their place of attachment, which is marked by the roots of the nervus oculomotorius (Lophius, Fig. xxxii; Gadus, Fig. li).

Now I proceed to the description of the tracts which originate from or terminate in the hypothalamus or pass through it. They will be divided into several groups:

1. Tracts connected with the tuber cinereum.
2. Fibers belonging to the saccus vasculosus.
3. Tracts which relate the groups of cells under and before the ventriculus opticus with the lobi inferiores.
4. Mutual relations of regions of the lobi inferiores themselves.
5. Relations of the hypothalamus with frontal parts.
6. Relations of the lobi inferiores with caudal parts.

To the tracts of the *first group* belong two which have already been mentioned. (1) The *tr. præthalamo-cinereus* (Figs. xxxv to xxxviii) which comes from the nucleus præopticus (Fig. xi = nucleus magnocellularis strati grisei, EDINGER, GOLDSTEIN) and terminates in the tuber cinereum. (2) The group of cells where this tract terminates and to which GOLDSTEIN gave the name of nucleus anterior tuberis is connected with the corresponding group of the opposite side by the *commissura tuberis*, of which mention was made when speaking of the præinfundibular connections (Fig. xxxviii).

(3) To these I have still to add another tract, whose origin is also situated in this region. In Gadus it is composed of small but compact feebly medullated bundles which first run upward (Figs. xxxix, xl) and then backward along the third ventricle and end in the anterior part of the lobi inferiores (Figs. xli, xlii), the *tractus lobo-cinereus brevis.* In Thynnus, however, the whole tract is much more developed than in Gadus, Lophius or Salmo and undoubtedly the greater part of the fibers which originate in this place and in separate bundles in the same way go higher up and end, after turning outward, in the region of the nucleus lentiformis, under the optic ventricle. This is the same tract

which GOLDSTEIN has described as *tr. tubero-dorsalis*, of which the tr. lobo-cinereus brevis probably represents only a part.

Regarding the *second group*, the *saccus vasculosus fibers*, the finely striped character of the saccus furrows in the teleosts has already been mentioned by STIEDA, USSOW and RABL RÜCKHARD. Only USSOW mentioned that he considered this to be nervous tissue. GORONOWITSCH describes in Acipenser a ganglion in the infundibulum which receives fibers from the saccus and doubtless has secondary connections with higher centers. JOHNSTON mentions in addition to this ganglion one tract for the cyclostomes and two tracts for the ganoids, a centrifugal and a centripetal one, the latter of which originates from the saccus, where its fibers arise from the ciliated epithelium, of whose cells they are the neurites. This tract according to JOHNSTON terminates in the thalamus. The other tract arises between the epithelium. This ciliated epithelium was first described in 1891 by C. L. HERRICK in Carpiodes.[1]

Such striped tissue strongly colored by paracarmin is found between the folds of the saccus, partly arising from the epithelium, which is distinguished by strong tufts. The fibers gather at the insertion of this sac upon the thalamus laterally of the connection with the third ventricle and then go under the floor of this ventricle for some distance forward. Where they terminate or what connections they make I cannot say. It seemed to me that they decussate in the median line, but on this matter I shall be able to say more when I treat of the selachians, merely pointing out here that it is an interesting fact in connection with the different origin of the hypophysis and saccus vasculosus that this kind of epithelium, as well as these nervous tracts are confined to the saccus.

To the *third group* of tracts connecting the nuclei directly under and before the ventriculus opticus with the lobi inferiores belong four systems.

(1) A group of fibers partly unmedullated and not very compact (Figs. xlii, xliii) which I have already mentioned as the *tractus thalamo-lobaris* connects the *nucleus thalami anterior* with the central part of the lobi inferiores. This tract after an inward

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[1] Some years ago BOEKE described sense epithelium in the ventral infundibular wall in larvæ of Murena. It seems to me more than probable that it is this which is later found in the saccus, the more so because JOHNSTON told me that in young ganoids he found a part of this saccus epithelium still ending in the infundibulum.

curve runs under the fibers of the commissura posterior and then, accompanying the fasciculus retroflexus for some distance, goes downward medially of the tr. strio-thalamicus, then bends again laterally without crossing ending in the lobes above the ventricles.

(2) The second connection of this kind arises in the *nucleus corticalis* and *nucleus prærotundus* (between which the terminal loops of the commissura transversa run) and goes downward (Fig. xliv) in the same way but more nearly in a single vertical plane than the first tract, mesad of the tr. strio-thalamicus, to end in the central part of the lobus inferior where the tr. olfacto-lobaris medialis (or tr. olfacto-hypothalamicus medialis) also ends (Fig. xlv). I have called this the *tractus mesencephalo-lobaris anterior.*

(3) The third connection of the hypothalamus with regions situated more dorsally is formed by the *tr. rotundo-lentiformis*, which I have named after the nuclei which are connected by it. This tract leaves the nucleus rotundus proprius together with the fibers of the commissura horizontalis and accompanies the fibers of this commissura to the region directly behind the commissura posterior. Perhaps the same tract has been seen by CATOIS, who considered it to be the same as the dorso-laterale-ventrale Zwischenhirnbahn of HALLER, who saw a similar connection. CATOIS describes this tract as originating "en arrière de la commissure blanche postèrieure," but his opinion was that its fibers also go into the commissura inferior. The latter, I think, were the fibers of the horizontal commissure which accompany this tract, which is also accompanied by a large tract originating behind the commissura posterior and going to the cerebellum.

(4) To this group of shorter connections belongs the *tractus mesencephalo-lobaris posterior*, consisting of a series of heavily medullated fibers which connect the back part of the lobi with the region of the nucleus lateralis mesencephali and the adjacent tectum along the exterior side of the brain. The strong development of this tract is correlated with the importance of the regions connected by it (Figs. xlvii, xlviii).

The *fourth group* of fibers consist of short but large strongly medullated bundles, part of which probably pass caudad into the tractus mesencephalo-lobaris posterior, while the greater part constitute:

(1) *Fasciculus intralobaris.* This connects the most anterior

region of the lobi anteriores with its posterior parts without decussation (Figs. xlvi to xlviii).

(2) An equally short but stronger tract (Figs. xlviii, il) gathers around the nucleus rotundus proprius and passes over into the mass of cells situated immediately under this nucleus. I call this the *tractus rotundo-lobaris*, which has been already correctly figured as far as its origin is concerned by BELLONCI, to which, however, no special name was given either by him or by DAVID, who gives an excellent figure of it without mentioning it.

(3) The last intralobular connection is formed by the *commissura supra-infundibularis*, or *com. post-infundibularis*. This very slight commissure connects the subventricular as well as the supraventricular parts of the inferior lobes (Fig. xlv).

A few words now about the *fifth group* of our scheme, comprising the tr. strio-thalamicus and tr. olfacto-lobaris lateralis et medialis.

(1) As I have already given the course of the *tractus strio-thalamicus* in the thalamus, I can now confine myself to the description of its ending in the lobi inferiores. Gradually the fibers of this bundle pass more ventrally and toward the median line from the nucleus prærotundus backward (Fig. xliv) and finally lie close to the median line (Fig. xlvii). After this they bend laterally at a sharp angle and end in the cell masses of the back part of the lobus partly in the nucleus rotundus but chiefly in the nucleus subrotundus. The terminus of the tr. strio-thalamicus is caudad to the ending of both tractus olfacto-lobares, the lateral of which ends somewhat more caudad than the medial.

(2) The *tr. olfacto-lobaris lateralis* ends at the point where the tr. strio-thalamicus runs as a circular bundle along the nucleus prærotundus (Fig. xlvi). This tract for the greater part ends decussated, but not above the ventriculus lobi inf., like the tr. strio-thalamicus, but below it.

(3) Of this group of frontal tracts, the one which ends most frontally is the *tr. olfacto-lobaris medialis*, which passing quite sharply laterally under the tr. strio-thalamicus, terminates in front of the nucleus rotundus, as represented in Figs. xliii and xliv.

It now remains to describe the *sixth group*, containing the caudal tracts of the lobi.

(1) *Tractus lobo-cerebellaris*. The region of origin of this tract extends over the whole pars posterior lobi. The fibers arise in the center and gather chiefly in the upper lateral angle where the

lobus passes over into the central brain mass (Figs. xliii, li). A part of the fibers of this tract pass anterior to the first decussation of the lemniscus, another part between the first and the second decussation, into the base of the mid-brain. Their further course will be treated beyond.

(2) The second caudal connection is much smaller than the first one and forms the *tractus lobo-peduncularis*, a small bundle containing but little myelin but sharply delineated arising from the pars posterior of the lobi (Figs. xlix and l) and breaking through the com. ansulata to end in the corpus interpedunculare together with the fasciculi retroflexi. It seems to me that EDINGER and CATOIS have described the same bundle as tr. mammillo-peduncularis.

Nuclei of the Hypothalamus and Adjacent Parts of the Thalamus. Owing to the course of these tracts and those described before, and also on account of the differences in the cells, one can distinguish several groups of cells in the hypothalamus and adjoining parts of the thalamus. The first group of cells, situated most dorsally, proximally and laterally, is the *nucleus prærotundus.* This group is related to the com. transversa and the tr. mesencephalo-lobaris anterior and gradually passes backward into a much larger group situated under and lateral to the level of the nucleus rotundus and ending where the real nucleus rotundus has its largest size. This latter group, which belongs entirely to the lobi inferiores, I shall distinguish as the *nucleus subrotundus* from the *nucleus rotundus proprius*, as it extends in part under the real nucleus rotundus so that the com. horizontalis, before it enters the lower border of the latter, lies for some distance over it and between it and the nucleus rotundus proprius. It is in the foremost part of this group of cells that the greater part of the tr. olfacto-lobaris medialis terminates, while in its posterior part the greater part of the tr. strio-thalamicus ends, bending downward in the same way.

Evidently this nucleus subrotundus has always been considered to belong to the nucleus rotundus. GOLDSTEIN alone describes it separately in his work and he also states that a part of the strio-thalamic fibers end here. Accordingly, investigators generally have considered most of the above-mentioned tracts to end in the nucleus rotundus; BELLONCI his tr. olfacto-rotundus, and others the greater part of the tr. strio-thalamicus. This group of cells must be considered separately if we are ever to obtain a more thorough knowledge of the 'tween-brain centers. It remains to be mentioned that the tr. mesencephalo-lobaris posterior goes from the anterior as well as the posterior part of this nucleus to the region of the nucleus lateralis mesencephali and the tectum.

The *nucleus rotundus proprius* (nucleus ventralis thalami of GOLDSTEIN) is clearly defined: (1) on account of the peculiar structure of its cells, already referred to by FRITSCH who compared them with the glomeruli olfactorii, as BELLONCI also did; (2) by the way in which the tr. rotundo-lobaris gathers on its periphery. As already mentioned, the com. horizontalis of FRITSCH goes through the nucleus rotundus, entering at the inferior side and leaving at the top, then bending forward with the tr. rotundo-lentiformis and ending in the nuclear region behind the com. posterior under the ventricle.

Finally I have still to mention as belonging to the nucleus rotundus proprius a tract which has been mentioned several times before. It is short, but large and strongly medullated and enwraps the nucleus, covering it, as it were, with a layer of myelin, after which it goes into the nucleus subrotundus and the *stratum griseum lobi inferioris proprius* and ends there. It is most remarkable that I do not find this latter tract, which is so strongly developed in Gadus, mentioned either by EDINGER or by CATOIS, while it is so excellently represented by BELLONCI and described by DAVID. C. L. HERRICK seems to have seen it, as he speaks of "fibers embracing the nidulus from all sides except dorsad," which must be the fibers of this tract.

Now, having mentioned the connections of the nucleus rotundus proprius and having described those of its "Nebenganglien," as EDINGER calls them, I must speak further of the *substantia grisea lobi inferioris*, as I term the rest of the gray substance of the hypothalamus, which cannot be regarded as a distinct nucleus and therefore has been justly called nucleus diffusus hypothalami by GOLDSTEIN. I have divided this substantia grisea lobi inf. into two parts, both situated in the more inferior, lateral and central parts of the lobi.

The *pars anterior* is connected with fibers of the tractus lobocinereus brevis, the tractus thalamo-lobaris, or bundle of VICQ D'AZYR, and the fasciculus intralobaris, while the *pars posterior* is connected with the tr. olfacto-hypothalamicus (or -lobaris) lateralis, a part of the tr. strio-thalamicus, the fasciculus intralobaris, the commissura supra-infundibularis or post-infundibularis, the tr. lobo-cerebellaris and finally the tr. lobo-peduncularis. From this it results that the back part of the lobi, which, moreover, is connected with the dorsal regions by fibers of the tr. mesencephalo-lobaris anterior et posterior, is the most important part of the lobi. It must, however, be stated that it is very difficult to place an exact limit between these two parts, especially because the tr. lobo-cerebellaris seems to get its fibers from both.

I must mention still that a basal optic tract such as has been mentioned by GOLDSTEIN could not be found in the basal thalamus regions or in the so-called ganglia ectomammillaria either in Lophius, Gadus, Thynnus or Salmo, nor a commissura postchiasmatica which should connect such basal regions. However, it is possible that there are variations in this point in different fishes. Nor did I find a second cerebellar connection between the nucleus rotundus (nucleus ventralis of that author), or the medullary tract which C. L. HERRICK describes for the nucleus rotundus (his nucleus ruber).

2. *The 'Tween-brain of the Selachians.*

The 'tween-brain of the selachians in its general features shows the same structure as that of the teleosts, but is distinguished from the former, among other things, by a much less compact arrangement of its tracts and nuclei, which makes the investigation very difficult, as EDINGER rightly observes. While in the bony fishes I could follow the different tracts—and there were many of them—very definitely and with good results, and find out their origins and terminations, the number of fibers of the 'tween-brain of the selachians, even of the full-grown animals, is so considerable that many systems go quite close to and even through each other. Moreover the groups of cells are so diffusely scattered that it is very difficult to distinguish many nuclei here.

Accordingly, it is no wonder that the number of investigators who have been successful in the examination of this material is much smaller than in the teleosts. The most important results (after the older authors of the period before WEIGERT) have been obtained by EDINGER, and afterward by HOUSER, HALLER and CATOIS. Especially the first named has clarified this region, which was only poorly explained by the investigations of VIAULT, ROHON and SANDERS.

The macroscopical structure of the so-called peduncular part of the 'tween-brain, also called *præthalamus*, situated between the fore-brain and the place where the optic nerve enters ventrally and the ganglia habenulæ dorsally, resembles very much that of the teleosts. Both show dorsally a plicated ependymal membrane and ventrally a small base of gray material and laterally the walls thickened by the fore-brain tracts which pass through them. The roof of the mid-brain overlaps the 'tween-brain less than in the teleosts and does not touch the ganglia habenulæ laterally. The lobi inferiores, whose saccus vasculosus is more developed in the selachians than in the teleosts, extend caudad farther than the superficial origin of the oculomotorius (Figs lxv to lxix, Plate IV).

The tracts of the præthalamus are partly the same and partly different from those of the teleosts (see Fig. 6, Plate XIII). For the latter fishes I was able to mention as fore-brain attachments: (1) tr. strio-thalamicus; (2 and 3) tr. olfacto-lobaris medialis et lateralis, and (4) tr. olfacto-habenularis. For the selachians there are to be mentioned: (1) tr. strio-thalamicus; (2) a part of the tr. medianus running along with the former in the back part of the fore-brain; (3) tr. pallii and (4) tr. olfacto-habenularis.

That the tr. strio-thalamicus is homologous in both fish types is evident on account of the fact that it begins and ends in the same place in the selachians as in the teleosts.

Whether one may consider the two tr. olfacto-lobares of the teleosts which begin in the secondary olfactory regions and end in the lobi inferiores as homologous with the tr. medianus and tr. pallii, which also originate in the secondary olfactory regions of the fore-brain, is a question which I may not answer before having described their further course.

I saw a small part of the terminal fibers of the *tr. olfacto-habenularis*, which is situated directly inward from the tr. pallii, pass over into a small homolateral group of cells belonging to the area of the ganglia habenulæ (Fig. liv, Plate III), but situated somewhat lateral and ventral to the chief group of the anterior ganglion. I have formerly mentioned this group, the cells of which are distinguished by a polygonal shape from the more round cells of the true ganglia, and called it the "ganglion intercalatum tracti olfacto-habenularis." It is certain, however, that not all fibers of this tract end here; a larger part goes through the commissura habenularis to the contralateral ganglion.

The *tractus pallii*, running at the very outside of the præthalamus and lying like a ribbon upon it, goes downward laterally of the tr. olfacto-habenularis and then comes to lie ventro-laterally to the nervus opticus (Fig. lvi). It then goes more and more ventrad (Figs. lvii to lxii) and caudad of the opticus and ends in the lobi inferiores (Figs. lxiii, lxiv), after having wholly decussated in the præinfundibular thalamus region.

EDINGER, who initiated these investigations, said in his article on the 'tween-brain in 1892, "Nach der Kreuzung ziehen die Fasern des Mantelbündels schräg aufsteigend über das Zwischenhirn weg und sencken sich an dessen caudalen Theilen angelangt in die Tiefe des Mittelhirndaches." HALLER and CATOIS are of a contrary opinion. The latter considers the fibers of this bundle to end in the lateral parts of the lobi inferiores, while HALLER also thinks that they end there but only partly decussated and partly uncrossed. Founding his opinion on GOLGI preparations, HOUSER, however, has recently confirmed EDINGER's original statement, though EDINGER himself is no longer convinced of this fact, according to his last publication on this point in his "Vorlesungen," for he there says that perhaps it is a cortico-mammillary tract, ending in the posterior part of the lobi inferiores, and this I can confirm.

The second group of fibers going from the fore-brain into the 'tween-brain is a combination of two tracts, the *tr. strio-thalamicus* and a part of the *tr. medianus*, forming a single whole during their course in the posterior part of the fore-brain and in the præthalamus and thalamus. In the præthalamus their fiber mass is situated mesad almost in the wall of the ventriculus tertius (Fig. lvi, Plate III), and in this position it runs over the optic nerves where they enter the thalamus (Fig. lviii), after which it is crossed at right angles by the com. transversa (Figs. lix, lx). It then ends in the pars posterior of the lobi inferiores, dorsally of the end of the tractus pallii.

The whole course of the tr. strio-thalamicus is easily followed. so that on this bundle, which was only vaguely mentioned by ROHON and SANDERS, authors are pretty well agreed. In his first investigations EDINGER mentioned, however, that only a part of the basal tract ends in the infundibular region and that another part goes farther caudad through the mid-brain. Yet in his "Vorlesungen" he mentions only the thalamic and hypothalamic termination. HALLER also mentions only hypothalamic termini, while CATOIS, whose opinion is that it is not impossible that some fibers may end in the basis mesencephali, nevertheless also considers the hypothalamus to be the end of the greater part, in which HOUSER also saw its termini.

Comparing now the fore-brain tracts of the selachians with those of the teleosts, we find that two connections are quite the same, viz., the tr. olfacto-habenularis and the tr. strio-thalamicus. Besides these the teleosts have two tr. olfacto-lobares, medial and lateral, of which the first ends uncrossed in the same level of the hypothalamus as the tr. strio-thalamicus, while the second crosses and ends in the most inferior parts of the inferior lobes. These two tracts are very much like the median bundle constituent of the tr. strio-thalamicus of selachians and the tr. pallii, which crosses and ends in the more inferior parts of the lobes. Moreover, in both types of fishes these two sets of tracts originate in secondary olfactory regions.

From all this it is probable that these two sets of tracts are to be regarded as homologous, and this is another proof of the homology of some parts which in the selachians lie in the pallium and in the teleosts in the lobi anteriores, as has already been made probable by the fact that a great many of the secondary olfactory fibers, which, in the teleosts, all end in the lobi anteriores, in the selachians end in the most dorsal regions. And, further, while the bilateral connection between these secondary olfactory centers is represented in the teleosts by a part of the com. anterior (which is, therefore, so much larger in these fishes than in the selachians), in the selachians these connections are situated in the dorsal region of the pallium. So we find that all the facts, as brought out by others and by myself, lead us to believe that in the lobi anteriores of the bony fishes there are parts which in the selachians are represented in the pallium, a fact of very great importance.

A second question is whether we may extend these homologies any further by stating that the secondary olfactory centers in teleosts related to the tractus olfacto-lobares are in other respects also the complete homologues of the pallial centers of the selachians described in the second part of the first chapter from which the tr. medianus and the tr. pallii originate. Regarding this question I may say that, though I am quite sure that the functions belonging to these tracts are homologous, it certainly may be that in the same pallial region of the selachians there are still other functions not in direct relation with the tracts in question which may be absent in the lobi anteriores of the teleosts. The functions to which I refer are the cortical functions, which, as JOHNSTON correctly pointed out, are related to higher tertiary connections and which must be studied by GOLGI preparations. Though it would have been very interesting to investigate this question, time did not permit me to take it up and I hope that some one else will do this, as JOHNSTON has already done for the ganoids and BOTAZZI partially for the selachians.

Now, we pass to the description of the commissures and decussations of the præinfundibular part of the 'tween-brain, of which I have already mentioned the most ventral one, the *decussatio tr. pallii.* The remaining decussations found here and not yet mentioned are those of the opticus fibers and the commissura transversa.

As far as my series of sections show, the opticus fibers seem to decussate wholly both in Galeus and in Angelus squatina. This, of course, could be settled for certain only by experiment. After their decussation the opticus fibers go between the mantle bundle and the commissura transversa in the direction of the *corpus geniculatum laterale* (Fig. lix), under which a part goes as the so-called ventral or lateral opticus root, while the other part goes into the medio-dorsal region of the tectum opticum. As for the *brachia tecti*, about which, when treating of the teleosts, I was able to give such positive information, I can only mention here that the corpus geniculatum is supplied with fibers from the tectum. This group of fibers may be recognized in Figs. lvi and lvii. The section first mentioned is taken more frontally than the second, so that perhaps the first one shows the entering of the brachium anterius, the second that of the brachium laterale or posterius. This, however, is only a possibility; certainty in this matter could be obtained only by degeneration experiments.

Now, I have still to describe the third præinfundibular decussation, the *commissura transversa,* situated dorsal to the optic decussation, the course of whose fibers is clearly to be seen in Figs. lix and lx, anterior to the commissura pallii. This commissure, which is but little developed in Angelus squatina, cannot be followed so distinctly to its end in Galeus as in the teleosts, where all the tracts are more compact. EDINGER, who considers it more a decussation than a commissure, saw its fibers end under the tectum opticum, while CATOIS describes it as a commissure between the posterior and lateral regions of the mesencephalon. HALLER, who calls it "commissura post-optica superior," says that it contains only decussating fibers of the tecti optici. I do not think that they are tectal decussating fibers (HALLER), but rather subtectal ones (EDINGER) and consider them to be the homologue of the com. transversa of the teleosts and not the homologue of the commissure of HERRICK of those fishes. As EDINGER has already observed, almost the whole commissure is to be seen in one section, of which Fig. lx is a good example. I could not follow them any farther backward, certainly not as far as the extreme posterior part of the mesencephalon, and indeed it seems very improbable that they should go so far backward. It seems to me that their place of termination is situated in the cell layer under the ventriculus opticus which is to be considered as homologous with the nucleus lentiformis and corticalis of the teleosts and is continued ventrally into the region in which in Gadus I described the nucleus prærotundus. Neither in Galeus nor in Angelus squatina can there be any sharp limitation of the boundaries of these groups of cells. It is only by means of the course of the tracts that the homologies of these regions can be determined.

Fortunately the relations in the *epithalamus* are more distinct. Of the *ganglia habenulæ* I have to say, in the first place, that they seem to be more developed in the selachians than in the teleosts; at least in Galeus canis they are much larger than in the cod, a fish of about the same size. In Fig. liv, Plate III, the situation of both the ganglia, the anterior or lateral, and the posterior or medial, is to be seen. In the posterior part of the whole complex runs the *commissura habenularis*, consisting of two kinds of fibers, some medullated and the others unmedullated. The medullated fibers take their origin from the *tr. olfacto-habenularis*, which contains a rather considerable quantity of myelin and ends partly in the antero-lateral ganglion of the same side, but for the greater part in that of the other side, describing a curve whose convexity is directed backward, so as to give the impression that the anterior ganglia are not related to one another, but only the posterior.

But besides these medullated fibers, the commissure has another medullated tract (Fig. liv) running for the greater part separately from the fibers mentioned above and ending decussated in the medial ganglia. It is more difficult to state the function of this tract, which, indeed, is evident from the literature which contains only a few data on this point given by EDINGER and HALLER. In his studies on the 'tween-brain EDINGER mentioned this bundle as a decussated tract, which next to the fasciculus retroflexus (still to be described) is the strongest tract which originates from the ganglia. He also describes its decussation as caudad to the ganglia habenulæ but could not be certain about its ventral end, which, according to him, perhaps lies in the 'tween-brain. In order not to prejudicate it, he calls this tract the *tr. descendens gangl. habenulæ*, which name I shall retain. Evidently HALLER observed the same bundle, of which he, however, says that it partly ends as "Hauben-Zwischenhirn Bahn" in the most anterior region of the thalamus and partly passes over into the opticus, which habenular opticus root has also been mentioned by VIAULT and DUMÉRIL. Indeed, it seems to me most probable that this tractus descendens joins the opticus fibers, though not as an opticus root to the eye, but first descends for some distance and then rises again backward. In this case it might be a crossed part of the "tr. ganglionis habenulæ ad mesencephalon," mentioned by EDINGER. More investigations, especially experimental ones, would perhaps explain many questions in this connection.

The bundle now to be described has been seen in all fishes by all investigators and in appearance and situation is one of the most constant, viz., the *fasciculus retroflexus*, also called the bundle of MEYNERT. This bundle which arises entirely without decussation from the postero-median ganglion and runs under the com. habenularis may be followed in all sections adjacent to the ventriculus tertius and the aquæductus Sylvii into the mesencephalon. It is remarkable that in Galeus canis the left tract contains no myelin at all, while the right one is medullated. The latter evidently does more work than the former (experimental investigations of AMBRONN and HELD concerning the formation of myelin), which is in conformity with the fact that the left ganglion is less developed than the right. The latter point has also been stated for the cyclostomes (AHLBORN, JOHNSTON) as well as for the ganoids (GORONOWITSCH, JOHNSTON), but has never been observed in the teleosts either by my predecessors or by myself.

Ahlborn, moreover, found the left fasciculus of Meynert to be smaller than the right one.

The fibers of this tract end in the basis of the mid-brain, in the region where the oculomotorius roots leave the brain, in the *corpus interpedunculare.* The decussation, which is a complete one there, takes place in Galeus (Fig. lxi, Plate IV) in three separate little bundles which do not decussate at the same point, but one after the other almost in the same level. After the decussation the fibers gradually disappear in the basal gray substance of the mid-brain described as the interpeduncular nucleus. I could not determine that any fibers went farther back, as has been stated to be the case in the cyclostomes and ganoids by some investigators.

Before leaving the epithalamus I have still to mention a decussation which as far as I know, has not been separately described in selachians by any one of my predecessors, but which has probably been considered by all as a part of the commissura posterior, with which its fibers afterward are mingled. It consists of thin but medullated fibers represented in Fig. liii, which do not decussate like the com. habenularis before the epiphysis, but behind it and before the folding of the dorsal wall up into the tectum. The dorsal thalamus roof forms a somewhat deeper fold so that this group of fibers is just as distinctly separated from the com. posterior as the root of the epiphysis separates it from the com. habenularis, which besides is situated at a higher level. Its fibers, running downward, join the most anterior fibers of the com. posterior and seem to end along with these. I cannot say whether there may exist relations with the nucleus prætectalis or whether this is the same bilateral connection which Holt mentions in the same region in the teleosts. Johnston, who saw a similar commissure in Acipenser, describes it as the epiphysial decussation, and states that these fibers partly originate from, and partly end between, the epithelial cells of the epiphysial sac and can be traced downward within and in front of the optic bundles into the region of the nucleus anterior, as seems to be the case here.

Now, passing over from the epithalamus to the thalamus, in Galeus I must mention a group of fibers (Fig. lvi) which originate laterally of the most anterior part of the thalamus immediately under the insertion of the tectum, medially to the *corpus genicu-*

latum laterale, then bend mesad to the third ventricle (Figs. lx, lxi), and going ventrad through the tr. thalamo-spinalis, end medially in the lobi inferiores (Figs. lxii, lxiii). Probably these fibers include the *tr. thalamo-lobaris* (also called VICQ D'AZYR's bundle), as well as the *tr. mesencephalo-lobaris anterior* of the teleosts. These fibers have been described by both EDINGER and HALLER.

The *thalamo-spinal bundles* of Galeus, already referred to, are of much more importance than in the bony fishes and are also rather easily followed. They arise in the so-called "centrales Höhlengrau" of EDINGER, or nucleus strati grisei of HOUSER, a diffuse mass of cells situated medially to the ventricular walls which extends backward almost in a straight line so that it lies mesad to the tr. lobo-cerebellaris and immediately under and adjacent to the fasciculus longitudinalis posterior. Soon after their origin these fibers are joined by the tecto-spinal fibers which arise farthest in front and the two tracts cannot be separately distinguished in their further course through the mid-brain, as their fiber-caliber is the same.

The post-infundibular tracts of selachians, which I have still to describe, conform closely with the relations in the teleosts. Two post-infundibular decussations have been described by EDINGER, one under the name, "Commissur des centralen Höhlengraues," the other as "Decussatio infundibuli." In his opinion the first commissure lies under and near to the ventricular epithelium ventrally to the fasciculus retroflexus and its fibers go to the posterior part of the 'tween-brain. As to the second decussation he says that it consists of strongly developed but unmedullated fibers descending from the dorsal region of the 'tween-brain or from the mid-brain. After decussation these fibers go backward into the lateral wall of the lobi inferiores, where they may be followed as far as the furrows of the saccus vasculosus: "Es scheint dass diese 'Tractus sacci vasculosi' sich dort aufsplitteren." A little further on he says that fibers from the "centrales Höhlengrau" also decussate in the decussatio infundibuli, after which they disappear in the saccus vasculosus. He again divides the decussation of the substantia grisea centralis into two parts, a ventral and a caudal decussation. HALLER describes the com. infundibularis as a connection of both the lateral post-infundibular regions with one another. It is said that its loops reach nearly as far as to the commissura posterior. Their observations in this matter evidently do not agree.

The relations as they are found in Galeus are as follows: In Fig. lxviii one sees a considerable quantity of clear unmedullated bundles gather from the furrows of the saccus vasculosus in the dorso-caudal wall of the lobi inferiores from the saccus epithelium. In Fig. lxvii this system (first neurone) runs upward and forward until it ends on the same side in two ganglia (Fig. lxvi). These ganglia, which, as far as I know, are not described by other investigators, except GORONOWITSCH and JOHNSTON who saw them in Acipenser, I shall call, "ganglia sacci vasculosi," as they receive their fibers from the saccus vasculosus. They consist partly of round cells and partly of middle-sized polygonal cells and they are abundantly provided with blood-vessels. From each of these ganglia fibers cross the median line, of which it is difficult to say whether they are a commissure between the ganglia or a crossing of fibers of the second neurone which go upward. The latter interpretation seems to be the most probable. It seems to me that this commissure is also found in the teleosts, where these fibers decussate before passing upward. Neither they nor the saccus itself, however, are as large as in the selachians; nor could I find there a separate ganglion, but only small round cells dispersed between the fibers of the first neurone. The fibers of the second neurone of the saccus sense-organ, which are also unmedullated, end probably in the substantia grisea centralis. It is impossible to follow them any farther, at any rate, on account of the great quantity of fibers between which they run.

Besides this decussation, there is a second decussation in that region. Near the ganglia of the saccus there is a considerable mass of cells in the lateral, dorsal and ventral walls of the lobi. HALLER has given a very exact description and sketch of their ventral layer under the name of "ventrale Zwischenhirn Kern," which passes over dorsally into the "Vereinigungsgebiet" of this author. From this cell mass, which is much larger dorso-caudally (HALLER's Vereinigungsgebiet) than ventro-frontally, a great many medullated fibers gradually assemble, of which one part connects the largest masses of this cell region, a connection which I shall call the *com. postinfundibularis superior.* This commissure (Fig. lxv) lies dorsal to the com. postinfundibularis inferior, is medullated and broader, but less compact than the commissure of the ganglia sacci vasc. mentioned above and evidently is the same as the one referred to in Scyllium by HALLER as a connection of the two lateral cell regions of the lobi inferiores. In my opinion it is homologous with the postinfundibular commissure which I described in Gadus and which is also a bilateral connection of the two lateral regions of the lobus.

It now remains only to treat of the *tr. lobo-cerebellaris*, or *tr. tegmento-cerebellaris*, which has already been mentioned several times. The fibers of this tract which originate farthest caudally gather in the most distal part of the lobi from the extensive cellular layer which surrounds its ventricle (Figs. lxv and lxvi). After having curved slightly forward, the fibers again turn backward in the base of the mid-brain. These relations are similar to those in Gadus, though in Galeus the lobi infundibuli protrude somewhat farther backward than in Gadus, so that more of the fibers have to make the curve forward before turning backward. In both Galeus and Gadus this nucleus is very extensive and is dark in color, due, it seems to me, not only to the abundance of small medullated fibers, but also to a slight pigmentation.

The lobo-cerebellar fibers gather in small bundles which form almost the whole base of the posterior hypothalamus region. Medially they border on the thalamo-spinalis fibers, and, farther back in the mid-brain, on the tecto-spinalis fibers which are situated partly above them and partly run along their lateral side. After their decussation, which takes place along with the commissura ansulata near the origin of the oculomotorius, the fibers disappear in the anterior part of the cerebellum.

Accordingly, we find in the lobi inferiores of the selachians the main features in the same relation as in the teleosts. In both the tr. strio-thalamicus ends without decussation in the higher layers of this region. In both the tr. lobo-cerebellaris arises in the posterior half and the tr. sacci vasculosi in the ventral half. In both a comparatively poorly developed commissure is found between the nuclei of origin of both of the tracts mentioned, the com. postinfundibularis superior. In both the tr. thalamo-lobaris ends in the more frontal part of the lobus. The 'tween-mid-brain connection, described as tr. mesencephalo-lobaris posterior in the teleosts, is most probably to be found in the selachians also, although it is difficult to follow it among the very numerous fibers of this region.

No certain conclusions could be reached by my method as to the shorter connections between the tuber cinereum and the lobi inferiores and in the lobi inferiores themselves. GOLGI preparations alone could show these connections which certainly do not form distinct tracts. The most important connections, however, those with other parts of the brain, were found and exhibit a resemblance to those of the bony fishes. The homology of the three frontal attachments has already been pointed out and does not need to be repeated here: the tr. strio-thalamicus with its median bundle constituent and the tr. pallii, with the three frontal tracts of the teleosts, viz., the tr. strio-thalamicus and the tr. olfacto-hypothalamicus lateralis et medialis.

The conclusion of my comparative study of the histology of the fore-brain and 'tween-brain of the bony fishes and selachians was that in the lobi anteriores of the former there are regions which in the selachians are situated in the pallium. This was proved (1) by the ending of the secondary olfactory tracts in the fore-brain; (2) the situation of the bilateral commissure of the secondary olfactory centers; (3) by the hypothalamic attachments of these centers. The fact that in the selachians the tr. pallii is strongly medullated, while in the teleosts the tr. olfacto-lobaris lateralis is unmedullated does not invalidate this homology. On the contrary, the region connected with the tr. pallii in the sharks is much more extensive than the corresponding region related with the tr. olfacto-lobaris lateralis in the teleosts. This difference was to be expected, as well as the difference we found between the two fasciculi retroflexi of the sharks, one of which, attached to the larger ganglion habenulæ, is medullated, while the other, attached to the smaller ganglion and less highly functional, is unmedullated. Even this is not so surprising as the fact that until now Haploidonotus (C. L. HERRICK) and Gadus are the only fishes in which this lateral tract has been found with absolute certainty (certainty at least in Gadus), for I did not find the tract in Lophius, nor in Thynnus, Salmo, nor Gobius capito, nor did GOLDSTEIN find it in the fishes examined by him. In the other fishes the function of the two olfacto-hypothalamic tracts of the selachians and Gadus and Haploidonotus must be included in the medial tract of that name, which I have found in all of the fishes examined.

HALLER has already suggested the homology of part of the lobi anteriores of the teleosts with the pallium of the selachians. The reasons which HALLER gives for his opinion do not agree with my observations. For his hypothesis is founded on the constitution of the tr. strio-thalamicus itself, described by him as, "die aus dem jederseitiger Vorderhirn aus je zwei Theile besteht, aus einem Thalamus Theil und einem caudalen Theil, der wieder in eine gekreuzte und eine ungekreuzte Portion zerfällt." Moreover, he saw in Scyllium in the mantle-bundle also a decussated and an undecussated part. In both the teleost and the selachian which he examined he saw the decussation mentioned in the same commissure, and by reason of this fact he believes that in the striatum of the bony fishes there are pallial parts which, as I have already said, is not in conformity with my observations, although I am quite ready to allow that the final results of our investigations in this matter agree in the chief point.

CHAPTER III.

THE MID-BRAIN, MESENCEPHALON.

1. The Mid-brain of the Teleosts.

From the description of the 'tween-brain it has already appeared that the dorsal wall of the mid-brain is much larger than the dorsal wall of the 'tween-brain and that a part of the latter is overarched by the tectum opticum. For the dorsal part of the 'tween-brain does not extend farther caudad than the commissura posterior, while its ventral part with the lobi inferiores extends under the base of the mid-brain. Under these circumstances it is, of course, difficult to mark a sharp boundary line between the 'tween-brain and the mid-brain, which extends from the commissura posterior above and in front to the posterior insertion of the lobi inferiores ventro-laterally.

This is why I found it difficult to omit the description of some systems belonging to the mid-brain in the second chapter. I there treated particularly and in detail the direct and indirect optic connections of the tectum; accordingly in this place it will be sufficient to give an account of the relations of the tracts. For a more detailed study of the nerve cells and the relations of the different neurones among one another I refer to the treatise of AICHEL and to the works of NEUMAYER, FUSARI, MIRTO, VAN GEHUCHTEN and BELLONCI, who made their investigations on the structure of the tectum for the most part with GOLGI preparations (BELLONCI with osmium preparations).

The outer fiber layer is formed by the termini of the optic nerves. These fibers join the fibers of HERRICK's commissure, entering at the antero-lateral part. Immediately under this layer, which contains medio-dorsally also the fibræ tectales N. optici, and connected with it are the fibers of the brachia tecti. These brachia tecti consist of two chief groups of fibers, a smaller one, situated dorso-medially and a larger one, situated laterally; the latter one may be followed under the ventral opticus root as far as the most caudal part of the tectum. The brachia end in the corpus geniculatum laterale.

I shall now describe the deeper layers of the tectum. I mention first the lowest which is very broad, extending over almost the whole tectum (Figs. xlv, xlviii) and rightly described as *lamina commissuralis tecti.* A part of the most anterior medullated fibers are connected with the ganglion cells of the *torus longitudinalis,* in which I cannot confirm for the cod AUERBACH's statement for the trout that this torus does not receive fibers. In fact, P. RAMÓN Y CAJAL and SALA and after them CATOIS have already described similar connections after GOLGI preparations.

The most frontal fibers of this deep layer (Figs. xli, xliv) gather and form some small bundles lying in an oblique plane, and after first going a little forward and then backward form a part of the anterior portion of the commissura posterior, whose fiber relations will be treated later. These fibers of the *stratum album profundum tecti* do not take part in the formation of the lemniscus, but end in groups of cells situated in and laterally from the eminentia medialis of the subventricular gray substance, *nucleus lentiformis* and *n. corticalis.*

Before continuing I should treat of the macroscopic structure of this subventricular wall, the nomenclature of whose different parts is in some confusion. The earlier anatomists described in this region the so-called *torus-semicircularis* as an important semicircular elevation of its postero-lateral part (Figs. xlv, li). This name, however, has evidently been abused. Thus, for instance, MAYSER, BELLONCI, KRAUSE and others call the place where the com. transversa enters into the anterior part of the subventricular gray substance, stratum zonale tori semicircularis, a very incorrect name which should not be used any more, as the torus semicircularis (or semilunaris) is not yet found there but lies farther backward and more dorsally. The slight medial vaulting of the ventricular floor, which lies anterior to and more medial than the torus semicircularis I shall hereafter always call *eminentia medialis*. Under the stratum zonale of the eminentia medialis the commissura transversa enters, which is in no way connected with the torus semicircularis. In the lateral part of the eminence mentioned where it borders on the tectum FRITSCH found the nucleus corticalis (in which the com. transversa ends for the greater part), a very unfortunate name which, however, has been accepted by most authors. It indicates an imperfectly defined group of cells which immediately passes over into another flatter, more medial cell-layer of the eminentia medialis which has been described as *nucleus lentiformis mesencephali*. Both cell-layers together are indicated by AUERBACH by the name "basal gray substance" and by GOLDSTEIN as "nucleus dorsalis." I should like to see the name torus semicircularis for the part posterior and lateral to this given up and replaced by the name "colliculus" given by RABL RÜCKHARD and C. L. HERRICK. This *colliculus* is a definite well-defined cell-mass of which I shall speak further in connection with the fasciculus longitudinalis lateralis and which I consider the homologue or pro-stadium of the corpus quadrigeminum posterius of higher vertebrates.

Now I shall continue the description of those fibræ profundæ tecti that do not form part of the lamina commissuralis or the commissura posterior. These, the *lemniscus* fibers, gradually gather from all the remaining regions of the stratum profundum, forming a lateral bundle situated between the brachium laterale tecti and the stratum zonale eminentiæ medialis (Fig. xliv, not numbered). These are the most frontal lemniscus fibers which consequently remain most lateral during their entire course in the mid-brain and do not form part of the com. ansulata. None of the most frontal fibers of the lemniscus decussate, in which I agree with EDINGER who gives excellent descriptions of these features.

The next following fiber group is the first decussating group (Figs. xlviii, il). In order to reach its lateral situation it has to pierce through the colliculus; it also sends fibers to and receives fibers from the *nucleus lateralis mesencephali* (which forms the colliculus), as has been stated also by JOHNSTON for Acipenser. Its decussation (represented in Fig. l, Plate III) forms the most frontal part of the so-called *commissura ansulata* and it is important to note that it lies at the level where the union of the lobi inferiores with the brain floor is still rather broad. After the decussation this loop of the commissure lies directly adjacent to the median line (Fig. lii, *lemniscus cruc.*). The first loop which does not decussate lies more dorsally at the most lateral border of the mid-brain.

Now follows a second decussating group, in Lophius (Fig. xxxi) going through and around the fasciculus lateralis longitudinalis to the ventral surface, but in Gadus situated at the outer border of the mid-brain. This group of fibers decussates at the caudal border of the insertion of the lobi inferiores upon the brain and also caudad of this point (Fig. li) and is separated from the first decussation by the most caudal fiber bundles of the tr. lobo-cerebellaris, which go from the lobi inferiores through both these decussations of the com. ansulata into the base of the mid-brain. The pars anterior of the tr. lobo-cerebellaris penetrates into the base of the mid-brain in front of the first part of the commissura ansulata mentioned above.

It is peculiar that the connections of the tectum with the colliculus are mentioned by most authors, but on the contrary the connection of this nucleus with the lemniscus is treated of only by JOHNSTON, who besides, like C. L. HERRICK, describes the nucleus lateralis mesencephali as derived from the fourth layer of the tectum. That a part of the lemniscus fibers end in the colliculus is a fact which need not cause surprise, but which can be only an additional reason for considering the rather important elevation in which the nucleus lateralis is situated as the homologue of the corpus quadrigeminum posterius of the higher vertebrates. A part of the lemniscus ends in both, as also does the fasciculus longitudinalis lateralis, which will be discussed directly.

As appears from the second separate lemniscus decussation of more medial fibers and from the fact that even in Lophius these fibers first take their course medially to and through the fasciculus longitudinalis lateralis (Fig. xxxi), we must consider the posterior part of the com. ansulata of the bony fishes as the pars superior of that commissure of the amphibians and reptiles (EDINGER).

In fact, EDINGER has already mentioned that in the bony fishes the medial part also goes to the base, but without adding that the decussation of this part is separated from the so-called lateral decussation (pars anterior) by the caudal fiber groups of the tr. lobo-cerebellaris.

But this does not exhaust the number of the lemniscus fibers. A fourth very considerable group from the most caudal part of the tectum runs through the posterior part of the colliculus and unites with the first uncrossed part (Figs. li, lii), with which it runs in a caudal direction at the lateral side of the mesencephalon. This part also contains fibers from the colliculus.

Accordingly, to recapitulate, the lemniscus consist of four parts (Figs. xlviii to li):

(1) The most frontal part, arising directly behind the com. posterior, continues to occupy a lateral position in the mesencephalon and *does not decussate.* This contains only tectum fibers.

(2) A part, which contains colliculus fibers, forms the *pars anterior of the com. ansulata* (pars inferior of the higher vertebrates), crossing between the frontal and the caudal parts of the tr. lobo-cerebellaris.

(3) A group which contains, besides tectum fibers, many fibers from the colliculus decussates behind the most caudal bundle of the tr. lobo-cerebellaris at the level of the most posterior attachment of the lobi inferiores with the brain and forms the *pars posterior commissuræ ansulatæ* (homologous with the pars superior of amphibians and reptiles).

(4) A part, also containing fibers from the colliculus, but going *without decussation*, in a caudal direction together with the first mentioned undecussated part.

Accordingly, we find three lemniscus groups in the caudal part of the mid-brain (Fig. lii) lying peripherally on both sides of the median line. The part lying highest and most lateral contains the undecussated fibers of the first and fourth groups, followed more basally by the decussated third group, and finally close to the median line, the second group, also decussated, the two tracts separated only by the corpus interpedunculare. The fibers of the lemniscus go caudad in these relations and end for the most part in the medulla oblongata (and spinalis), and in smaller numbers enter the cerebellum, so that their further course will be taken up under the metencephalon.

Now, taking up the *commissura posterior*, I have already mentioned that its *anterior fibers* originate from the stratum profundum tecti and end partly in the homonymous stratum of the opposite side, as has already been described by MAYSER, and partly lead to the gray substance of the eminentia medialis. To this *first part* of the commissura posterior I must add those fibers which connect the eminentiæ mediales with the tori longitudinales and which certainly are in direct or indirect connection with those fibers of the stratum profundum tecti which enter the torus longitudinalis from its superior side (*cf.* Fig. xlv with Fig. xlvi).

The *second part* of the commissura posterior is formed by fibers which connect with one another the nuclei lentiformes mesencephali, or the medial subventricular cell layers of both sides. This is by far the larger part. The fibers belonging to it form the pars media of the commissure, the more caudal bundles of which (*third part*) bend downward and backward and run along the aqueduct above the tr. thalamo-spinalis into the most anterior part of that cell-mass from whose posterior part the fasciculus longitudinalis dorsalis arises.

That fibers of the *fasciculus longitudinalis dorsalis* continue into the commissura posterior, as C. L. HERRICK and EDINGER think, is an opinion which I can contradict on the basis of exact investigations on Lophius, Gadus, Thynnus, Salmo and Cottus. The results of my investigations agree with those of AUERBACH and VAN GEHUCHTEN, who state that in the anterior part of the same cell-group from which the fasc. long. post. originate the commissure fibers end. I do not consider that thalamus fibers belong to this fasciculus, as EDINGER and JOHNSTON do. It arises with heavily medullated fibers in a group of cells of the mid-brain which is the frontal extension of the oculomotorius nucleus, situated immediately behind the most posterior nucleus of the commissura posterior, as VAN GEHUCHTEN also mentions. After having arisen (probably with total decussation) in this group of cells, the fibers go backward laterally of the median line immediately under the ventricle and are augmented to a considerable extent by fibers from the oculomotorius and trochlearis roots and nuclei.

As already mentioned in the account of the 'tween-brain, the fibers which EDINGER judged to belong of the fasc. long. post. are evidently fibers which have been described by myself and others as thalamo-spinal bundle. These fibers go backward and are increased in the oblongata by the addition of short association tracts and they are distinguished from the dorsal fibers by their more delicate medullary sheaths and by the fact that they do not get their myelin as soon as the fasc. longitudinalis dorsalis, which, moreover, is more heavily medullated. While the dorsalis fibers have the appearance of primary and secondary motor fibers, the thalamo-spinalis lacks these qualities. Since, however, the fasciculus dorsalis is merely a collective name for different kinds of fibers, there is no objection in principle to considering the other longer and shorter association fibers as belonging to the fasc. dorsalis. But even in this case I must deny that they form part of the com. posterior or of the fibræ ansulatæ thalami.

As belonging to this tract I must mention also a connection with the lateral part of the valvula cerebelli (not figured), which has been mentioned also in Acipenser by GORONOWITSCH and JOHNSTON, in the region of the trochlearis and oculomotorius nuclei. I regard these fibers as a crossed connection between these nuclei and the cerebellum, of which, however, I shall have more to say in the fourth chapter.

In the same place where these fibers leave the cerebellum another tract enters the valvula directly mesad of those fasc. long. posterior fibers. It is the *tr. mesencephalo-cerebellaris superior* (Figs. xlvii to lii, Plate III, and Fig. 5, Plate XII), already referred to when speaking of the com. horizontalis and the tr. rotundo-lentiformis, with which it originates from the nucleus lentiformis in the most anterior part of the eminentia medialis directly behind the com. posterior. In Figs. xlvii and xlviii the fibers designated as *37*, *42b*, *23* contain the beginning of this tract which, continuing its course in the same direction backward, runs mesad of the colliculus and mesad of the colliculus-bundle, the fasciculus lateralis, and directly adjacent to the latter, as Figs. l and li show. But while the lateral fascicle runs backward into the oblongata, the medial tract enters the valvula cerebelli and is still visible at the base of the cerebellum in Fig. lii. In this region of the cerebellum, which must be regarded as the velum, the tr. mesencephalo-cerebellaris superior runs through two roots of the nervus trochlearis which unite more laterally and then leave the velum (Figs. lxxxvi and lxxxvii, Plate VI).

This tract was first described by C. L. HERRICK in his work on the thalamencephalon and mesencephalon as arising in the region of the com. posterior "in the mesal denser part of the nidulus corticalis," which agrees with the situation of the nucleus lentiformis which laterally fuses with the nucleus corticalis. GOLDSTEIN saw the same tract as HERRICK describes it, and as I saw it running along with the com. horizontalis, as mentioned above, but he regards the com. horizontalis as a part of it, viz., as a cerebellar commissure, and he saw its frontal curve passing upward into the tectum, which I cannot confirm. My results are the same as those of C. L. HERRICK, with the qualification that I doubt whether the tr. mesencephalo-cerebellaris superior afterward decussates in the cerebellum. If some of its fibers cross there, it is surely only a small part. JOHNSTON probably saw the same connection in Acipenser and gave it the name of tr. tecto-cerebellaris, as he, too, saw its fibers going upward into the anterior part of the tectum. He does not describe any decussation of its fibers.

The *fasciculus longitudinalis lateralis* runs parallel with, and lateral to, the bundle last described, arising from the *nucleus lateralis mesencephali*, which is situated in the *colliculus*, or *torus semicircularis*, where its fibers are assembled from a large area (Figs. xlviii to li, Plate III). The tract is very distinct in Gadus and more easily traced than in any of the other fishes examined. It runs backward into the oblongata as a compact medullated bundle and ends after decussation in the acoustic lobes, forming in this region the greater part of the dorsal arcuate fibers (Fig. xciv, Plate VI). The tract must be regarded as a secondary acoustic tract and has been described in higher vertebrates also as a connection between the acoustic center and the corpus quadrigeminum posterius, of which, as I pointed out above, the colliculus must be regarded as the homologue, or rather as a prostadium, in the teleosts.

JOHNSTON, who apparently described the same tract in Acipenser, saw the greater part of its fibers ending in the tectum, which agrees with the fact that the colliculus must be regarded as derived from the deeper layer of the tectum and with the ending in the colliculus of a part of the lemniscus fibers and with the fact that in the ganoids the colliculus is far less strongly developed than in the bony fishes (*cf.* the account of the selachians in the second part of this chapter). The name which JOHNSTON gave to his secondary frontal acoustic tract is tr. bulbo-tectalis, which

I think a good one, though it is surely better to keep the name already known to every one who has studied the acoustic connections—fasc. longitudinalis lateralis.

I have next to mention the *tr. lobo-cerebellaris* which merely passes through the mid-brain and whose origin was described in the second chapter when treating of the hypothalamus. It is evident that this tract is the homologue in the fishes of the *tr. tegmento-cerebellaris* of the higher animals.

In agreement with C. L. HERRICK, whose opinion I am more and more inclined to accept, we are to believe that the posterior region of the lobi inferiores is the homologue of nuclei of the tegmentum of the higher vertebrates. With the disappearance of the lobi inferiores this region would have come into the basis mesencephali. In view of this fact I consider it not impossible that C. L. HERRICK is correct in considering the recessi inferiores of these lobes as the homologue of the corpora mammillaria. EDINGER, who in both the selachians and the teleosts places the tegmentum in the hypothalamus, describes the tr. tegmento-cerebellaris as "exceedingly constant." In Gadus it consists of very important bundles, almost all medullated, and decussating behind the exit of the oculomotorius after which they enter the cerebellum.

I could find no more mid-brain tracts forming connections between the hypothalamus and the cerebellum, though more have been described by other authors. Thus, GOLDSTEIN describes behind the nucleus rotundus a nucleus ruber from which a tract runs through the mid-brain into the cerebellum, just as has been described by CATOIS. The latter author, however, seems not to be quite convinced of this fact. GOLDSTEIN described still another connection of his nucleus ventralis (nucleus rotundus of other authors) and the cerebellum which I could not find, nor the medullated connection of the same nucleus mentioned by HERRICK.

Two other mid-brain tracts, however, must be mentioned here. They are the *fasciculus retroflexus* and the *tractus lobo-peduncularis*, both described in the second chapter as ending in the *corpus interpedunculare*, the first after crossing, the second uncrossed, the first originating from the ganglia habenulæ and the second from the medial posterior part of the lobi inferiores. Their origin and course have been described in the second chapter. Fig. 5 (Plate XII) gives a good idea of their ending.

Finally, I must demonstrate the origins of the eye-muscle nerves. This I have already done when treating of the fasc. long. dorsalis for the *N. oculomotorius* whose roots arise, about half crossed and half uncrossed, from a mass of rather large polygonal cells situated behind the nucleus fasciculi long. dorsalis near the medial line under the aqueduct (Figs. xxxi and li). The fibers run downward and somewhat laterally and leave the brain in the fissure formed by the lobi inferiores and the base of the mid-brain.

A nucleus caudad from this situated in the same region and composed of the same kind of cells as those just mentioned is the nucleus of the *N. trochlearis*, which, in Lophius sends its fibers around the aquæductus and then in a single bundle almost perpendicularly upward (Fig. xxxiii). In Gadus, on the contrary, it runs obliquely upward through the velum in two bundles, of which the upper lies over and the lower under the tr. mesencephalo-cerebellaris superior which enters there (Figs. lii, lxxxvi, lxxxvii). The most dorsal of these roots leaves the upper side of the velum between the cerebellum and the most posterior part of the tectum opticum and then unites with the lower root which leaves the brain separately. Thereupon they unite and pass forward, for a short distance accompanying the trigeminus.

2. *The Mid-brain of the Selachians.*

The structure of the mid-brain in the selachians, though in the main the same as that of the teleosts, differs by the lesser development of the tectum which does not overlap the adjacent parts of the brain as much as in bony fishes. Under the tectum, however, there is a greater difference in the structure of the sub-tectal mass, due to the absence of the torus longitudinalis and the very much smaller development of the colliculus (torus semicircularis), which has not been mentioned by any of those who have made the selachians the subject of their investigations. CATOIS supposes the analogue of the torus to be situated in the more central layers of the mid-brain. HALLER also mentions that the torus semicircularis in the teleosts is a specially developed region, and neither HOUSER nor EDINGER mention it for the Plagiostomata. As in the bony fishes, the posterior part of the mid-brain is chiefly a passage for tracts; but in the most anterior dorsal part immediately under the ventricle important systems of fibers originate and terminate.

The course of the *optic fibers* I have already mentioned when treating of the 'tween-brain, indicating both their division into two roots, a dorsal and a ventral, about the corpus geniculatum laterale and their termination in the upper layer of the tectum. Though with much less certainty than in the teleosts where the degenerated condition of one N. opticus proved very useful to me, I was, nevertheless, able to see in Galeus also the fibers of the tectum situated directly mesial to the optic fibers terminating in the corpus geniculatum laterale as *brachia tecti.*

For the finer structure of the ganglion cells and their mutual relations I am obliged to refer to HOUSER, who examined them by the GOLGI method, and proceed at once to the description of the deep medullated layer, the *stratum album profundum.* Here, as in the teleosts, there is a *lamina commissuralis tecti*, a flat but very large dorsal commissure of the two parts of the tectum (clearly to be seen in Fig. lv). As in the teleosts, the most anterior fibers of this commissural system constitute a part of the *commissura posterior* (Fig. lv), of which by far the greater part consists of fibers which disappear in the cell layers which are situated immediately under the optic ventricle (Fig. lvi).

Before continuing the description of the tracts I must mention that the differentiation of this gray substance under the optic ventricle is by no means so clear as in the teleosts, either in the outlines of this region or in the distribution of the ganglion cells.

The *eminentiæ mediales* are scarcely visible and the only thing to be stated here about the *torus semicircularis* is that in Galeus I found a distinct but small protrusion of the postero-lateral subtectal region of the mid-brain (Fig. lix), which I must suppose to be the homologue of the *colliculus*, or torus semicircularis. That this is the case I conclude (1) from its situation in the posterior subtectal region; (2) from the fact that, as in the teleosts, it is provided with numerous ganglion cells (*nucleus lateralis mesencephali*); (3) from the fact that there is a very distinct medullated tract which arises in the stratum album profundum tecti and terminates here. This tectal relation was also found in the teleosts, where its fibers were situated between those lemniscus fibers which pierce through the colliculus. This is not the case here because the situation of the colliculus in the selachians is more medial than in the teleosts, so that all the real lemniscus fibers run to one side of it. (4) A small number of fibers of this nucleus run caudad, of which I shall speak later.

I shall next describe the course of the principal mass of the deep layer of the tectum, whose fibers do not form a part of the com. posterior, but just as in the teleosts form the *lemniscus*, or fillet, which, together with the thalamo-spinal tracts, in the selachians fills nearly the whole central mass of the mid-brain (see Fig. 7, Plate XIV). The division of the lemniscus fibers into four parts, as in the teleosts, is not so easy in the selachians. The resemblance, however, is easily seen to this extent that part of the fibers decussate and part take an uncrossed course. One gets the impression that the more medial fibers of this system decussate, while the more lateral fibers generally take the direct course and continue to be more lateral in the oblongata also, while in this part of the brain the crossed fibers lie, as in the bony fishes, nearer the ventral surface and the raphé. It is, however, extremely difficult to distinguish in the oblongata the three groups which are so plain in the teleosts. In the latter fishes, moreover, a part of the lemniscus took its origin from the nucleus lateralis mesencephali in the colliculus.

We found, as already mentioned, a fiber tract originating in the colliculus of the selachians and running backward and mingling with the fibers of the thalamo-spinal and tecto-spinal bundles. Naturally it is quite impossible to say whether these fibers represent a colliculus portion of the lemniscus or whether they represent the fasciculus longitudinalis lateralis. The latter tract differs fundamentally from the lemniscus (though in human anatomy very often included with it) in that it is not direct like a part of the lemniscus, nor crossed in the com. ansulata like the other part, but it passes on to the acusticum region and constitutes the greater part of the fibræ arcuatæ dorsales of that region. It is quite impossible to say whether the caudal attachment of the colliculus in the selachians is lemniscus or lateral tract; but this can be regarded as sure that in the selachians, whose acoustic centers and lemniscus fibers are so strongly developed, the colliculus can represent only a small part of that structure in the teleosts, and we must surely assume that the greater number of fibers which in the teleosts arise from (or more properly terminate in) the colliculus end in the selachians in those layers of the mid-brain from which the colliculus of the teleosts has been derived, *i. e.*, in the place where the tectum is attached to the ventral wall and in the deep layer of the tectum itself. In connection with this deduction, two facts are very interesting: first, the great radial dimensions of the roof, especially the broad base by which the tectum is inserted on the ventral wall of the mid-brain in the selachians as compared with the teleosts (*cf.* the figures of the tectum of the two fishes); and, second, the fact that JOHNSTON found a tract ending in the tectum of the ganoids (where the colliculus, moreover, is very small), which in the teleosts certainly does not end there, his tr. bulbo-tectalis, my fasciculus lateralis, the secondary acoustic tract.

I cannot leave the description of the tectal attachments without mentioning a tract which EDINGER has also described in his publication on the cerebellum, and which he calls the *tr. cerebello-tectalis*, a connection of the cerebellum with that part of the lobi optici in which the *nucleus magnocellularis tecti* is found (Figs. liv to lix). This particular nucleus has already been mentioned by ROHON and SANDERS. The former did not make any mention of its neurites, but SANDERS described their axis cylinders as running over the median line in the lamina commissuralis tecti. HOUSER gives an extensive description of its cells and also records that not all of their neurites take their course over the median line. He is of the same opinion as P. E. SARGENT that the most anterior fibers of this nucleus enter into the aqueduct and afterward into the sinus rhomboidalis, thence backward into the medulla spinalis, while the most posterior cells of this group form the cerebellar tract mentioned.

I have not seen these intra-ventricular fibers, nor even one of the neurites turned in the direction of the optic ventricle, but can state clearly that almost all of them cross the median line and mingle with the fibers of the deepest layers of the tectum. I do not know whether they afterward run into the cerebellum as HOUSER stated for these fibers and as EDINGER and JOHNSTON think possible, forming the *tr. tecto-cerebellaris* which disappears in the velum anticum. But it is quite certain that a tract of a few thick and strongly medullated fibers is easily to be distinguished in the velum crossing there and running forward and then going upward into the deep layer of the tectum. This is as described by JOHNSTON for the ganoids save that he does not speak of a decussation of these fibers in the velum, and it may be that the large cells of the tectum are related directly or indirectly to this tract, which I have called the *tr. tecto-cerebellaris superior* to distinguish it from a part of the commissura ansulata fibers which also form a cerebellar connection. This nucleus magnocellularis tecti has been generally considered as the place of origin of a mesencephalic radix trigemini, from the time that BURCKHARDT described it as such and homologized it with a nucleus which in higher vertebrates is found laterally of the aquæductus Sylvii and gives rise to the tractus trigemini. That the nucleus magnocellularis tecti forms the nucleus of a radix quinti I cannot believe. At least I am not able to advance any proof for it, but can adduce two points against it. The first is the nonexistence of this nucleus or of such a root in the teleosts, in which the trigeminus is at least as strongly developed as here. In the second place, I have been able to recognize those fibers which have been described as the tr. quinto-tectalis by EDINGER as being in no relation whatever to the tectum. I shall have more to say about this tract in the next chapter.

Regarding the *commissura posterior*, I have already mentioned that its most anterior part is provided by fibers originating in the deep layer of the tectum, while the second part, which is the strongest, begins in the median subventricular substance, and both end in this substance of the opposite side, as has been described for the teleosts. Farther backward the fibers decrease in number and now pass more directly caudad and at a little distance in front of the origin of the fasciculus longitudinalis dorsalis they divide into fine bundles which evidently terminate there. This is the reason why I cannot believe that either here or in the teleosts the commissural fibers pass into the fasc. long. posterior. But the fibers of this fascicle begin in the same group of cells in whose anterior part the fibers of the commissure terminate, from which it follows that an indirect relation between these two systems is more than probable.

The dorsal longitudinal fascicle first appears as thick, strongly medullated decussating fibers which increase greatly in number near the nucleus of the oculomotorius. It then runs backward into the oblongata under the ventricle close to the raphé.

Three other tracts must be described here, of which only one passes out of the mid-brain, the others terminating within it.

The *tr. lobo-cerebellaris*, whose origin has been described in the second chapter, enters the mid-brain at its junction with the inferior lobes and runs backward in its latero-basal part, crossing at the same level as the ansulate commissure and then going upward into the cerebellum (Fig. lxx, Plate IV) between the ascending fibers of the tr. mesencephalo-cerebellaris frontally and the cerebellar fibers of the lemniscus caudally. This tract is as strongly developed in the selachians as in the teleosts and follows the same course.

Regarding the *fasciculus retroflexus*, I have already mentioned that this compact bundle before entering the interpeduncular ganglion divides into three or four smaller bundles which cross the median line at the same horizontal level (Fig. lxi, Plate IV) and then enter the strongly developed ganglion interpedunculare (Fig. lxxii).

The *tr. lobo-peduncularis* is much more difficult to trace with certainty. This tract which is so compact and easily traced in the bony fishes as an uncrossed feebly medullated connection of the posterior and medial parts of the inferior lobes with the corpus interpedunculare has been described by JOHNSTON under the name of tr. mammillo-bulbaris, and surely is present in the selachians, where we find mesad of the tr. lobo-cerebellaris a very clear unmedullated tract which cannot be followed further than the base of the mid-brain. Though I was not able to see its terminus in the interpeduncular body, I am convinced that these fibers represent the lobo-peduncular connection of the bony fishes.

As for the origin of the *oculomotorius* and *trochlearis*, I must mention first that it may be that the greater part of the fiber tract described as tr. mesencephalo-cerebellaris or tecto-cerebellaris superior does not enter the tectum at all, but enters the nuclei of these nerves, representing the similar connection in teleosts and ganoids. The more I investigate this region the more is this impression strengthened, which would find some further support in the fact that the fibers which will be described in the second part of the fourth chapter as tr. cerebello-motorius cruciatus, arise in the same part of the cerebellum as these fibers, have similar heavily medullated sheaths and take the same course.

I can confirm CATOIS that the decussation of the eye-muscle nerves is not total, but partial. The *oculomotorius* leaves the brain at its base and the *trochlearis* dorsally just anterior to the velum.

CHAPTER IV.

THE HIND-BRAIN, METENCEPHALON.

1. The Hind-brain of the Teleosts.

The medulla oblongata in the teleosts forms the transition between the posterior part of the mid-brain and the medulla spinalis. The region where the mid-brain and hind-brain join is covered dorsally by a highly developed wall through which several groups of fibers continue their course. This roof of the aqueduct is the velum anticum cerebelli. Under and behind the velum the aqueduct continues into the ventriculus quartus, or rhomboidalis, which is larger and deeper in immature Lophius and whose upper part, which is roofed by the widely extended cerebellar arms (Fig. lxxiv, Plate V), is in the full grown fishes narrowed to a fissure by means of a mass, the *nucleus lateralis cerebelli* (Figs. lxxxvii to lxxxix, Plate VI), situated at the union of these cerebellar-arms and the oblongata, protruding them outward and especially inward. This nucleus has been described by others as "Rindenknoten," or secondary vagus nucleus.

Behind the cerebellum the fourth ventricle is for a short distance covered by the tela choroidea, from which the plexus choroideus grows into the ventricle. In Gadus the part of the ventricle which is covered by tela is still less than in this young specimen of Lophius, though in the latter a commissure appears a little farther caudad in this part of the roof between the caudal ends of the tubercula acustica (Fig. lxxviii, Plate V). In the full-grown codfish there is not only a commissure between the posterior parts of the acustica (Fig. xcvii, Plate VI), but the tubercula acustica themselves are fused (Figs. xcv, xcvi). Accordingly, the whole roof of the sinus rhomboidalis is of nervous character and this greatly reduces both the membranous covering and the cavity of the ventricle itself. Behind the acoustic region the roof is again for a space ependymal, but soon again becomes massive by the union of the lobi vagi, behind which both in Gadus and in Lophius another small commissure connects the two sides, the *commissura infima Halleri* (Fig. lxxx).

At the plane of this commissure in Lophius a new and more important enlargement of the sensory field begins to appear, in which, among others, the tractus descendens nervi quinti terminates—the *nucleus spinalis trigemini,* or nucleus ROLANDI. This sensory mass extends with diminishing circumference for some distance into the medulla spinalis and in Lophius is the terminal nucleus of sensory spinal roots.

Over its posterior part are the giant ganglion cells previously examined by USSOW, and FRITSCH and after them, among others, by TAGLIANI, SARGENT, DAHLGREN, HOLMGREN, JOHNSTON and STUDNICKA, who, though not always of the same opinion, describe the course of their neurites and their characteristic vascular supply. Here they are more numerous than farther caudad (*cf.* Figs. lxxxiii, lxxxiv with lxxxv).

After this short description of the most important external features of the oblongata, we may proceed to the course of the tracts, the entrance of the nerves and the position of the nuclei. I shall begin with the description of the fibers which connect the more frontal regions with the oblongata, afterward taking up the nerves (*cf.* Fig. 8, Plate XV).

As I have already treated of the mesencephalo-cerebellar and thalamo-cerebellar connections, I can begin with the *fasciculus longitudinalis lateralis,* which in the most caudal parts of the midbrain appears as a round tract not divided by any septa or only by very small ones (Figs. lxxxvi, lxxxvii, Plate VI). In Gadus it continues caudad till near the entrance of the motor trigeminus, where the nucleus of this nerve divides it into two parts (Fig. xci), of which the most lateral part touches the secondary communis tract and seems to belong to it. This, however, is not the case. Both frontal and caudal of the trigeminus this bundle again joins the rest of the fasc. lateralis which does not give off any fibers as far as the trigeminus region extends. But farther back it is first divided by several septa into smaller bundles and afterward (see Fig. xciv) decussates entirely and enters the acustico-lateralis region. These decussating fibers form there an important part of the *fibræ arcuatæ dorsales,* as also EDINGER describes for the reptiles. Accordingly this tract relates the terminal nucleus of the nervus octavus (inclusive of the nervi laterales) with the colliculi, and consequently is to be considered as connecting the static center with a region indirectly connected with the optic system.

As a second connection of the oblongata with the frontal parts of the brain, I mention the important tracts to the deeper layers of the tectum opticum, *the fibræ tectales or lemniscus*, of which I have already mentioned when describing the mid-brain that after decussating they deliver a contingent of fibers to the cerebellum. This is the reason why its fibers are not so numerous in the oblongata as in the mid-brain. Its fibers at the beginning of the oblongata are all situated ventrally of the superficial origin of the trochlearis (see Fig. lxxxvii) and at the entrance of the trigeminus also they are all situated ventrally of the fifth root. During this part of their course the fibers do not diminish in number. Further down, however, they diminish and one separate bundle bends inward from the most laterally situated group and can be traced into the abducens nucleus. This agrees with AUERBACH's statement that he saw tectal fibers end in the oculomotorius and trochlearis nuclei, as HALLER afterward confirmed (Fig. xcii). That I was not able to make the latter observation myself I explain as due to a less fortunate direction of my sections at that point, for in view of the certainty with which I can demonstrate this connection for the abducens nucleus I can no longer doubt these statements, the more so as physiologically it can awaken no surprise that centrifugal fibers of the tectum should pass toward the nuclei of the eye-muscle nerves.

These fibers, however, form only a very small part of this enormous ventro-lateral mass of fibers about whose exact terminations the statements of authors differ. EDINGER conceives that they end in the nuclei of the sensory nerves and accordingly would form a centripetal tract in which in the higher animals it is possible to trace even the different fascicles from each sensory nucleus separately. HALLER is of a different opinion and considers them as connections between the tectum and secondary motor regions, as far as I can make out his meaning. The undecussated groups of the lemniscus situated laterally which give off the abducens tract described above decrease greatly between the region of the trigeminus and the acustico-facialis, as MAYSER has already noted (*cf.* Figs. lxxxix and xcii, Plate VI). In this same region a gray mass is formed ventrally which contains only small cells and was described also by HALLER and there is no doubt that these fibers end here. This gray mass extends very nearly down to the glossopharyngeus and vagus, but is most extensively developed about the tuberculum acusticum (Figs. xciv to xcvi). At this level there terminates the first decussated part of the tr. tecto-bulbaris which runs from the com. ansulata along the raphé and which JOHNSTON, who found almost the same relations in the sturgeon, calls tr. bulbo-tectalis. Only a small part of the more lateral undecussated fibers of this tract run farther backward (Figs. xcvii to xcix), turning gradually ventrad so that the two groups of each side are very near each other and are separated from the gray mass by the fibræ arcuatæ externæ, whose origin I shall take up later. These bundles are the only ones of the tectal fibers which continue farther caudad than the regio acustico-facialis, reaching even beyond the regio glossopharyngeo-vagalis. I am of exactly the same opinion as HALLER regarding the termination of the main mass of tectal fibers in the regio acustico-facialis. HALLER, however, upon the examination of GOLGI preparations considered this region related with the motor nuclei, though he does not positively say so. I am of the other opinion that this region is connected with the area of the sensory nucleus by the ventro-dorsal arcuate fibers which are here so numerous. For this region I consider the tectal fibers as tertiary sensory tracts from the nuclei of the oblongata.

The third group of fibers which can be followed from the mid-brain into the oblongata is the *fasciculus longitudinalis posterior* or *dorsalis.* The situation of this tract, which is constant in all animals, is the same in the mid-brain, immediately under the aqueduct close to the raphé, in the oblongata and still farther back. While I can recommend the summary which VAN GEHUCHTEN gives of all that has been said about this tract in the higher vertebrates and also EDINGER'S "Vorlesungen," yet I wish to point out here what is known of this bundle in fishes.

All investigators state that its fibers increase greatly in the region of the nuclei of the oculomotorius and trochlearis and GORONOWITSCH, JOHNSTON, EDINGER, HALLER and VAN GEHUCHTEN are all of one opinion that it also receives fibers from the motor nuclei of the oblongata. The statements about the other relations of the fasciculus dorsalis, which are certainly not less developed or of inferior interest, are far less numerous. GORONOWITSCH observes in his work on Acipenser, "a part of these fibers come from the valvula cerebelli," and JOHNSTON describes as passing into the most anterior part of the cerebellum "fibers—heavily medullated—emerging from among those of the fasciculus longitudinalis posterior," which he thinks originate from the region of the trochlearis, while Haller saw in this bundle indirect decussated connections of the cerebellum with the motor seventh nerve.

Regarding my own results, I can confirm Van Gehuchten's information that this tract both in the teleosts and in greater measure in the sharks increases as it passes caudad, particularly near the origins of the fifth and seventh nerves. The fascicle receives fibers from all motor nerves, as well as from the continuation of the ventral motor column, which is situated in front of the trigeminus and of which Haller also speaks (Figs. lxxxviii, lxxxix). The course of the motor fibers of the fasciculus dorsalis is frontal in almost all cases, as the motor nuclei lie for the greater part behind the entrance of their roots. This particular relation of the motor nuclei to their roots has also been stated by Johnston. He justly observes that the only exception to the rule is a part of the fibers of the trigeminus. In the facialis the difference in position is greatest.

These decussating motor fibers form the *first group* constituting the fasc. long. dorsalis. To these we must undoubtedly add still other connections between the motor nuclei themselves which permit the coördinated functions of the different muscles of the eyes.

Its *second group* comprises fibers belonging to the static centers, the cerebellum and the acustico-lateralis center covered by the cerebellar crest: The cerebellum gets its connection with the fasc. long. posterior later than the regio acustico-lateralis; for, while in all adult fishes examined both groups of fibers were present, the cerebellar group was lacking in the immature Lophius. The fibers which have already been mentioned by Goronowitsch and Johnston for Acipenser must be regarded as the most anterior members of this cerebellar group. They are found at the junction of the mesencephalon and the oblongata, and crossing through the fasc. long. posterior, disappear in the region of the trochlearis nucleus, just as Johnston found it in Acipenser. I have already mentioned this in Chapter III.

I am not so sure, however, about the character of these fibers as I am of the compact medullated tracts which, coming from the fasc. long. posterior, pass in an elegant curve (marked *53* in Fig. lxxxvi, Plate VI) mesad of the lobo-cerebellar fibers, after the decussation of the latter. These tracts seem to run on frontally in the fasc. long. posterior, after having crossed in this fascicle. But immediately behind them the crossed oblongata connection begins, sending its fibers first to the motor column which lies in front of the trigeminus nucleus. I could follow this bundle (Figs. lxxxviii, lxxxix), from the cerebellum into this nucleus easily, crossing in the posterior longitudinal fasciculus, in which it takes only a short course.

Immediately following this are the cerebellar connections with the motor trigeminus, abducens and facialis nuclei. It is very probable that the group of fibers which go farther backward terminate in the motor column of the medulla spinalis. We have here a whole system of fibers passing for a longer or shorter distance in the dorsal bundle and going to the nuclei of the motor nerves and which, therefore, I should prefer to call *tr. cerebello-motorius cruciatus*, as this name better indicates the connection forming this system than the name tr. vestibulo-nuclearis, given to that part of it which has been discovered by Ramón y Cajal in mammals as being the connection between Deiter's nucleus and the nuclei of the eye-muscle nerves.

After I had already finished my work I received Banchi's description of the cerebellar connections, in which this author has not only described this connection of the cerebellum with the fasc. long. posterior, but has also found by Marchi experiments that it degenerates after the destruction of the cerebellar lobe. He could follow the fibers in the fasc. long. posterior frontally up to the third nerve and caudally to the spinal cord, so that there can be no doubt about the existence of this tract. A similar connection, moreover, has also been found by Köppen in the reptiles. This first part of the second group was not yet developed in my specimen of Lophius, as indicated above; on the other hand the second part of the same group was present. This has still to be described and I mention here merely that it is a similar motor connection for the whole octavus region, the latter being an enormously developed static center which, covered by the cerebellar crest, extends far behind the cerebellum on the dorsal and lateral aspect of the oblongata.

The posterior part, however, of this static region is situated more ventrally, laterally of the tr. descendens N. quinti. By this peculiar downward extension of the octavus region its decussating association fibers are divided into two bundles (Figs, xcv, xcvi, Plate VI), one of which originates from the dorsal region caudad of the beginning of the fasc. long. lateralis while the other and smaller one arises more laterally and bends down above and around the tr. descendens nervi quinti, after which it joins the more dorsal fibers in their passage through the raphé.

Now, in Gadus some bundles of the dorsal part of these fibers may be followed into the motor cell column after decussation through the dorsal longitudinal bundle. These may be called *tr. octavo-motorius cruciatus.* This tract arises in the tubercula liniæ lateralis in the same way as the analogous cerebellar fibers in the cerebellum, for it forms the most medial bundles of this region. They form a considerable part of the *fibræ arcuatæ internæ*, or *dorsales*, which a little farther frontally also include the decussating fibers of the lateral longitudinal bundle, already described.

This static-motor connection, accordingly, is the continuation of the cerebellar tract described; or rather, conversely, the cerebellar tract is an extension of this static-motor connection, of more recent origin. This appears from its absence in younger animals, as the cerebellum itself arises late as we know from SCHAPER'S investigations, where its bilateral origin from the lateral wall of the oblongata is described. The static function of these two regions and their general agreement in structure has been abundantly confirmed by physiologists and histologists. As far as this connection of the primary center is concerned, I believe that the experiments of QUIX on the labyrinth of the sharks may also prove the presence of this simple connection between the octavus region and the motor nuclei, in this case the oculo-motor nuclei, as after stimulation of the labyrinth he observed several immediate ocular movements, as Professor BOLK once demonstrated to me in Naples.

The presence of fibers, partly uncrossed and partly decussating in the median line of the oblongata, going from the static center backward into the motor nuclei was demonstrated by BETHE by physiological experimentation in his investigations on the locomotion of Scyllium. Although it would be very interesting indeed to look for further relations between his experiments and those of LOEB and STEINER with the structures described, the scope of my investigations does not allow this and I must now leave the dorsal longitudinal bundle and pass to another complex of short and long paths which many authors consider to belong to the group last described—the *tr. thalamo-spinalis.*

Its fibers are distinguished from the dorsalis fibers only by a somewhat smaller caliber and lighter color after the WEIGERT stain, in this respect resembling the sensory tracts of this region more than the motor ones, which have the same appearance as the fasc. long. dorsalis, as I mentioned when treating of the midbrain. They are present through the whole length of the oblongata under and at the side of the last mentioned system and caudally their number is greater than frontally. These fibers also seem to increase in the octavus region and doubtless this complex must be considered as composed, like the dorsal bundle, of shorter and longer longitudinal tracts forming a fronto-caudal and a caudo-frontal association system, probably connecting regions situated laterally to the motor column. It certainly does not contain thalamic fibers exclusively in all parts of its course. As I described when treating of the 'tween-brain, its fibers assemble first in the substantia grisea centralis and in a still more lateral region.

Now, passing to the nerves of the oblongata, I will describe the situation of their roots, their intra-medullary courses and their terminal nuclei and nuclei of origin, some of which I have already mentioned in connection with the frontal tracts.

The *nervus trigeminus* enters the oblongata laterally with its sensory and motor fibers (Lophius, Fig. lxxiv, Plate V; Gadus, Figs. xc, xci, Plate VI). The motor root, consisting of thicker, more heavily medullated fibers, originates from the large motor ganglion cells which in the younger Lophius still lie immediately under the fourth ventricle, but in the full-grown cod are removed downward between the two bundles of the fasc. long. lateralis, as already mentioned when describing that tract. They are situated in a plane which forms with the raphé an angle of about 45 degrees and extend backward into the motor facialis nucleus and forward into the ventral cell column which was described when speaking of the cerebello-motor tract. The motor fibers originate partly without decussation, while another part goes through the fasciculus dorsalis and ends in the nucleus of the other side. I have already mentioned that this nucleus has a crossed connection with the cerebellum by means of fibers which run through the fasciculus dorsalis.

The sensory fibers of the trigeminus enter at the same level as the motor, but only a very small part of them end there. Nearly all of the fibers of the sensory quintus remain in a ventral situation and go backward as a compact bundle accompanied as far as the lobi glossopharyngeo-vagales by the secondary communis tract (secondary vago-trigeminus tract of MAYSER) behind which the bundle continues and is soon divided into two parts. One part which is always situated most dorsally in the posterior vagus region turns upward and enters the *nucleus Rolandi* (Fig. lxxxi) where it ends. I have already mentioned that this region is very large in the teleosts, especially in Lophius piscatorius. Accordingly, KINGSBURY, who examined many species, rightly says, "the enlargement of the metatela produces corresponding ectal swellings resembling the clavas of the mammalian brain; and from this the spinal fifth root can be traced."

This, however, is not the only terminus of the tr. descendens nervi quinti. A considerable part goes farther backward under the nucleus of ROLANDO between the posterior funicles of the medulla spinalis beyond which it cannot be separately followed (Figs. lxxix to lxxxii, Plate V). This last part is by no means small, but is about one-third of the whole tr. descendens and between the entrance of the sensory root and the *nucleus Rolandi* it always lies ventrally of the fibers destined for this nucleus.

I am of the same opinion as C. J. HERRICK and VAN GEHUCHTEN about the so-called radix ascendens of the trigeminus and must differ from most other investigators. HALLER (teleosts), EDINGER and MAYSER (teleosts) and GORONOWITSCH (ganoids) agree that such an ascending root is quite well developed, but I must, after careful and repeated examination deny that such a root exists, though at first I felt rather inclined to consider such a bundle present. This was due to the fact that from the nucleus lateralis cerebelli (or secondary vagus nucleus) I followed fibers down to the level of the trigeminus where they lie at the side of the sensory root of this nerve and seemed to be a true radix ascendens. But this is contradicted not only by the fact that in following these fibers more carefully it could be determined with certainty that they go farther caudad accompanying the tr. descendens and end in the lobi glossopharyngei et vagi but by the further fact that this secondary communis tract is not yet developed in the young Lophius so that here there was no trace of the supposed radix ascendens. This tract, having received not a single fiber of the trigeminus, goes forward or upward, so that I must deny the presence of the mesencephalic root, as JOHNSTON and KINGSBURY did. These arguments seem to me sufficient for denying the presence of this radix in Gadus and Lophius, and also the direct cerebellar trigeminus root of HALLER, EDINGER and JOHNSTON.

Immediately caudad of the entrance of the nervus trigeminus compact bundles of medullated fibers which at first were situated dorsally of this nerve (Fig. xci) go in a ventral direction along the outer border of the oblongata. These are bundles which originated in the cerebellum farther forward. Between the trigeminus and the first roots of the facialis they pass to the ventral side of the oblongata where, somewhat farther caudad, they take the place formerly occupied by the tr. tecto-bulbaris et spinalis, the latter having partly terminated and partly turned more medially. In this situation they go farther caudad (Figs. xciii to xcix) giving off successive bundles into the nuclei situated more dorsally, these bundles decussating to form part of the fibræ arcuatæ externæ. They disappear behind the vagus region.

EDINGER also mentions a *tr. cerebello-spinalis ventralis* in the selachians and considers it to be a connection between the sensory nuclei and the cerebellum, while BANCHI traced its fibers down into the spinal cord. HALLER, on the contrary, describes this same tract in Salmo as descending into the trigeminus region and going to the motor columns. JOHNSTON also describes the tr. cerebello-spinalis ventralis, as far as its origin and early course are concerned, in the same way for Acipenser; but although he worked with GOLGI preparations, he could not be sure about its termination; which perhaps is due to the fact that he did not see its connection with the fibræ arcuatæ externæ which he explains in another way.

There are still other cerebellar fibers to be mentioned in the post-trigeminal region. These are bundles connecting sensory centers with the cerebellum. A considerable tract must be considered as belonging to this system which descends along the outer side of the cerebellum and after a short course ends in the posterior part of the nucleus lateralis cerebelli behind the end of the secondary communis tract (Fig. lxxxvii, Plate VI, marked *54a*). But the fibers which probably belong to the same category destined for centers farther caudad (chiefly for the static centers, in my opinion, and perhaps for the glossopharyngeus and vagus also) upon leaving the cerebellum take a longitudinal course and run backward through the static field.

Probably we must reckon among these also the direct cerebellar connections of the octavus which have been so well demonstrated in Scyllium by EDINGER, so that this tr. cerebello-spinalis dorsalis must be considered as HALLER'S indirect cerebellum tract as well as the direct continuation of the funiculi posteriores of the spinal cord mentioned by BANCHI, for which, however, no sure proof could be obtained.

Before passing to the static center I must first treat of the *nervus abducens* and *facialis*. The *abducens* is treated of here in order to follow the sequence of the official numbers, in spite of the fact that it leaves the brain behind the nervus facialis and acusticus. This eye-muscle nerve receives its fibers from a nucleus situated more ventrally than the motor trigemino-facialis cell column. This ventral situation of the nucleus, so different from that of higher vertebrates, has already been noted by MAYSER and also by HALLER. A similar elevation in higher vertebrates has also been asserted by KOCH for a part of the hypoglossus nucleus. That the abducens nucleus receives tecto-spinal fibers has already been mentioned. A part of the root fibers of the sixth nerve cross in the most ventral part of the fasciculus longitudinalis dorsalis.

As it leaves the oblongata the *nervus facialis* contains fibers which come from two different regions of which only the motor fibers are really genuine facialis fibers; *i. e.*, these are the only ones which originate from a separate region which can be considered as a facialis region, for the sensory fibers originate farther back from the glossopharyngeus region. The motor facialis fibers arise from large motor cells situated somewhat caudad of the origin of the facialis from the oblongata and for the most part in the backward continuation of the cell column which I have already described in connection with the origin of the motor trigeminus. The motor facialis cells may be divided into two groups which, however, are not sharply separated but gradually merge into each other.

The most dorsal group is situated laterally to the fasc. long. posterior, as has been correctly described by VAN GEHUCHTEN. The fibers of this group first rise up for a short distance and then, after a partial decussation in the upper half of the raphé, take their position immediately under the ventricular wall. This is VAN GEHUCHTEN'S "branche radiculaire interne." JOHNSTON also gives a figure of these motor facialis fibers in the ganoids, while EDINGER gave a sketch of the subventricular bundle in Barbus fluviatilis, without, however, giving it a name. In this position this bundle now turns frontally and forms VAN GEHUCHTEN'S "branche radiculaire ascendente." This course it follows for quite a long distance (about half as long as the sensory facialis lying above and laterally of it) and then bends outward near the downward bend of the sensory root and always below the latter. Accordingly, the course of this geniculate motor facialis root is in large measure similar to that of the mammals and man, but differs in that in the latter cases it originates from a nucleus situated lower and its fibers bend up and over the abducens nucleus which is higher up.

Another part of the motor facialis fibers do not take the dorsal course, but after partial decussation take a latero-ventral direction through and immediately beneath the tr. descendens N. V. They gather latero-ventrally of this tract (Figs. xcviii, xcix, Plate VII) and after having followed it in a frontal direction for a short distance they leave the brain together with the upper geniculate facialis root. Of these fibers some originate more ventrally than the other facialis fibers in a cell group which, at least in Lophius, is situated at about the same level as that of the abducens (Fig. lxxvii, Plate V). Their course may easily be followed and has also been given by HALLER and JOHNSTON. Perhaps this is also the reason why VAN GEHUCHTEN, who describes only the most dorsal motor root, describes "prolongements protoplasmatiques" between the nucleus of this root and the tr. descendens nervi quinti, which he considers to have the function of short reflex tract between the sensory trigeminus and the motor facialis. Although I must admit the possible existence of such a reflex tract, yet I can state for certain that these "protoplasmatic prolongations" are *motor roots* of the facialis going *through* the descending fibers of the trigeminus.

The sensory facialis root in Gadus goes laterally of and above the wall of the ventricle, and, as has long been known, arises from the most anterior part of the lobi vago-glossopharyngeales. According to HALLER, C. J. HERRICK and JOHNSTON the root contains only sensory fibers, which KINGSBURY contradicts and considers it to have also a viscero-motor function. I cannot confirm KINGSBURY'S statement on this question, although it accords with KOHNSTAMM'S discovery that in the higher vertebrates, after resection of the chorda, large (secretory?) ganglion cells degenerate in the taste nucleus.

The course of the sensory facialis fibers caudad has been described in the highest vertebrates for the pars intermedia (WRISBERGI) of this nerve which in these forms also ends in the lobus glossopharyngei (HIS, DUVAL, EDINGER). That this root originates from the glossopharyngeus region might be a motive for not considering it a genuine facialis root but a part of the glossopharyngeus which runs out with the facialis. In this connection it is of great importance to determine what connection there is between the terminations of these sensory facialis fibers and the sensory glossopharyngeus fibers, in other words whether their agreement in central origin is borne out by their peripheral ramifications.

Investigations on their peripheral course have been made first by COLE (Gadus) and by C. J. HERRICK (Menidia), who both drew the conclusion that from the ganglion geniculi sensory facialis fibers originate which by reason of their course and mode of termination form the rudiment of the chorda tympani of man. That this peripheral relation does exist is positively proved by this fact together with the further fact that the chorda provides the anterior and the glossopharyngeus the posterior part of the tongue with taste fibers. JACOBSON'S anastomosis of Gadus, according to COLE, must also be considered as another argument for the close relation between the glossopharyngeus and facialis.

Nervus octavus and nervi laterales. Before describing these I must take up an important question which has been prominent in the literature for many years. The earlier investigators of the selachian brain, viz., ROHON, SANDERS and VIAULT, described in the sharks and rays a considerably elevated part of the gray substance at the most anterior latero-dorsal region of the medulla oblongata, in which originated a large medullated root which was evidently sensory from its mode of origin and termination. This root was considered by them as belonging to the trigeminus and for a long time was described as such. By reason of this conception the excrescence of the octavus field, where the lobus is really situated, was called the *lobus trigemini.* MAYSER, to whom we owe so many excellent observations, unfortunately used this name for a bilateral dorsal protuberance of almost the same size found in some teleosts, viz., the cyprinoids, whose two parts are sometimes completely fused in the median line (Cobitis fossilis, Carpio, Barbus, Brama) and consequently appear as a single "tuberculum impar," showing its bilateral origin only by a median groove situated dorsally. This lobus trigemini of MAYSER, however, has no relation whatever to the lobus which is developed farther frontally in the acoustic region, but is the continuation of the lobi vagales and glossopharyngei, originating from a more posterior and medial region.

This region of MAYSER is found in all teleosts as well as in all selachians (of larger or smaller size in all fishes) and is the most anterior part of the lobi vagales. From this region a medullated bundle arises which runs for some distance in a frontal direction immediately under the fourth ventricle and then leaves the brain along with the motor facialis forming the sensory root (pars intermedia) of this nerve as described above. This sensory root was also found by MAYSER, but since the lobe from which it originates in some bony fishes has somewhat the same appearance as the lobus trigemini of the selachians, this root was considered by him as the equivalent of the so-called superior geniculated sensory trigeminus root (from the "lobus trigemini") of the selachians. In consequence he made two mistakes: (1) he considered the most anterior part of the lobi vagales and the so-called lobus trigemini of the selachians to be equivalent; and (2) in consequence of this he identified the facialis root originating from these swellings in the teleosts with a root from the "lobus trigemini" of the selachians. Now, subsequently, it has appeared that the so-called superior geniculated sensory trigeminus root of the selachians is not a trigeminus root at all, but a lateral line root from a separate swelling of the octavus region which peripherally joins the trigeminus. For this root, the nervus lateralis anterior, there is no separate swelling in the teleosts. This root innervates a canal system of the head which probably has an important static function like the lateral line of the body.

Now, after this short exposition of facts and misconceptions I can proceed with the description of the *radix anterior lateralis*, as I shall call this most anterior static root, in agreement with JOHNSTON. After having entered the acusticum (Lophius, Fig.

lxxv, Plate V; Gadus, Fig. xciii, Plate VI) a small part of the fibers pass in a frontal direction, but a much larger part caudad at the outer margin of this region under the cerebellar crest (Figs. lxxvii, xcv.)

The descending fibers may be followed as far as the place where the ascending fibers of the radix lateralis posterior end, the two roots mingling and thus constituting a proof of the functional relation between the posterior root which enters with the glossopharyngeus and the anterior root entering with the octavus. In the young Lophius the anterior root enters as one root, and this is the case with Gadus morrhua also, as already stated by COLE, and C. J. HERRICK.

The part of the oblongata where the nervus lateralis ends is covered by the cerebellar crest, which we know from the investigations of SCHAPER, HALLER (teleosts and selachians), JOHNSTON (ganoids) and others to contain cells related to and very similar to those of the molecular layer and PURKINJE layer of the cerebellum, of which it is a continuation. Under, and in, this layer the nervus lateralis probably sends its final ramifications. I cannot state for certain whether the ascending fibers of the lateral nerves reach the cerebellum, as JOHNSTON states for Acipenser; in any case they reach as far as the cerebellum and it is more than probable that between the ascending cerebellar tracts of this region there are also direct cerebellar connections with the lateralis system, as is evident for the acusticus. The number of the bundles going in a backward direction is much larger, but I could not follow them as far as the *nucleus Rolandi* either in Lophius or in Gadus, in which they end in the posterior part of the tuberculum acustico-laterale.

In recent times this radix anterior lateralis has generally been considered as belonging to the facialis, as it leaves the brain in its immediate neighborhood. But two arguments contrary to this opinion may be mentioned: (1) its terminal region, which in the teleosts is identical with the terminal region of the acusticus; (2) the function of this radix lateralis, which, like the posterior root of the nervus lateralis, accords with that of the labyrinth. In my opinion it is better to treat the radices laterales separately, or to consider them to belong to the eighth nerve, especially the vestibular root.

Authors are in general agreement on the character and origin of the lateralis center. JOHNSTON states positively, "The lobus lineæ lateralis is shown by its structure to be an integral part of the acusticum," and "the central relations of the lateral line and VIII nerves add support to the hypothesis that the ear is derived from canal organs." In his work on Chimæra monstrosa COLE says, "doubtless all the lateral line nerves arose primitively by a single root from the tuberculum acusticum," and in his description of the Gadidæ, "There can be little doubt that the primitive lateral line organs gave rise both to the recent lateral line system and also to the vertebrate auditory organ"; and C. J. HERRICK also considers the organs which end in the acustico-lateral center as "kindred structures."

The radix anterior and posterior of the so-called nervus lateralis must be considered as the foremost and hindmost roots of the static system, of which I shall now briefly describe the only root which has remained in man—the *nervus octavus.*

This nerve, of which in fishes only the *vestibularis* is clearly visible, enters into its terminal region under the radix anterior lateralis. A small number of its large medullated fibers end at the place of entrance into the octavus nucleus, composed of large cells placed ventrally. A larger part end more dorsally in the chief nucleus, composed of small cells. The greater part of the vestibularis fibers, however, take a longitudinal course in the oblongata, part forward to reach the cerebellum, as described by C. J. HERRICK, EDINGER and JOHNSTON, but a larger part backward as far as the most posterior region of the tuberculum acustico-laterale, which is always covered by the cerebellar crest. Here the tr. descendens N. VIII (according to C. J. HERRICK'S statement containing a great many secondary eighth fibers) gradually goes along the side of the oblongata higher up, ending at the same level as the descending fibers of the lateral system.

As stated above, I cannot confirm for the teleosts JOHNSTON'S observation on Acipenser that fibers of the octavus end along with the descending quintus root in the *nucleus Rolandi,* although the terminal regions of these lie quite near to each other and both are evidently the continuation of the cornu posterior of the spinal cord. I could nowhere find a decussation of acusticus fibers in the oblongata. Yet, as mentioned in the description of the external form of the oblongata, the tubercula join and at their frontal end and especially their caudal end are united by considerable commissures, *com. acustica anterior* and *posterior*.

Among the other secondary connections of the octavus region I must mention first the *fasciculus lateralis longitudinalis* which, together with the *decussated octavo-motor connection*, also already described, forms the *fibræ arcuatæ dorsales* of this region. The remaining *fibræ arcuatæ internæ* and *externæ* are doubtless partly formed by secondary connections with the ventral gray substance described above in which the tecto-bulbaris fibers end, while finally some very distinct little bundles are decussating ventral cerebello-spinal fibers probably not belonging to the acusticum.

The *nervi glossopharyngeus* and *vagus*, of which the former enters the brain with the radix lateralis posterior, consist of two kinds of fibers, motor and sensory. The sensory fibers of the ninth end in the same region as the pars intermedia facialis and, farther back, the sensory vagus. This whole sensory region is situated medially to the caudal continuation of the static area and has been distinguished by HALLER from the latter (his "äusseres sensorisches Gebiet") as "inneres sensorisches Gebiet."

The American school calls it "fasciculus communis system," following OSBORN and STRONG who studied its structure and also clearly distinguished it from the "acusticum" situated more dorsolaterally. Now, this "communis region" may be very greatly enlarged in some teleosts, as never occurs in the selachians, and when treating of the nervi laterales I already mentioned that this was the cause of MAYSER's mistake in considering the most anterior part of the lobi vagales of the cyprinoids as the homologue of the swelling so strongly developed in the selachians in which the nervus lateralis anterior ends. The size of the communis region in bony fishes is really so considerable that generally the two regions unite and in some bony fishes the formation of the so-called *tuberculum impar*, mentioned by the earlier investigators takes place.

That the posterior part of these regions is always connected by a commissure has already been described by A. VON HALLER, his *commissura infima cerebri*, or *com. infima Halleri*. Behind it decreases in circumference. In Lophius it is vaulted over by the sensory enlargement in which the *nucleus Rolandi* lies and it gradually passes into that region of the medulla spinalis of which it constitutes the frontal continuation and which is situated immediately over and laterally from the central canal.

Into this communis region there enter without decussation the sensory glossopharyngeus and vagus roots which will be treated here together as they present exactly the same character in fishes. That the vagus gives part of its fibers to the tractus descendens N. V. (VAN GEHUCHTEN, C. J. HERRICK), I have not been able to confirm. KINGSBURY records that it is found in some teleosts and not in others. The greater number of the sensory fibers terminate immediately in that nucleus, thus differing from the higher vertebrates in the fact that there are no descending or ascending tracts such as have been described for the amphibians where the descending sensory ninth and tenth fibers form a bundle of which a part decussates in the com. infima cerebri (STRONG and JOHNSTON).

In his first publication on the oblongata of ganoids JOHNSTON did not mention this decussation of descending ninth and tenth fibers; in his complete description of the brain of Acipenser, however, he describes a decussation of direct root fibers in the commissura infima, which, moreover, also contains connections of the *nucleus commissuræ* which is situated immediately under the commissure. In the bony fishes MAYSER described, among others, two sorts of fibers in this commissure: (1) thinner fibers which he thinks are root fibers of the tenth nerve, thus agreeing with JOHNSTON; and (2) thicker fibers which he considers as a secondary commissure of the motor vagus nuclei. Later this region of the teleosts has been examined by KINGSBURY and better by C. J. HERRICK in Menidia.

The latter author says of the fasciculus communis behind the lobi vagi that this "is chiefly, if not wholly, composed of secondary fibers from the lobus vagi and not of root fibers." These secondary fibers participate in the com. infima HALLERI, but no root fibers.[1] Nor can I see in KINGSBURY any mention made of descending root fibers of the vagus which decussate in this commissure, and the result of my investigations is in perfect accord with theirs. The teleosts differ from the higher vertebrates in

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[1] In his most recent work on cyprinoids, however, C. J. HERRICK mentions root fibers from the sensory vagus to the commissura infima HALLERI and he presumes that similar fibers exist in smaller numbers in other fishes.

that the glossopharyngeus and vagus, at least in Lophius and Gadus, have no descending fibers, from which it results without doubt that the part of the nucleus vagi of higher animals, which is situated more spinalward and receives the terminations of root fibers has been taken up in the lobi themselves which are consequently better developed. The commissura infima in teleosts, as far as I was able to ascertain, contains only secondary decussated communis fibers, of which such as originate behind might be considered as fibers of the nucleus commissuræ infimæ (Fig. lxxx, Plate V).

Another secondary system of the vagus has been already slightly noticed. It consists of small, compact medullated uncrossed bundles which run from the communis region ventrad to a position mesially of the tr. descendens N. quinti. They then turn forward along this tract and continue in the same direction after the separation from the brain of the sensory root of the trigeminus and terminate in an important enlargement between the cerebellum and the oblongata, the *nucleus lateralis cerebelli*, which has been described above. This is the secondary communis tract which has been described by MAYSER, as "secondary vago-trigeminus tract," and also by HALLER, KINGSBURY and JOHNSTON. MAYSER called it the "Rindenknoten" and JOHNSTON "secondary nucleus vagi" after the tract which ends here. But since there are other fibers which begin or end here, I prefer to use a more general term, "nucleus lateralis cerebelli," the name given to it by EDINGER for the selachians. These nuclei of the two sides are connected by a commissure, the *com. inferior cerebelli* (Fig. lxxxvi, Plate VI), or as JOHNSTON calls it, the "secondary vagus commissure."

These, however, are not all of the secondary communis connections. First, I mention a small group of fibers which relate the communis region with the acusticum and perhaps with the cerebellum, a connection which JOHNSTON seems also to have observed in Acipenser. Secondly, there is a tract from the sensory vagus nucleus running in the fasciculus dorsalis and appearing to terminate in the contra-lateral nucleus, of which, however, I cannot be sure (Fig. xcix, Plate VII).

As for the motor glossopharyngeus and vagus fibers, I may briefly note that they pass from their source, the *nucleus ambiguus*, partly without decussation and partly decussated through the upper part of the fasciculus dorsalis. In Lophius this nucleus extends generally in a double row of rather large motor cells, along the lower wall of the ventriculus quartus. By further development these cells are crowded together so that some of them take a more ventral position, while others remain immediately under the floor of the ventricle nearer the sensory terminal nucleus. This is the appearance of the motor region in Gadus, in which I quite agree with C. J. HERRICK, who, like myself, failed to observe the origin of motor ninth or tenth fibers from a ventral column as HALLER describes it.

That the most posterior vagus root may be considered as *N. accessorius* appears from the investigations of C. J. HERRICK, who succeeded in following the course of this root in Menidia into the m. trapezius.

I will not bring this part to a close without returning to the question, with what parts of the medulla spinalis the lobi vagi, glossopharyngei et facialis sensibilis on the one hand, and the *nucleus Rolandi*, tubercula acustica (lobus lineæ lateralis) and the cerebellum on the other hand correspond, and the grounds and consequences of this correspondence.

As for the communis region, this passes directly into the sensory splanchnic region of the medulla spinalis. The fact that the sensory fibers of seventh, ninth and tenth are visceral fibers (seventh for taste) is in perfect accord with this. The fact which several investigators of the peripheral nervous system of fishes have been able to state, that the end-buds on the barbels of fishes and on their fins are innervated from this system (C. J. HERRICK), would not contradict this visceral character, as JOHNSTON records, whose view I repeat, because these end-buds in his opinion are intended for detection of the composition of the surrounding water and would immediately transfer their impressions to the viscera to regulate their functions.

The somatic sensory region of the oblongata, on the other hand, which both by its position and by its structure is distinguished from the communis region, evidently forms the continuation of the dorsal horns and the dorsal tracts of the spinal cord. It contains the sensory trigeminus, which actually passes back into the funiculi posteriores, as well as the octavus region (static region) from which the cerebellum is developed, as is well known since SCHAPER'S work on the subject. This somatic sensory region receives impressions of non-splanchnic character which are not in immediate relation with the viscera.

Though I could not control by personal examination the published data about the peripheral distribution of the different sensory nerves of this region, yet I willingly acknowledge that during my examination at first undertaken in a rather skeptical spirit in this matter, I never met with any fact which I might advance against the opinions of the American school. The truth lies rather on the other side. I consider the conclusions of this school and the methods of investigation by which STRONG, KINGSBURY, HERRICK and JOHNSTON reached their conclusions about the microscopic structure of the centers and the peripheral courses of the nerves as necessary to complete the interesting and excellent work which BURCKHARDT began in the selachians of getting by the microscopical method a better insight into the problem how the medulla oblongata has developed from the medulla spinalis.

2. *The Hind-brain of the Selachians.*

The hind-brain of the sharks is distinguished by its form in some very important respects from that of the teleosts. The velum anticum cerebelli in the teleosts is more voluminous than in the selachians, this difference being very great between Galeus and Gadus. While in the latter fish the velum has a large dorso-ventral dimension and not only contains tracts, but is richly supplied with gray substance which is directly continuous with the nucleus lateralis cerebelli, we find this region in Galeus to consist only of a relatively smaller number of decussating medullated fibers, as shown in Figs. lxx and lxxiii, Plate IV.

While in the codfish the strongly developed tr. mesencephalo-cerebellaris runs through this velum and the valvula cerebelli itself has a very broad attachment to it, we find in the same part of the brain in Galeus and Angelus squatina only the much smaller upper tecto-cerebellar tract. The lateral nucleus, which in the teleosts is the direct backward continuation of the velum, is smaller here and lies farther backward in the lateral arms of the cerebellum (Figs. lii to lxxiii).

It is chiefly this last factor, the fact that this nervous mass projects inward very much less, that explains why in the sharks the fourth ventricle is here larger. There are, however, very many more points of difference between the two kinds of fish. The mode of subdivision of the cerebellum itself is different. The part generally called the valvula cerebelli which, in most bony fishes, extends in so characteristic a way under the roof of the mid-brain and which some older anatomists considered as corpora bigemina is not represented in this form in the sharks. Here the anterior part of the cerebellum overlies the tectum opticum and looks more like the anterior half of the true cerebellum, while macroscopically the valvula seems more like an appendage of it, at least in Gadus, Lophius, Salmo and the greater number of other bony fishes. From the investigations of C. L. HERRICK, in Haploidonotus grunniens and those of MARCUSEN in Mormyridæ it results, however, that the valvula may also be developed into a very strongly plicated organ, as it also appears in Thynnus. BURCKHARDT considers it as the homologue of the pars anterior cerebelli of the selachians, whose cerebellum, he contends, is always divided into two parts by a dorsal transverse furrow, which in some representatives of these fishes is only feebly marked but which is generally clearly to be seen. I can state that this transverse groove clearly appears in the selachians which I have examined. In Galeus it is far deeper, as a superficial examination could show; in Angelus squatina it is far less clearly seen. Another point of difference lies in the auriculus cerebelli found in the plagiostomes, a continuation of the cerebellum caudad and characterized by the sharp elevation which it causes and the folding of its surface (Figs. c, ci, Plate VII).

Another part which in the bony fishes is united with other regions is distinct in the selachians and known as the *lobus nervi lateralis anteriores*, also called lobus facialis sensibilis and formerly generally lobus trigemini, according to the opinion the naturalists had regarding the important geniculated root which terminates there and which some say belongs to the trigeminus and others to the facialis, but which as a static nerve might best be said to belong to the octavus, with whose region this terminal nucleus is united, as is the case in the bony fishes, though in the selachians it has grown out as a separate lobe.

The fusion of the static regions across the median line, which in bony fishes is caused by the fact that so many roots enter the same region in consequence of which the region is greatly extended, does not occur in the selachians, nor do we find there the commissura acustica dorsalis. The lobi vagales are here much less voluminous than in the codfish and no fusion over the ventricle takes place, which is the explanation also of the fact that in the posterior part of the oblongata the sinus rhomboidalis is so much more spacious.

Where the medulla oblongata passes into the medulla spinalis and the sinus rhomboidalis closes into the central canal, of course the backward continuations of the acustica and of the communis regions of the two sides finally amalgamate, as shown in Fig. cvii, Plate VII. Here we find a fiber tract connecting both sides, the *commissura infima*.

The *nucleus Rolandi*, which with the surrounding sensory mass causes in Lophius such an important ectal swelling in this place, though not developed in so great measure in Gadus, is, however, in this fish of still greater extent than in the selachians, where it lies dorsally embedded in the spinal cord, as is the case also in reptiles.

As for the microscopic structure, I can repeat what was already observed when treating of the 'tween-brain, that the strong development of the longitudinal tracts produces so complicated a microscopic aspect in the oblongata that it is a difficult, and in many cases an impossible, task to follow the course of each tract accurately by itself when the investigator does not make use of the embryology or, what is still better, of experimentation after the methods of GUDDEN, MARCHI and NISSL, as EDINGER did successfully for some nerve roots. In treating the microscopical structure of the oblongata I shall follow the same order as I did with the teleosts.

My treatment of the *fasciculus longitudinalis lateralis* must be very restricted. Already when treating of the mid-brain I observed that the frontal end of this tract, which is so strongly developed in Gadus and Lophius, cannot be separated between the great mass of longitudinal fiber-tracts chiefly belonging to the deeper tectum-layer. A slight elevation of the posterior part of the wall under the optic ventricle is present, but different arguments mentioned in the third chapter make it probable that the greater part of the nucleus lateralis mesencephali is embedded in the deep tectum layer, where this layer joins the base of the mid-brain and so the homologue of the fasciculus lateralis of the teleosts runs probably with the tecto-bulbar tract, as it was shown by JOHNSTON for the ganoids. It is not easy, however, to state this with certainty. Nor do we find in Galeus with common methods of investigation a sufficient ground to state these relations near the acoustic field, where in the teleosts the fasciculus longitudinalis lateralis terminates after having formed the fibræ arcuatæ dorsales. A tract of decussating fibers situated under the ventricle, passing through the fasciculus longitudinalis dorsalis and losing itself in the acoustic field on one side and on the other side in a group of fibers immediately lateral to the dorsal bundle cannot be interpreted as such with any certainty. Though among the great number of fibræ arcuatæ of this region there are many which can be seen to take this course, this does not give me sufficient evidence to consider them as the homologue of the lateral fasciculus of the teleosts, even though I am personally convinced that it is to be found in the selachians, in which the static center is even more strongly developed than in the bony fishes.

Happily we can give a clearer report on the *tr. thalamo-* and *tecto-bulbares et spinales*, which I shall have to treat of here together, as it is impossible to separate the thalamic and the tectal fibers. After an important part of this group has entered the cerebellum (Figs. lxx, lxxi, Plate VI), the remainder terminates partly in the ventral gray layers of the medulla oblongata and in at least equal amount farther backward.

The gray mass of the oblongata which in Gadus is so clearly seen to begin in the region of the trigeminus and shows its greatest development in the octavus region is in Galeus canis a great deal more diffusely spread and is differentiated only in the region of the trigeminus (Fig. c, Plate VII) as a more compact scale-shaped mass on both sides of the raphé. In the octavus region, however, it is impossible to distinguish any such local concentration.

The tracts also extend farther backward and decrease only very gradually giving more fibers also to the *nucleus paraseptalis* which is so strongly developed in the whole vagal region, situated ventrally beside the raphé (Figs. cvi, cvii, Plate VII). Thereupon, the greater part of the tracts run backward into the spinal cord, where they occupy a lateral and ventro-lateral position. It is especially this spinal part of the whole complex which seems to make this group of fibers so much larger in the selachians. It need hardly be mentioned that it is out of the question to follow the course of any separate tract into the nucleus of the abducens.

Contrary to my expectations, I could trace here the different components of the *fasciculus longitudinalis posterior* or *dorsalis* almost as well as in the teleosts. There is no doubt at all about the *first group* of fibers which join this fasciculus after its origin in the mid-brain, the decussated nerve roots. The entrance of motor fibers into the fasciculus may be demonstrated in selachians as clearly as in other animals. This is seen for the motor trigeminus in Fig. ci, and for the motor facialis in Fig. ciii. It follows from the whole theory of the coördination of eye movements that there must be other fibers in addition to these short ones, in this fasciculus to effect this coördination, and it has been proved by others that there are fibers coming from the motor nuclei which continue their course in the dorsal longitudinal bundle a great deal farther than the root fibers. These components, however, form only a part of the tracts which appear in this complex and do not sufficiently explain the fact which is so striking in the selachians that where the lobus nervi lateralis anterioris appears the fasciculus longitudinalis posterior assumes greatly increased dimensions (*cf.* Figs. cii and ciii, Plate VII). This augmentation may be attributed in part to the entrance of motor trigeminus fibers, but more to the entrance of quite different tracts which run for a much greater distance in the fasciculus.

In Figs. lxx, lxxi, lxxii, Plate IV, we see, after the tr. tecto-cerebellaris superior has ascended along the inner side of the cerebellar arm, immediately behind this tract fibers descending along almost the same course (marked *53*) running backward in a longitudinal direction adjacent to the lateral walls of the ventricles. But as the configuration of the cerebellum changes by reason of the formation of what is generally called its under lip this tract is pressed downward, becomes more compact and more mesially placed under the ventricle (Fig. ci, Plate VII) and where finally the lateral wall is still more reduced by the beginning of the lobus nervi lateralis anterioris these fibers are pushed still farther toward the median line, while the most medial of them enter the fasciculus longitudinalis dorsalis whose dimensions are thereby increased. In the following sections (Figs. cii, ciii) this is still more the case since now, even before the sensory facialis has occupied the place which they formerly occupied, all of the fibers have entered the upper half of the fasc. long. dorsalis, which has, moreover, been augmented by fibers originating from the whole octavus region.

After they have attained this great size after the addition of these cerebellar fibers, the fasciculi longitudinales on both sides run backward decreasing very slightly in volume. To be sure, farther caudad in the vagus region they do not project so strongly, but this is caused by the fact that the dorsal displacement of the lateral parts has already begun here. Estimating their circumference, this appears to have remained almost the same.

I think there is left no room for doubt that this is the same part of the fasciculus dorsalis which could be followed so clearly and sharply in Gadus into the motor cell column, the *tr. cerebello- et octavo-motorius cruciatus.* EDINGER figures this tract, but differently, and I think did not accurately interpret it. In Fig. 70 of the fifth edition of his "Vorlesungen" he calls this tract "tr. quinto-tectalis," a name which he also uses for it in his last publication on the cerebellum of Scyllium canicula. He also sees this tract in its subventricular course, but evidently considers it as originating from the tectum, and connected with the trigeminus, running through the velum. I can most positively state that the *tr. cerebello-motorius cruciatus* does not go through the velum and that this false impression is produced only by the tecto-cerebellar tract, which ends in the region of the cerebellum where this tract begins. I am more and more doubting the existence of the mesencephalic quintus root in fishes, like the other investigators whom I mentioned in the first part of this chapter, and I think I may conclude from EDINGER's way of expressing himself on this subject that he is by no means positively convinced of his interpretation. The strong development of the fasc. long. posterior of the selachians EDINGER himself has already brought into relation with a supposed connection between this fasciculus and the cerebellum. I am, accordingly, happy to prove as a certainty what he supposed.

Now that I have described the frontal relations of the oblongata (and part of the cerebellar), I may proceed to the description of the nerves.

The *nervus trigeminus,* which contains sensory and motor fibers, enters the oblongata at the level at which the most anterior part of the lobus nervi lateralis becomes visible in the ventriculus quartus (Fig. c, Plate VII). The motor and sensory fibers enter at almost the same place, the motor in part somewhat anterior to the sensory. From the former root one part immediately takes its course to the nucleus of the same side, which is chiefly situated farther caudad (*cf.* Figs. c and ci). Another part about as large enters the fasciculus dorsalis, but does not immediately leave it at the other side, but farther caudad like the other motor fibers, as I found in the teleosts and as JOHNSTON also observed in the ganoids.

Only very few of the sensory fibers end at the place of their entrance. By far the greater part pass backward as the *radix descendens trigemini*, and its course may be followed through the whole oblongata, decreasing but little in circumference and at the inner side always accompanied by a thin long strand of small cells into which it sends neurites and especially collaterals (VAN GEHUCHTEN). In the octavus region it lies farther from the outer surface, as it is covered there by the fibers of the descending octavus and ascending posterior lateralis roots (Figs. c to cv). Behind the most anterior vagus roots, with which the posterior lateralis enters, it approaches the surface again and terminates in the most anterior part of the medulla spinalis in the *nucleus Rolandi* or *nucleus trigemini descendentis*, while another part of its fibers seems to run farther caudad (Figs. cvii, cviii). This region has far smaller dimensions in Galeus than in Lophius where a thick spinal root also ends here.

I was not able, either in Galeus or in Angelus squatina, to be absolutely certain whether or not there is a *radix ascendens trigemini*. Much more than in the bony fishes I got the impression that there is really such a root (Fig. c, at the right), which ends not far away under the cerebellum. However, since I know that in the teleosts this same impression was given by the course of the secondary communis tract, I am inclined to believe that the tract which gives the impression of being the ascending or cerebellar trigeminus root is, just as in the teleosts, the secondary communis bundle connecting the communis region with the nucleus lateralis cerebelli. As already noticed for the bony fishes, VAN GEHUCHTEN and C. J. HERRICK are of the opinion that we are to deny the existence of this root in the teleosts, nor is it mentioned by KINGSBURY. In his latest publication EDINGER describes sensory fifth fibers (though without proving their trigeminus relations by degeneration) which ascend into the cerebellum, as JOHNSTON found in the ganoids. Without having undertaken degeneration experiments, I do not venture to pronounce positively in the matter as the enormous quantity of fibers of the oblongata and corpora restiformia is so great that even the very best preparations cannot give anything like certainty in this matter.

Now, before going on with the nerves I must mention an important cerebellar connection which is found in the same place in plagiostomes and teleosts, the *tr. cerebello-spinalis ventralis*, which originates from the cerebellum and leaves it by the auriculus behind the trigeminus and in front of the facialis, descending along the lateral wall of the oblongata (Fig. ci), taking such a course that it lies close to the mesial side of the nervus octavus where it enters the oblongata (Fig. civ). Then it approaches closer to the raphé, through which it sends some fibers which, however, cannot be followed to their termination without experimental examination. Under this name EDINGER described a tract in Scyllium which leaves the cerebellum through the decussatio veli and which he could follow only to the trigeminus region. But I have given the same name to the tract which I have described by reason of its likeness in both origin and course through the oblongata to the tract described under this name in the teleosts.

The *nervus abducens*, consisting of motor fibers only, leaves the oblongata behind the facialis as in the bony fishes. Its nucleus lies laterally of the deeper fibers of the dorsal longitudinal bundle and consists of rather large polygonal cells which extend somewhat farther dorsally in Galeus than in Gadus, where they really lie in the lower third of the oblongata. But in this respect both the selachians and the teleosts show an important difference from the higher vertebrates, where this nucleus lies very close under the ventricle. That a part of its fibers decussate through the fasciculus dorsalis, though more clearly apparent in Gadus, is also observable in Galeus (Fig. civ). As I have already observed, in WEIGERT preparations of selachians no separate tectal tract can be followed into the nucleus of the abducens. The enormous mass of fibers prevents such an observation.

The *nervus facialis*, leaving the medulla in almost the same place as the octavus, constitutes the most frontal group of fibers of the acustico-facialis complex. It is a mixed nerve, of which the sensory part is intimately related to that of the ninth nerve, as the situation of its terminal nucleus, near the glossopharyngeus and in intimate relation with it, falls in the most anterior part of the communis region. In Figs. cii and ciii its mode of entrance is clearly seen. The left side of these figures, which lies somewhat farther caudad than the right, shows that a part of the motor root fibers before turning upward run backward for some distance along with the tr. descendens nervi quinti as a small cap on the outer side of this tract which can be distinguished from the trigeminus fibers by its darker color. Later it turns upward and terminates partly decussated and partly uncrossed in the motor facial nucleus.

KINGSBURY also stated that fibers of the tr. descendens N. quinti in ganoids leave the medulla with the facialis root. I suppose, however, that he took them for spinal (and sensory) fibers. That this is not the case is proved by the origin of the dark cap on this tract in the motor facialis region and the origin of the fibers which have a thicker and darker colored medullary sheath like those from the motor facialis nucleus. By reason of this course of motor facialis fibers the tr. spinalis N. quinti grows thicker in the region of the motor facialis nucleus and when leaving this region decreases again, in the proportion of about 5 : 6 : 5. That such a course exists also in the teleosts I have mentioned before, but there these fibers are not situated dorso-laterally but ventro-laterally of the descending fifth tract.

These, however, are not all of the motor fibers. Nearly as large a part immediately runs dorsad, passes for some distance beneath the ventricle and finally terminates in the same place as those just described. The latter part is the homologue of the motor facialis bundle which, in Gadus, forms the larger part and was first described by VAN GEHUCHTEN in Trutta (in its different parts as branche interne, ascendente and externe). In the selachians, as in the bony fishes, the motor nucleus lies nearer the floor of the ventricle than the nucleus abducens.

The *sensory facialis* originates exactly as in other animals in the anterior part of the communis region, then passes frontad for a short distance immediately under the ventricle somewhat more dorso-laterally than the motor fibers. After their exit from the brain the fibers run into the ganglion geniculi so that this bundle represents the *pars intermedia Wrisbergii* of the higher vertebrates.

GREEN, following STANNIUS, described in the selachians (including Galeus canis) three nerves which originate from this ganglion, the ramus palatinus, ramus prætrematicus and a third branch which runs between the two others along the anterior border of the spiracle and then downward, forward and inward under the mucosa of the mouth between the hyoid and the mandibular arches, where it reaches to the ventral median line of that region. Thus, both in its peripheral course and in its origin it represents the chorda tympani of the higher vertebrates. COLE, who examined these branches in Chimæra, considers the ramus prætrematicus itself as the homologue of the chorda.

While I leave to those who have made a special study of the subject the many questions of comparative anatomy connected with this matter, I wish to point out merely the fact that the relations in selachians are proofs of the opinion that the tongue as far as the sense of taste is concerned is innervated in toto by fibers terminating in the communis region, a part which in man, was described by EDINGER as the *taste nucleus.*

Static center. As a counterpart of the greater development of the cerebellum and fasc. long. posterior we find in the sharks the terminal nucleus of the nerve of the lateral line canals of the head very strongly developed and separated from the rest of the static region as a distinct lobe. When describing this center in the bony fishes I have already given a summary of the different opinions and names which have been current about this lobe and the nerve which terminates in it, so that it may suffice to refer to what I said there. Agreeing with JOHNSTON, I call this lobe, *lobus nervi lateralis*, applying the name lateral nerve also to the root which innervates the canal system of the head. Perhaps it might be better to term it the lobus staticus, as there can scarcely be any further doubt that we are to regard this lobe as a static center, it is so intimately connected in position, structure and relations with that of the octavus.

As we see from Figs. cii, ciii, civ, this static nerve enters the brain behind the insertion of the auriculus, running over the cerebellar crest, which covers the terminal region of the octavus, into the lobus nervi lateralis, which is likewise covered with cerebellar formation, and which it pierces in small bundles. There it divides into ascending and descending fibers which course through the whole length of the lobus. Its terminal region is scarcely distinguishable in structure from that of the region of the octavus itself, with which in the bony fishes it constitutes a single whole. Both are also probably put into relation with the motor centers of the oblongata and myel through the fasciculus longitudinalis.

The posterior lateral nerve, which enters in the region of the glossopharyngeus and anterior vagus (Fig. cv), does not terminate in the lobus, but immediately under it in the region of the octavus itself where I could easily follow its course.

The third nerve of the static region is that of the labyrinth, the *nervus octavus*, commonly called nervus acusticus, a name which does not suit very well, as this surely has much more vestibularis fibers than acusticus fibers, which, however, for the teleosts at least, are very probable from PARKER's researches in this matter.

The octavus terminates in part in a nucleus at the place of its entrance, situated dorso-laterally in the oblongata under the cerebellar crest, as has already been described by EDINGER and HALLER. In my fish, however, a small part ends in larger cells which are more ventrally situated, as also mentioned by HALLER, of which rarely more than two or three are found in any one section (Fig. civ). I do not venture to say with certainty whether we may see in this nucleus the homologue of the more ventral nucleus which GAUPP described in the reptiles, which might have an auditory character. It is mentioned neither by VAN GEHUCHTEN for the teleosts nor by JOHNSTON for the ganoids.

But the greater part of the fibers terminate in other regions. One part goes straight on into the cerebellum, as EDINGER showed experimentally and as JOHNSTON stated for other fishes, while a much larger part runs caudad on the dorso-lateral border of the oblongata and may be followed, decreasing in circumference, nearly to the *nucleus Rolandi*. That there are any fibers entering ROLANDO's nucleus itself, as JOHNSTON maintains for Acipenser, I think not probable, even in the selachians, as this name is intended for the region where the tr. descendens N. quinti begins to terminate and which in carmin preparations is distinguished by a somewhat darker color. The terminal region of the fibers of the octavus, however, passes so gradually into the terminal region of the descending fifth tract and lies so near to it that the whole matter is one of individual judgment. It is, however, certain that the fibers of the octavus are reduced to a minimum by the time the descending trigeminus has reached the *nucleus Rolandi* (Figs. cvi, cvii).

From all this it appears very distinctly both in Galeus and in Angelus squatina that both the *nucleus Rolandi* and the static region are continuations of the dorsal sensory field of the medulla spinalis and are everywhere sharply contrasted to the communis region which is the continuation of that region of the spinal cord which is situated next to the central canal.

As for the secondary relations of the static region, I must mention first the strongly developed *fibræ arcuatæ internæ* and *externæ*, which as in the ganoids, pass through the raphé as diffuse fibers and not as in the teleosts as compact bundles which spread out laterally. As before observed, the lower arcuate fibers, the real fibræ externæ, are formed chiefly by decussating cerebello-spinal fibers, while the innermost might represent bilateral connections. In correlation with the strong development of this region their number is very considerable. Whether the fibers which are more dorsally situated are to be considered as decussating parts of the fasciculus lateralis, as I observed when discussing this bundle, cannot be made out. On the other hand, another secondary connection of this region has long been known, the *fasciculi mediani*, first described by STIEDA and after him by ROHON and HALLER. ROHON considered them as a separated part of the dorsal longitudinal bundle and thought he saw them still in the trigeminus region. SANDERS mentions them but does not say anything further about them. HALLER, with whose opinion I quite agree, records that they begin in the region of the acustico-facialis, from which they bend inward medially of the motor facialis root then run backward under the ventricle between the sensory region of the ninth and tenth laterally and the motor region of these nerves mesially (Figs. cv and cvi) and finally enter the spinal cord (Fig. cvii), where they are situated close to the central canal (Fig. cviii) and from time to time some of their fibers pass into the ventral column of motor cells. The size and medullation of their fibers are the same as in the fasc. long. posterior and I am of the opinion that we have here a caudal relation between the octavus center and the motor regions of the spinal cord corresponding to MAUTHNER's fibers in the dorsal longitudinal bundle itself in the bony fishes.

The *nervus glossopharyngeus* is just like the anterior root of the vagus. The motor fibers of this nerve enter with the sensory and terminate partly decussated and partly uncrossed in the group of cells situated under the ventricle laterally of the fasc. long. posterior. But before these fibers enter their nucleus they take a longitudinal course in a separate bundle laterally of the chief part of the fascicle, as has been figured for the vagus in Fig. cv.

The relations of the sensory radices are also very simple in Galeus and Angelus squatina where we see their fibers spreading out like a short pencil within the lobe, as already described by ROHON in his study of the vagus. Ascending or descending root fibers (the latter in higher vertebrates constituting the fasciculus solitarius) are scarcely observable, and, if present, are extremely short, as in the teleosts. From the tr. descendens nervi quinti I did not see any fibers passing into the glossopharyngeus, as KINGSBURY records for some ganoids and teleosts.

Between the vagus and the glossopharyngeus, and accordingly somewhat farther caudad than in the teleosts, the so-called *nervus lateralis vagi* enters the oblongata directly into the posterior continuation of the octavus field (Fig. cv). By reason of the great decrease backward of the lateral sensory field the vagus roots enter at a more dorsal level than those of the glossopharyngeus. The motor fibers of the vagus terminate in the same way as those of the ninth nerve and these decussating fibers before they enter their nucleus under the floor of the ventricle form a separate bundle immediately lateral to and belonging with the fasciculus dorsalis (Figs. cv, cvi).

The sensory fibers pursue the same course as those of the glossopharyngeus. Here, also, we see little tracts of ascending and descending fibers ending brush-like within the lobus. At about this level of the oblongata there begins an important collection of gray matter ventrally close to the septum, which reminds one of the gray mass beginning farther cephalad in the teleosts. EDINGER indicates it in Scyllium and calls it *nucleus paraseptalis.* It is rather difficult by my methods of investigation to give a complete account of it. It may be the same as that described by JOHNSTON in the ganoids as the lower olive, the neurites of whose cells this author says cross the ventral raphé and finally break up among the lateral tracts. As Fig. cvii shows that in the selachians this gray mass contains a great many fibers which take that course, this seems the more probable because the nucleus paraseptalis extends into the beginning of the cervical cord, where JOHNSTON found his lower olive. HALLER thought that in the region of the vagus some fibers of the fasciculi mediani of STIEDA might end or originate. I am able to contradict this for Galeus and I think that HALLER has considered decussating motor vagus fibers as such (Fig. cvi). These fibers run to their nucleus across the bundle of STIEDA and upon closer examination can be distinguished from them easily.

The posterior motor root of the vagus nerve was already considered as *N. accessorius* by CLAUS and ROHON, which was duly proved by FÜRBRINGER, who stated that in Hexanchus it innervates the m. trapezius. HALLER and EDINGER both consider this to be true. This root originates in the same way as the other motor vagus roots (Fig. cvii) and from a continuation of their nucleus.

CONCLUSIONS.

From the course of the secondary olfactory tracts, the tertiary bilateral connections of the secondary olfactory centers and the tertiary caudal connections of these centers it results that the lobi anteriores of the teleosts contain regions which in the selachians are situated in the pallium.

Only a part of the median tract joins the tractus strio-thalamicus in the selachians; another part ends in the ventral region of the fore-brain, so constituting a dorso-ventral connection in the prosencephalon.

The nucleus magnocellularis præopticus of the teleosts has a connection with the tuber cinereum.

The commissure of HERRICK ends in the same layer of the tectum opticum as the optic fibers themselves.

The centripetal optic fibers, the fibræ tectales nervi optici and the brachia tecti have been correctly described by KRAUSE. His doubt, however, regarding the fasciculi mediales nervi optici has no ground. These are optic fibers which join the commissure of HERRICK and end in the superficial layers of the tectum.

The saccus vasculosus is a sense organ.

The colliculi (tori semicirculares) of the bony fishes may be considered as a *prostadium* of the corpora quadrigemina posteriora of higher vertebrates.

The posterior commissure contains no direct fibers for the fasciculus longitudinalis posterior.

The difference of opinion about the thalamic or mesencephalic origin of this tract is due to the presence of a thalamic fiber system which joins the mesencephalic system and which, by some authors, evidently has been regarded as constituting a part of the fasciculus longitudinalis posterior. Since, however, the thalamic system becomes medullated later than the mesencephalic system and consists of finer less heavily medullated fibers, it is better to regard the thalamo-spinal tract as a separate tract.

A tectal root of the trigeminus does not occur either in the teleosts or in the selachians.

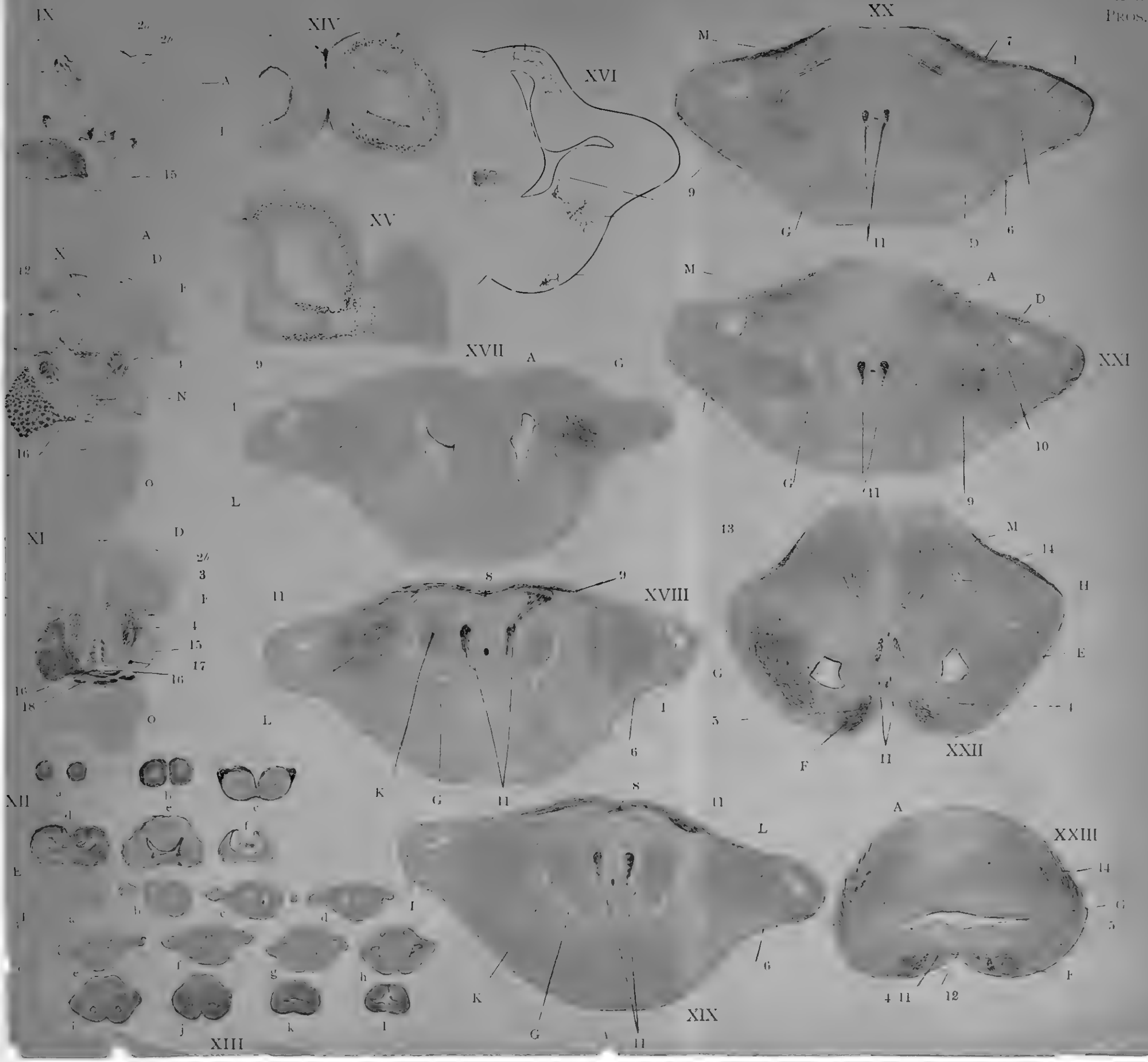
Researches on the peripheral and central nervous system of the teleosts and the selachians suggest that the tongue of higher vertebrates has a single sensory nucleus as taste nucleus, with which it is connected, partly by the nervus glossopharyngeus and partly by the pars intermedia Wrisbergii of the facialis.

The selachians and teleosts have a stato-motor fiber system which connects the whole static center (the center of the N. octavus, NN. laterales and the cerebellum) with the motor nuclei of midbrain, oblongata and spinal cord, running with decussation through the fasciculus longitudinalis posterior.

Descending vagus or glossopharyngeus fibers do not occur either in the teleosts or in the selachians.

The commissura infima HALLERI of the teleosts and selachians contains secondary vagus fibers, but no direct root fibers.

Plate I.
PROS.



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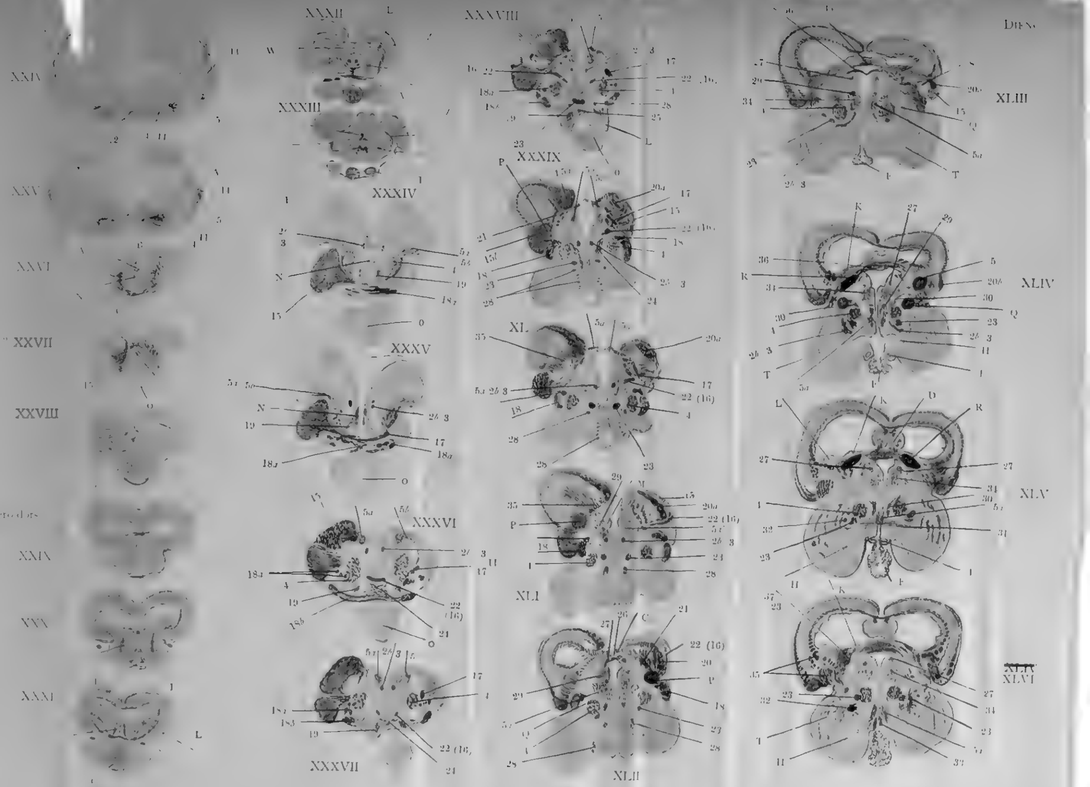
TAB. II. (DIENCEPHALON):

XXIV, XXV, Galeus canis; XXVI-XXXIII Lophius piscatorius; XXXIV-XLVI Gadus morrhua.

A	ventricul III.
B	epiphysis.
C	gang. habenulae.
D	tor. longitudin.
E	tuber cinereum.
F	saccus vasculos.
G	infundibulum.
H	ventric. lobi infer.
I	recessus inferior (mammill Herrick)
K	eminentia medial.
L	colliculus (tor. semicirc c. n. lat. mesenc.)
M	nucl. thalami ant.
N	nucl. praeopticus.
O	hypophysis.
P	corp. geniculat. later.
Q	nucl. praerotundus.
R	nucl. lentiformis.
S	nucl. corticalis.
T	subst grisea lob. inf.
V	valvula cereb.
W	velum anticum.
Z	tectum opticum.

Tracti:

2*b*	tr. olfacto. lob. med.
3	tr. epistri lobar.
4	tr. strio-thalam
5*a*	tr. olfacto. lob later.
5*b*	tr. olfacto-haben.
11	tr. medianus.
12	comm. anterior
14	tr pallii.
15	n. opticus
16	fasc. medial. n. opt.
17	fibrae tectales n. opt
18*a*	comm. transversa (ant. pars ventr.
18*b*	comm. transversa (post. pars ventr.)
19	tr. prae-thalamo-cinereus.
20 (*a*, *b*)	brach. tecti laterale, (ram. lat. ram ventr.
21	brachium tecti mediale.
22	comm. minor Herrick.
23	comm. horizontalis.
24	fibrae ansulatae.
25	comm. tuberis.
26	comm. habenularis.
27	fasc. retroflexus.
28	tr. lobo-cinereus brevis. et tubero-dors
29	tr. thalamo-lobaris.
30	tr. mesenc. lob. ant.
31	comm. supra-infundil.
32	fasc. intralobaris.
33	tr sacci vasculosi.
34	tr. thalamo-spinalis.
35	fibr. profundae tect.
36	comm. posterior.
37	tr. rotundo-lentiform.



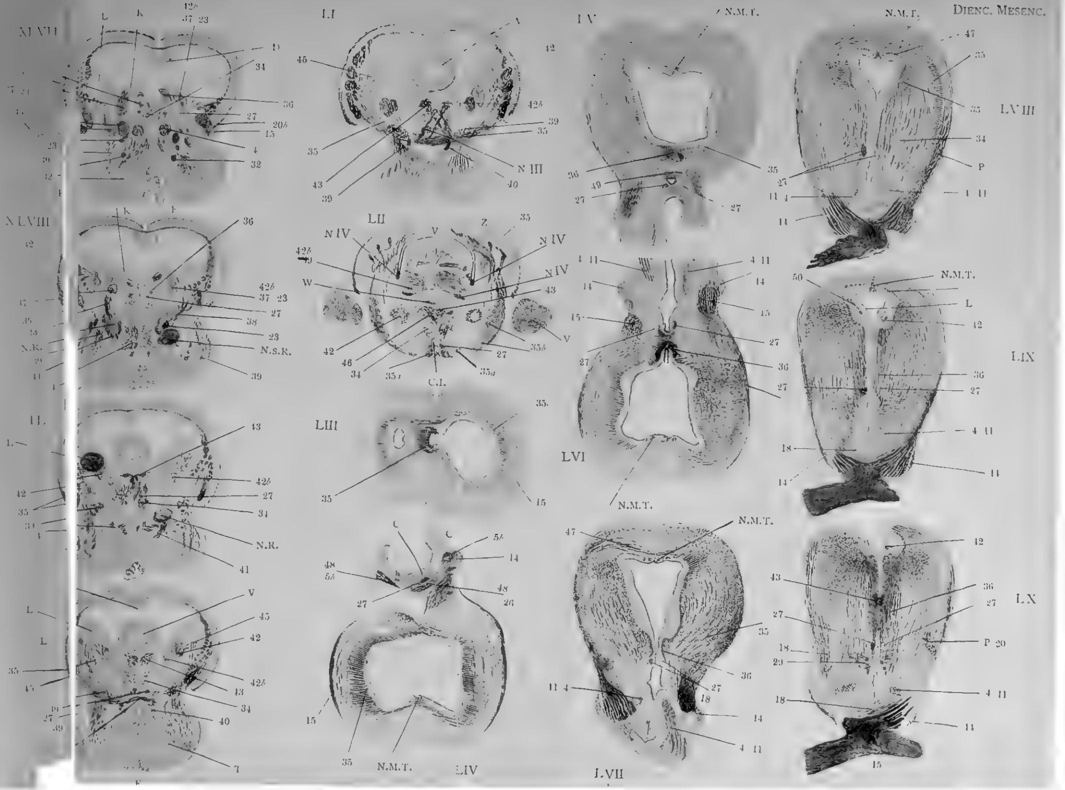
TAB. III. (DIENCEPHALON, MESENCEPHALON).

XLVII—LII, Gadus morrhua; LIII—LX, Galeus canis.

D.	. . . tor longitudinalis.
F.	. . . saccus vasculos.
H.	. . . ventric. lobi infer.
L.	. . . colliculus (c. nucl. lat. mesenc.).
P.	. . . corpus genicul. later.
T.	. . . subst. grisea lobi inf.
V.	. . . valvula cereb.
W.	. . . velum anticum cereb.
Z.	. . . tectum opticum.
N.R.	. . nucl. rotundus.
N sR.	. . nucl. subrotund.
C. J.	. . corpus interpedunc.
N. M. T.	nucl. magnocell. tecti.
P.	. . corpus genicul. later.
K.	. . eminentia medial.

Tracti:

4	tract. strio-thalamicus.
5*b*	tract. alfacto-hobenul.
11	tract. medianus.
15	n. opticus.
18	comm. transversa.
20*b*	rom. vent. broch. tecti later.
23	comm. horizont.
26	comm. habenularis.
27	fasc. retroflexus.
29	tract. thalamo-lobaris.
32	fasc. intra lobar.
34	tract. thalamo-spin.
35	fibrae profundae tecti.
35*a*	lemniscus cruc.
35*b*	lemniscus rectus.
36	comm. posterior.
37	tr. rotundo-lentiformis.
38	tr. mesencephalo-lobar. post.
39	tract. lobo-cereb.
40	tract. lobo-pedunc.
41	tr. rotundo-lob.
42	fasc. longit. later.
43	fasc. long. post.
44	comm. ansulata.
45	fibrae lemnisci ad colliculum.
46	tr. tecto-cereb. infer.
47	tr. tecto-cereb. super.
48	tr. desc. gangl. habenulae.
49	comm. pulvin.
50	fibrae profundae ad collic.
14	tr. pallii.
42*b*	tr. mesencephalo-cerebellaris superior.

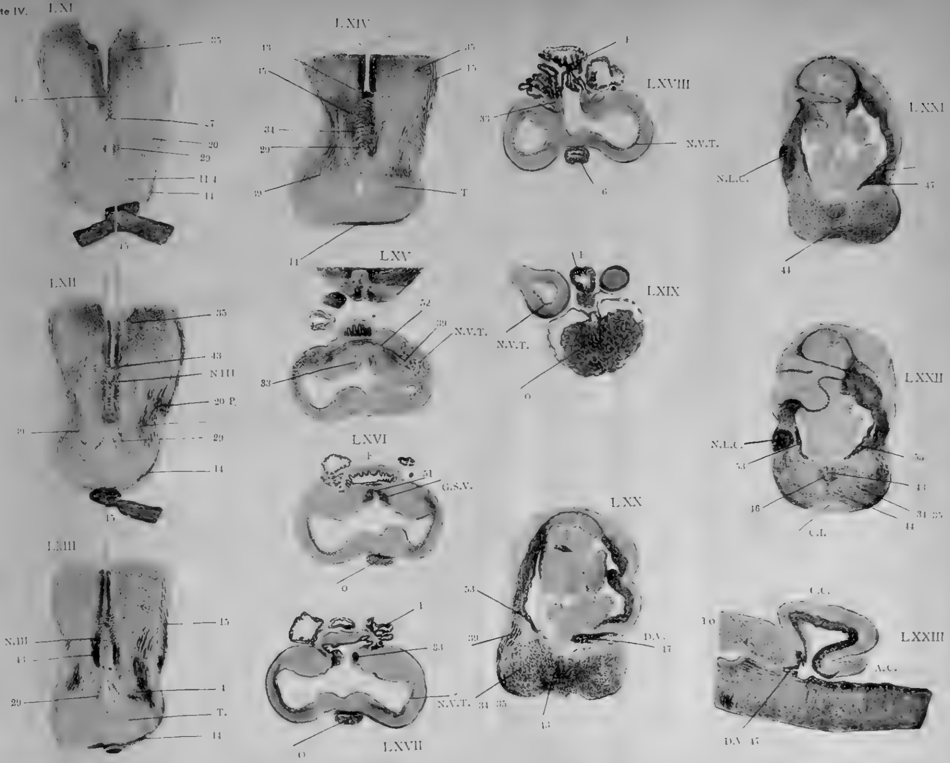


TAB. IV. (DIENCEPHALON, MESENCEPHALON);
LXI—LXXII GALEUS CANIS;
LXXIII ANGELUS SQATINA.

F . . saccus vasculosus.
O . . hypophysis.
P . . . . corpus genicul. later.
T . . substantia gris. lobi inf.
C I. . . . . corpus interpedunc.
N.V.T. . nucl. ventralis thalami (Haller).
G.S.V. . . ganglion sacc vasc.
D.V. . . decuss. veli.
C.C. . . corpus cerebelli.
N.L C. . nucl. later. cereb.
A.C. . . auric. cer.

Tracti:

4 tract. strio-thalamic.
11 tract medianus.
14 tract. pallii.
15 N. opticus.
20 brachium tecti.
27 fascic. retroflex.
29 tract. thalamo-lob.
33 tract. sacci vasc.
34 tract. thalamo-spin.
35 lemniscus.
39 tract. lobo cereb.
43 fasc. long. post.
44 comm. ansulata.
46 tract. tecto-cereb. inf.
47 tract. tecto-cereb. sup.
51 comm. post-infund. inf.
52 comm. post-infund. sup.
53 tract. cereb. motor. cruc.



TAB. V. (METENCHEPHALON).

LXXIV—LXXXV, Lophius piscatorius.

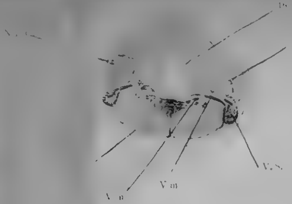
N. L. C.	nucl. later. cereb.	C. H....	comm. infima Halleri.
T. A. L.	tuberc. acust-later.	G. C....	cellul. gigant.
V. Q....	ventric. quart.	N. Sp. S..	nerv. spin. sens.
C. C....	corpus cerebelli.	L. S.....	lobus sensib.
C. A....	comm. acustica.	N. Sp. M.	nerv. spin. mot.
L. V....	lobus VII, IX, X sens.	C. M. Sp.	cornu mot spin.
N. R...	nucl. Rolandi.	R. M....	radices motor.

F.M.L. fibrae motor. long.

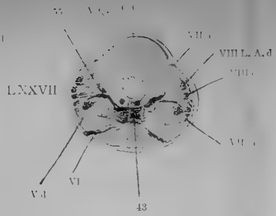
Tracti:

43	fasc. long. post.	55	fibrae arcuat. dors.
46	tr. tecto-cereb. inf.	56	fibrae breves.
54	tr. cereb. spin. dors.		
V s......	N. trigem. rad. sens.	VIII.....	n. acusticus.
V m.....	N. trigem. rad. mot.	VIII d....	tract. desc. N. acust.
V m c....	N. trigem. rad. mot. cruc.	VIII L. A.	rad. lateralis ant.
V d......	tractus descendens trigem.	VIII L. P.	rad. lateralis post.
V d *a*.....	tr. desc. trig. ad n. Rol.	VIII L. A. d	tract. later. ant. desc.
V d *b*.....	tr. desc. trig. spinalis.	VIII L. P. a	tract. later. post. ascend.
VI.......	N. abducens.	IX.......	N. glossopharyng.
VII m *a*...	N. facialis rad. mot. genicul.	X.......	N. vagus.
VII m *b*...	N. fac. rad. mot. infer.	X m c....	N. vag. rad. mot. cruc.

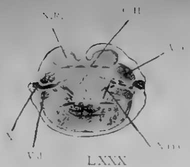
LXXIV



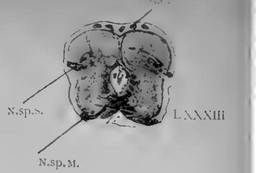
LXXVII



LXXX



LXXXIII



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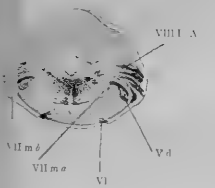

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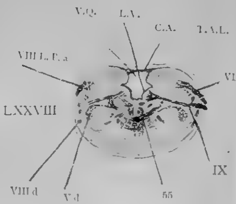
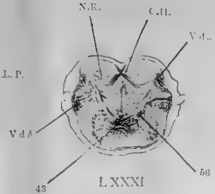


LXXXI



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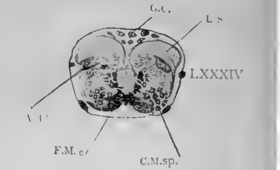

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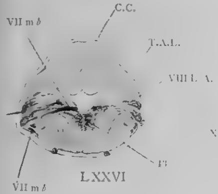
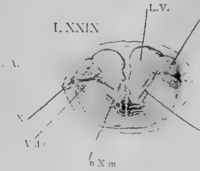
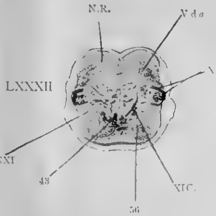


LXXIX

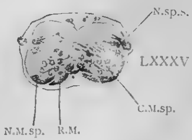


LXXXII



G.C.

LXXXV



TAB. VI. (METENCEPHALON): LXXXVI—XCVII, Gadus morrhua.

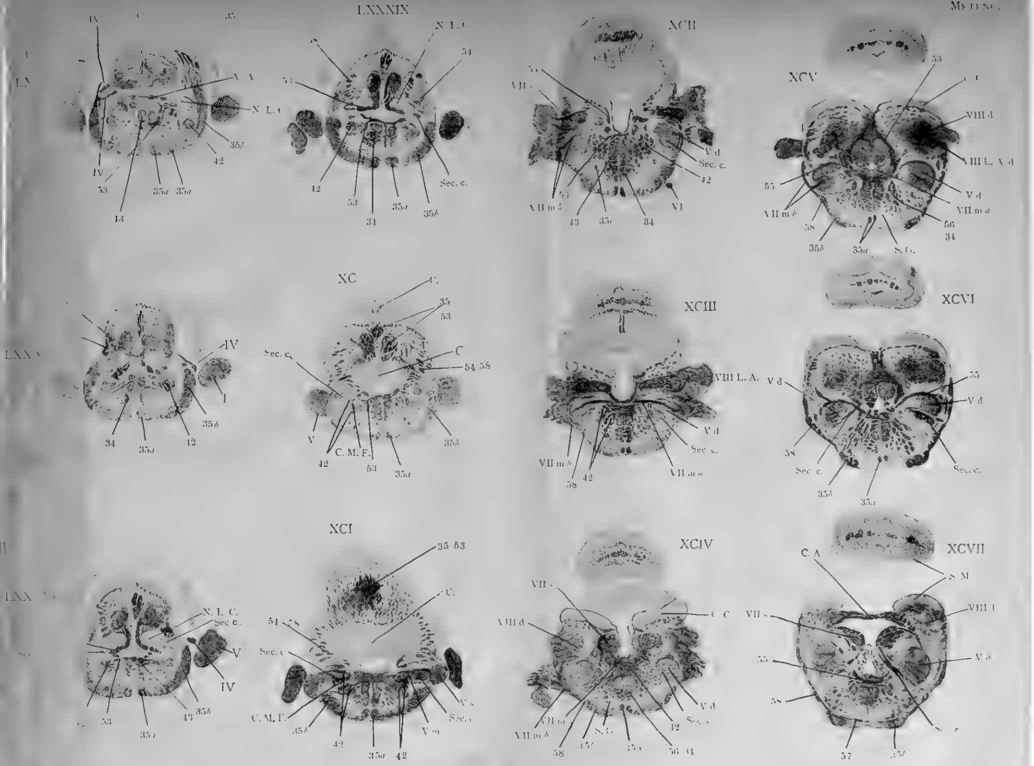
T. O. . . tectum opticum.
C. . . . cerebellum.
V. A. . velum anticum.
N. L. C. nucl. lateralis cereb.
C. M. F. cornu motor. frontal.

S. G. . . substantia grisea med. oblong.
C. C. . . crista cerebell.
C. A. . . comm. acustica.
S. M. . . strat. moleculare.

Tracti:

34 tract. thalamo-spin.
35 lemnisc. (fibr. prof. tecti).
35*a* tr. tecto-bulbaris cruc.
35*b* tr. tecto-bulbar. rectus.
35*c* tr. tecto-bulb. ad nucl. n. abduc
42 fasc. long. later.
43 fasc. long. post. s. dors.
IV . . . . . N. trochlearis.
IV*a*. . . . . N. trochlearis rad. infer.
IV*b*. . . . . N. trochlearis rad. super.
V . . . . . . N. trigeminus.
V s . . . . . rad. sensib. N. trigem.
V d. . . . . rad. sens. descend. N. trig.
V m. . . . . rad. mot. n. trigem.
Sec. C. . . . tr. secund. region. commun.
VI . . . . . N. abducens.

53 tr. cerebello- et octavo-motor. cruc.
54 tr. cerebello-spin. dors.
54*a* pars tr. cer. sp. dors. ad nucl. lat. cer.
55 fibrae arcuatae dorsales.
56 fibrae breves.
57 fibrae arcuatae externae.
58 tr. cereb. spin. ventralis.
VI c. . . . fibr. N. abduc. cruc.
VII . . . . N. facialis.
VII s . . . . rad. sens. n. facial.
VII m *a*. . . rad. mot. genicul. n. facial.
VII m *b*. . . rad. mot. infer. n. facial.
VIII . . . . Nervus octavus (vestibularis).
VIII d . . . fibrae desc. n. octav.
VIII L. A. . rad. later. anter.
VIII L. A. d fibrae desc. rad. lat. ant.



TAB. VII. (METENCEPHALON):

XCVIII, XCIX Gadus morrhua: C—CVIII, Galeus canis.

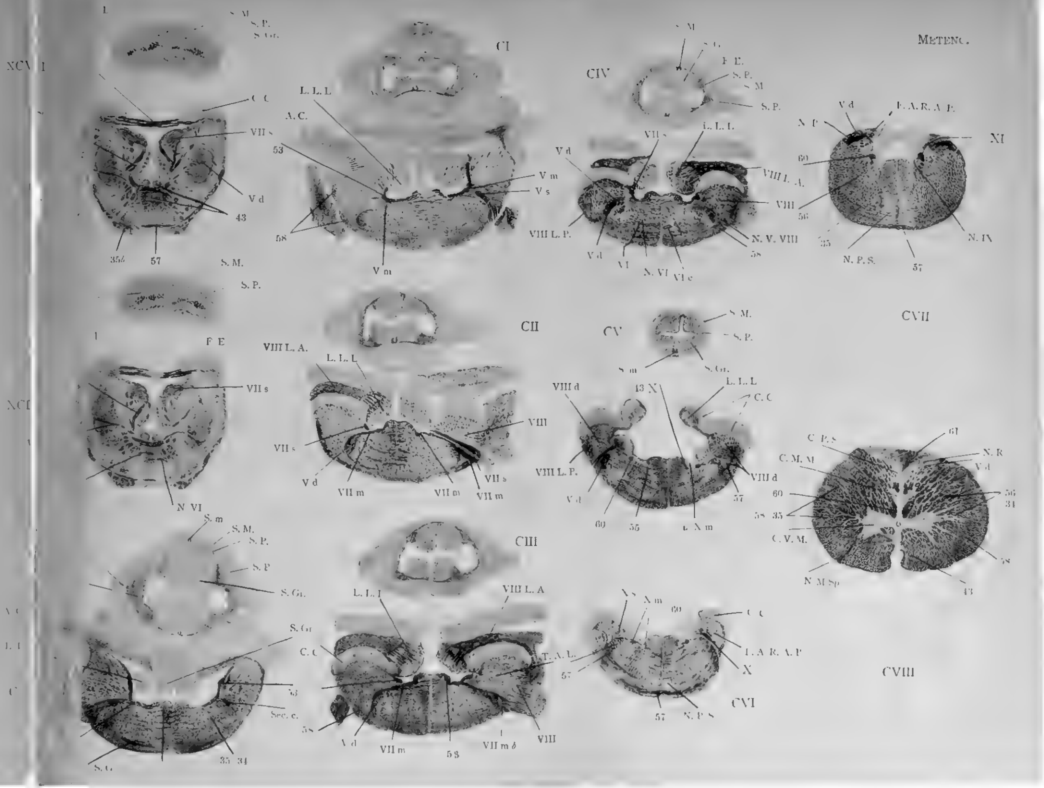
F. E.	fibrae externae cereb
F. I.	fibr. internae cereb.
S. M.	stratum moleculare.
S. P.	strat. Purkinje.
S. G.	subst. grisea ventr. med. oblong.
S. Gr.	strat. granulosum.
C. A.	comm. acustica.
C. C.	crista cerebell.
N. VI	nucl. n. ab-duc.
A. C.	auric. cereb.
L. L. L.	lobus liniae lateralis.
T. A. L.	tuberc. acustico-laterale.

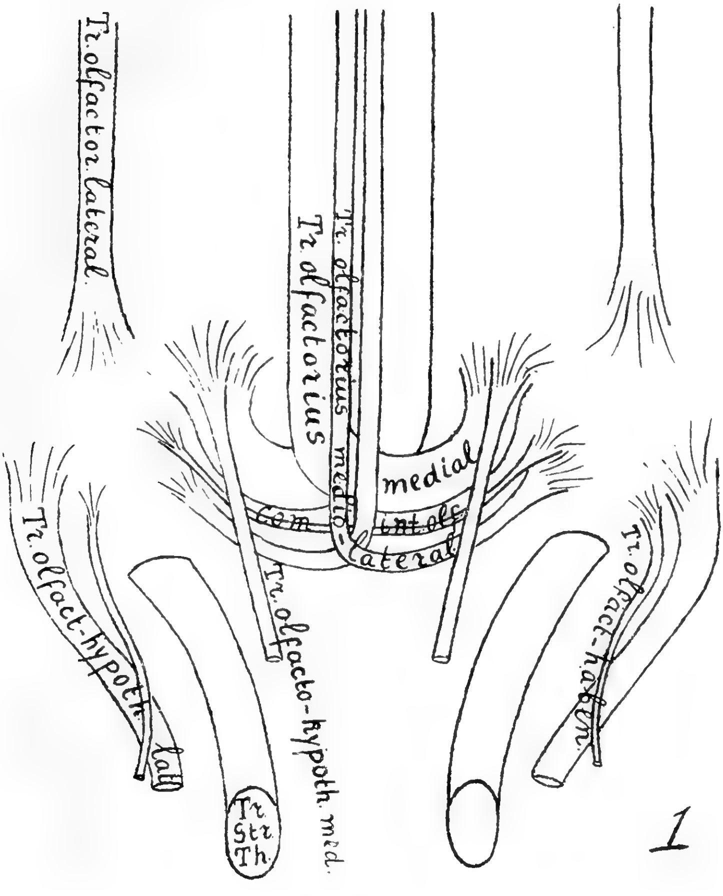
S. m.	sulcus medianus.
N. V. VIII.	nucl. vent. N. acust.
N. P. S.	nucl. paraseptalis.
N. X. m.	nucl. vagi motor.
N. R.	nucl. Rolandi.
F. A. R. A. P.	fibrae acusticae et regio acustica posterior.
N. XI.	nucl. N. accessorii.
C. P. S.	cornu post. sens.
C. M. M.	cornu med. motor.
C. V. M.	cornu ventral motor.

Tracti:

34	tract. thalamo-spinalis.
35	tract. tecto-spin. et bulbaris.
35*a*	tract. tecto-bulb. cruc.
35*b*	tract. tecto-spin.-rectus.
43	fasc. long. post.
43 X	fasc. mot. vagi fasc long. post.
53	tract. cereb. motor. cruc.
Sec. C.	tract. secund. region. comm. (VII, IX, X Sens).
V.	nervus trigem.
V s.	rad. trigem. sens.
V m	rad. trigem. motor.
V d.	rad. trig. descendens.
V d R	rad. trig. desc. ad nucl. Rolandi.
V d S	rad. trig. desc. spin.
VI	nervus abducens.
VI c	fibrae n. abd. cruc.
VII	nerv. facialis.
VII s.	rad. fac. sensib.

55	fibrae arc. dors.
56	fibrae breves.
57	fibrae arc. externae.
58	tract. cereb. spin. ventralis.
59	comm. interlobaris vagi.
60	fasc. medianus *Stieda*.
61	fun. posteriores.
VII m	rad. fac. motor.
VII m c	rad. fac. mot. cruc.
VII m *a*	rad. fac. mot. genicul.
VII m *b*	rad. fac. mot. cum tract. desc. trig.
VIII	nerv. acusticus (vestibularis)
VIII d	fibrae descend. N. acust.
VIII L. A.	rad. later. anterior.
VIII L. P.	rad. later. posterior.
X s.	rad. vagi sens.
X m	rad. vagi mot.
XI	n. accessorius.





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Scheme of the Fore-brain Tracts in Teleosts.
For Description See Chapter I.

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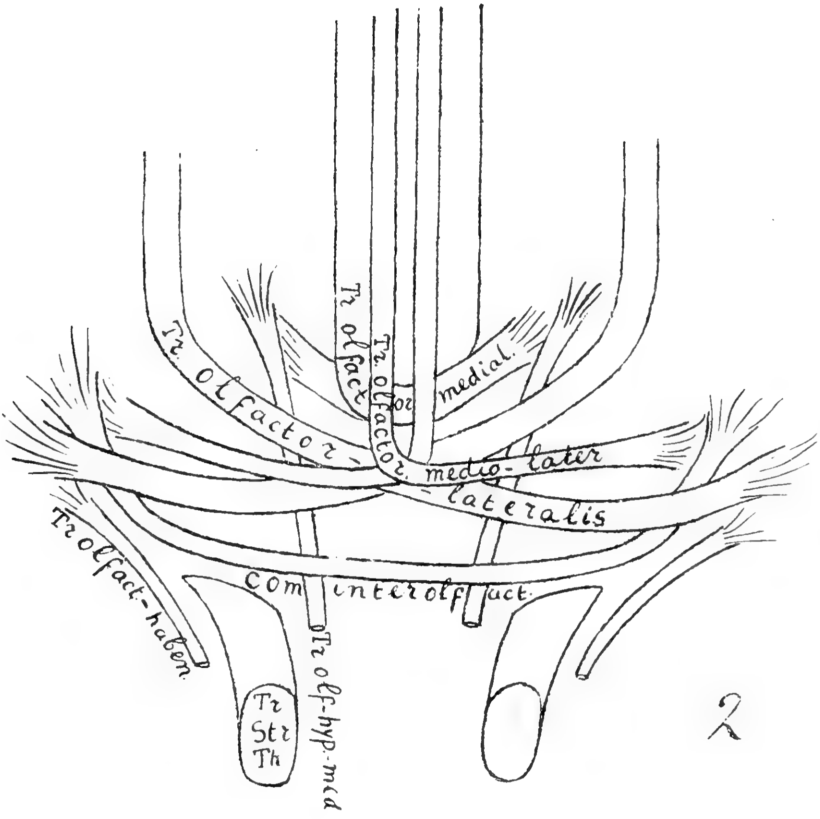
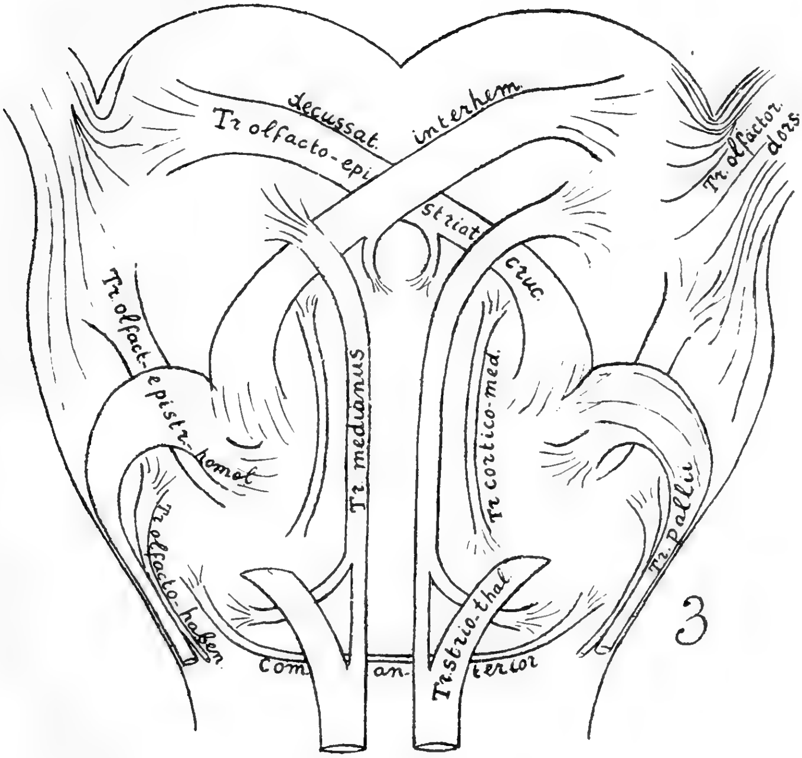
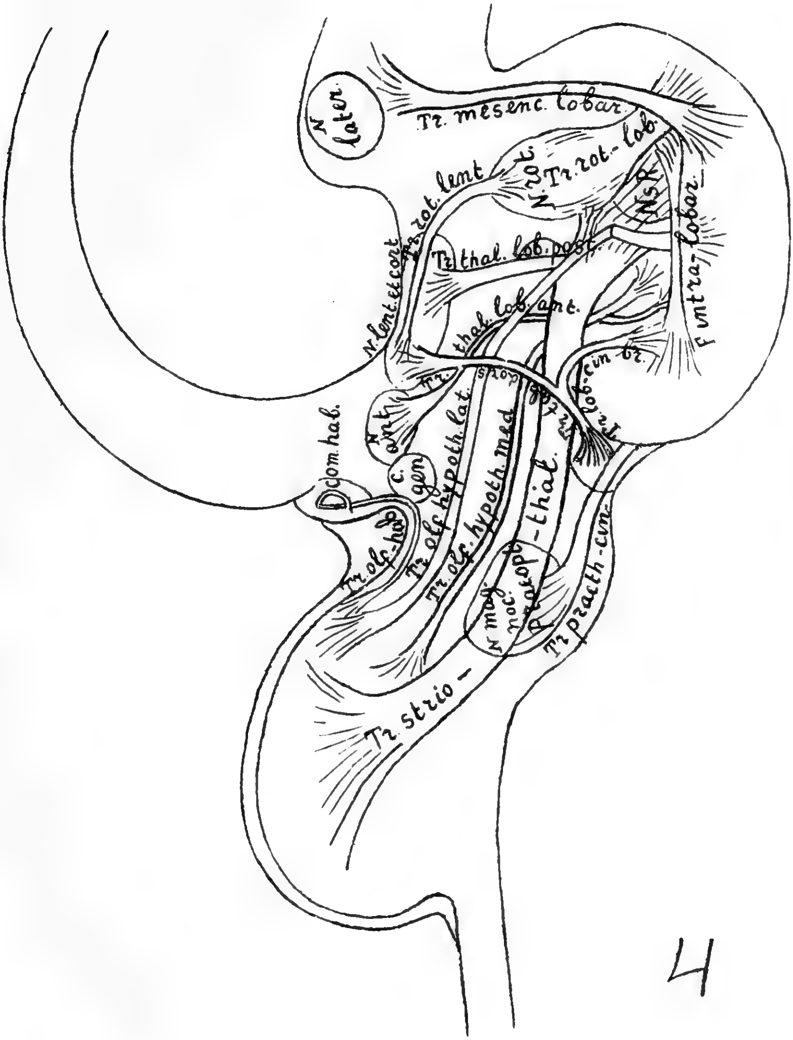


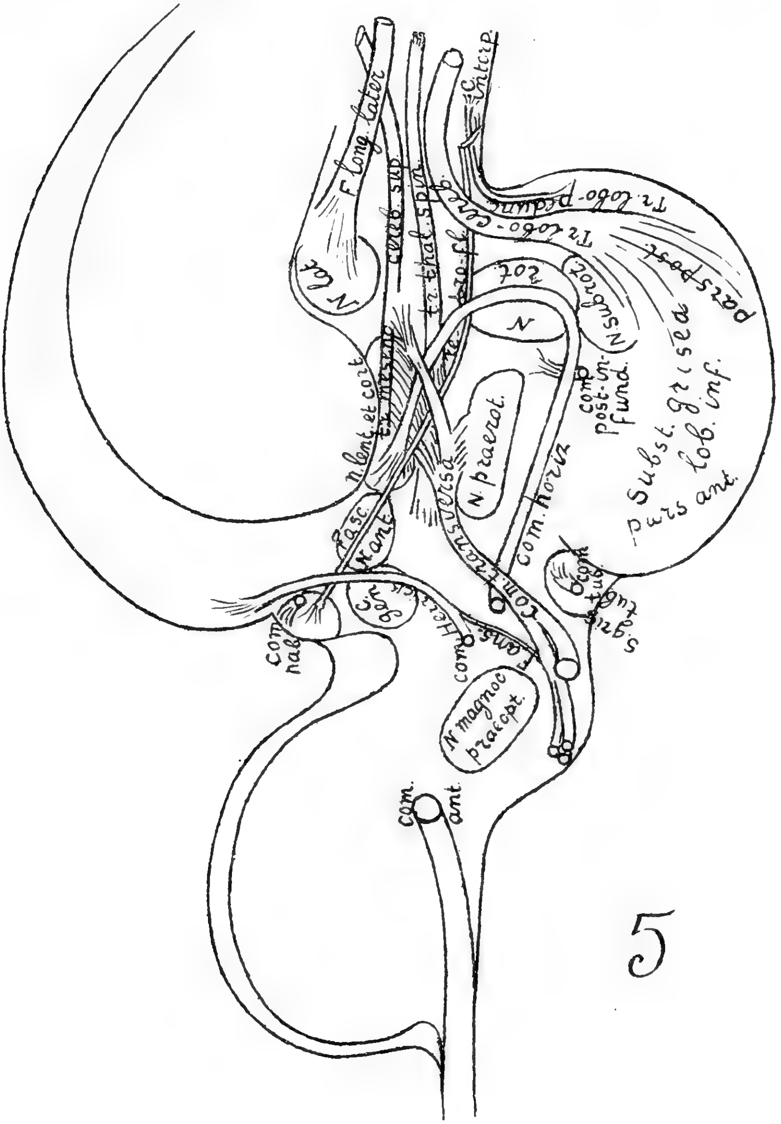
Scheme of the Fore-brain Tracts in Teleosts.
For Description See Chapter I.



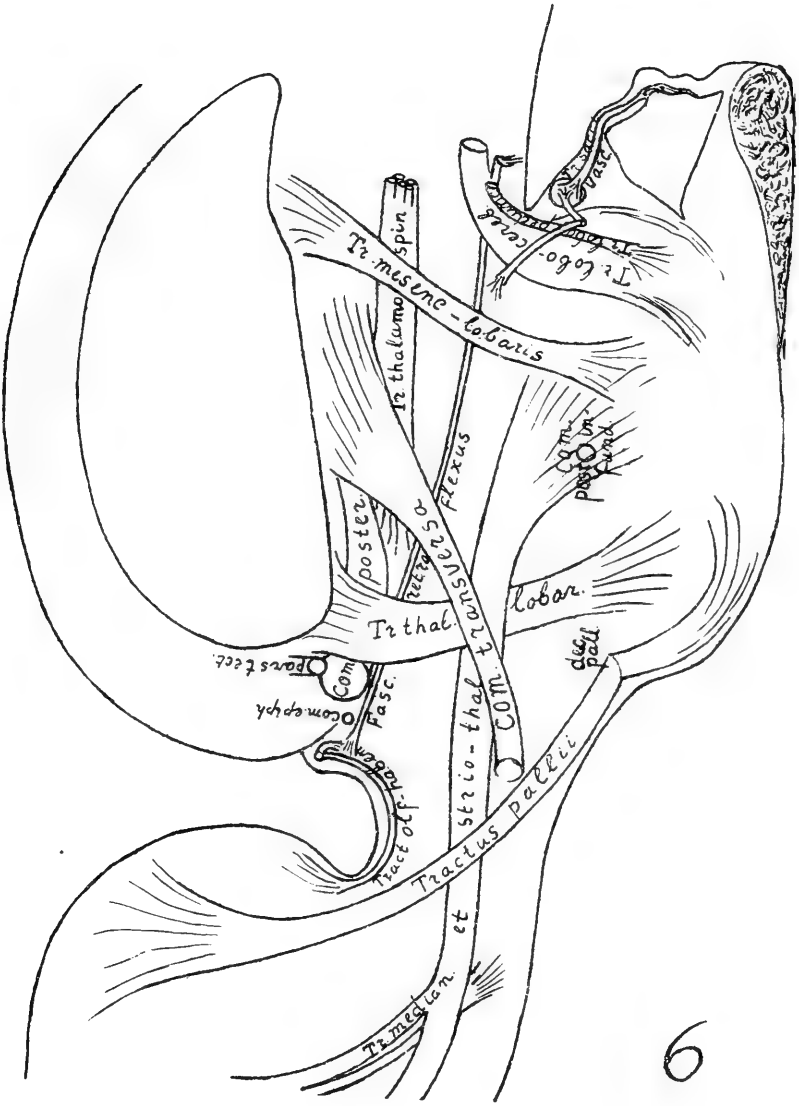
Scheme of the Fore-brain Tracts in Selachains.
For Description See Chapter I.



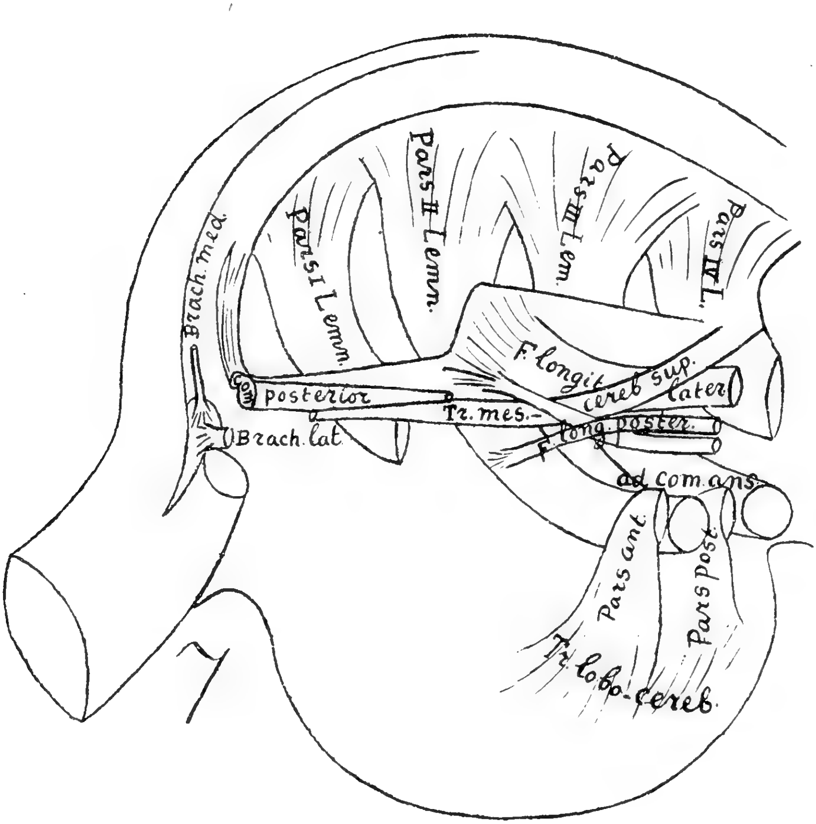
Scheme of the 'Tween-brain Tracts in Teleosts.
For Description See Chapter II.



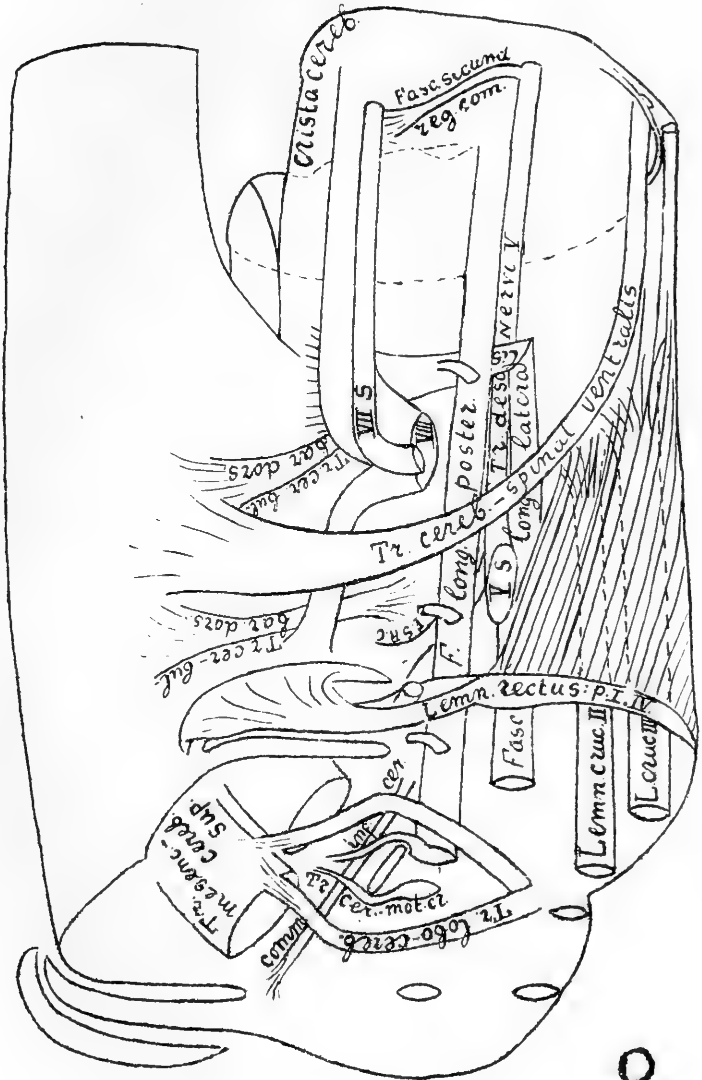
Scheme of the 'Tween-brain and Mid-brain Tracts in Teleosts.
For Description See Chapter II and III.



Scheme of the 'Tween-brain Tracts in Selachians.
For Description See Chapter II.



Scheme of the Mid-brain Tracts in Selachians.
For Description See Chapter III.



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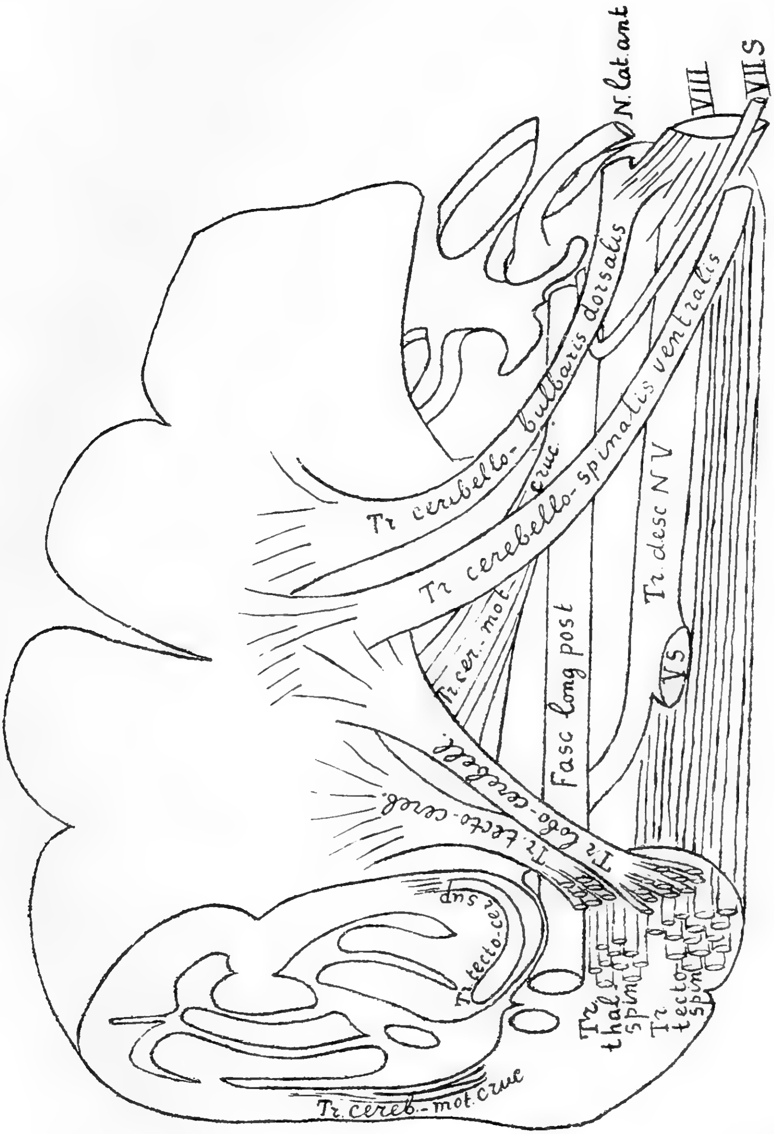
Scheme of the Hind-brain Tracts in Teleosts.
For Description See Chapter IV.



Scheme of the Hind-brain Tracts in Selachians.
For Description See Chapter IV.

9

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Professor Parker has shown that Rana pipiens is positively phototropic to intensities of light from 1 to 20,480 candle-metres, and also that the skin as well as the eye is a receptive organ for light. The central nervous system is not directly stimulated. R. M. Y.

Hunter, George William. Notes on the Heart Action of Molgula manhattensis (Verrill). *Amer. Jour. of Physiol.*, Vol. 10, pp. 1–27. 1904.

In this study of the heart action of Molgula the author has collected data concerning the normal action of the organ, its relation to the nervous system, and the influence of poisons. Removal of the ganglion in various ways causes modification of the beat—depression, irregularity, lack of coördination. R. M. Y.

Wixon, Howard H. The Principles of Soaring Flight. *Scientific American Supplement*, No. 1554, p. 24904, Oct. 14, 1905.

The writer attempts to account for the energy acquired by birds when soaring in circles, upon a principle much like that of the anemometer. When in that part of the circle in which it moves with the wind, the bird tilts its wing anterior edge down, thus presenting a hollow surface to windward and catching the air just as does the cup of an anemometer. But in the other half of the circle, in which the bird is returning against the wind, the wing is tilted in such a way as to offer much less resistance to the passage of the air.

Observations are needed to show that birds actually make such wing movements when soaring in circles. And an elaboration of the theory is needed to show how a bird has power to change its course when drifting before the wind, for at such a time the bird may be motionless with respect to the wind. But the reviewer believes that such an extension of the theory can easily be made, and that Mr. Wixon has given a suggestion which, when followed out, will go far toward explaining how birds soar in a spiral. WALLACE CRAIG.

Wheelock, Irene G. Regurgitative Feeding of Nestlings. *The Auk*, N. S., Vol. 22, pp. 54–70. 1905.

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The author details changes in the nesting sites of half a dozen American birds following upon the changed conditions due to advancing civilization.

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Clark, Austin H. The Migration of Certain Shore Birds. *The Auk*, N. S., Vol. 22, pp. 134–140, 1905.

The author suggests that the planetary winds are an important factor in guiding migrating birds, especially over the trackless ocean, the birds being always prone to fly at right angles to the wind. He suggests also that the peculiar routes taken by certain species are due to eastward and westward leeway caused by these winds

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Cole, Leon J. and Tooker, H. C. Habits of a Muskrat in Captivity. *Fourth Report of the Michigan Academy of Science*, pp. 199-205. 1904.

An interesting account of the food and feeding habits, general activities and space perception of a muskrat which was kept in captivity by the authors.

The chief points of the paper may be summarized as follows. The animal washes face and grates teeth before eating. It eats almost any vegetable, leaves, fruit, etc., and is especially fond of carrots. Surplus food is stored. No animal food is taken. Quiet during the day; active at night. "It does not fully appreciate height—a trait connected with its aquatic habits." R. M. Y.

Janet, Charles. Observations sur les Guêpes. *Paris*, pp. 85. 1903.

In this paper JANET has brought together descriptions of the activities of several species of Vespa, and of Polistes gallicus. Nest construction, care of larvæ, food, enemies, and general activities are considered. The paper contains almost too many "observations diverses" to be scientifically satisfactory, but it does present a great number of facts which are interesting and valuable from the natural history standpoint. R. M. Y.

Duret, H. Les Tumeurs de l'Encéphale, Manifestations et Chirurgie. 836 pp., 297 figures. *Paris, F. Alcan*, 1905.

This extensive monograph has grown out of the Report on Cerebral Tumors made to the French Congress of Surgery in 1903, and aims to present a comprehensive picture of the actual state of our knowledge in this field at the present time, including original contributions of importance.

The work is divided into four parts. The *first part*, General Manifestations, includes chapters on the Syndrome and Semeiology of encephalic tumors, comprising their constitution, variation, pathogeny and general symptomatology. The *second part* includes the local manifestations, taking up each part of the brain in detail and also the osseous walls at the base of the brain (pp. 170–471). The *third part* is devoted to diagnosis, taken up under the headings, semeiotic diagnosis, differential diagnosis, topographic diagnosis, diagnosis of multiple tumors and diagnosis of the nature of the neoplasm (pp. 472–591). The *fourth part*, Surgery (pp. 592–828), contains five chapters, entitled, Historical, Indications, Operative Procedures, Statistical Tables and Results of the operations.

The tables include an exceedingly valuable analytic summary of four hundred operations, gathered from the entire literature. They are followed by a detailed analysis of the cases on the basis of age, sex, the nature and location of the tumors, results, etc. It appears that in these 400 cases 19.5 per cent. succumbed to the primary effects of the operation, an advance from 25 per cent. in 1899. Seventy-three per cent. received positive benefit, and considerably more than half of the cases received permanent amelioration or cure. Attention is called to the fact that nearly half of the cases operated are sarcoma or glioma and we do not obtain better results with this class of neoplasms in other regions of the body. C. J. H.

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A very readable book written from a standpoint which will appeal to the general medical practitioner for several reasons, notably because of its emphasis on the significance of the earliest symptoms of mental disorder which, as a rule, he alone can meet and which are of the highest importance to successful treatment. The work will also prove attractive to those of our readers who, though not in the practice of medicine, desire a practical introduction to the leading facts of psychiatry. Starting from the position that psychiatry "not only forms a branch of general medicine, but should be classed with other biological studies," the author treats each topic conservatively on the basis of a clear scientific analysis of both old and new doctrines. Some of the chapters may prove disappointing to those accustomed to a more dogmatic treatment, but the sharp discrimination of definite clinical fact from theory is perhaps the most distinctive merit of the work.

C. J. H.

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THE ESTABLISHMENT OF AN ASSOCIATION INVOLVING COLOR-DISCRIMINATION IN THE CREEK CHUB, SEMOTILUS ATROMACULATUS.

BY

MARGARET F. WASHBURN AND I. MADISON BENTLEY.

The only experimental evidence hitherto existing, so far as we have been able to learn, that fish possess the power to discriminate colors is contained in the work by Vitus Graber, published over twenty years ago and entitled *Grundlinien zur Erforschung des Helligkeits- und Farbensinnes der Tiere.*[1] Graber experimented on a large number of animals, including two species of fish, Cobitis barbatula and Alburnus spectabilis. His method was to offer the animals the choice between two compartments differently illuminated, and at the end of a given period to count the number in each compartment. The results thus tested light-preferences rather than light-discrimination merely. Graber himself points out that the two do not coincide, inasmuch as an animal may be quite capable of distinguishing between two colors and yet find them so nearly equal in feeling-value that it seeks them equally often. There must also be reckoned with the possibility that apparent color-preferences are really brightness-preferences, due to the difference in brightness between the two stimuli employed. This latter difficulty Graber avoided in the following manner: If an animal showed itself to be, in our modern phrase, positively

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[1] Rough experiments performed some years later by W. Bateson (*Jour. of the Marine Biol. Assoc. of the United Kingdom,* N. S., Vol. I, 1889–90, p. 225) gave, as the author says, "chiefly negative results." Bateson fed young mullet with minced worms sprinkled on tiles of various colors and noticed that the light-colored tiles were first cleared of food. It is to be remarked that Bateson was working for *preference* and not for discrimination of color and also that he neglected to control the element of brightness.

or negatively phototropic to a marked degree, and also showed a preference for one color or another, the preferred color was taken much darker than the other, if the animal was positively phototropic, or lighter if negatively phototropic. The persistence of the preference under these conditions showed it to be a true color-preference. GRABER'S results for the two species of fish were approximately the same and showed decided preference for white over black, a lesser degree of preference for blue without the ultra-violet rays over blue with the ultra-violet rays, for red over green, and for green over blue (ultra-violet). The last-mentioned could hardly be called a preference at all, and the difference between red and green was so slight as to be reversed when the green was made decidedly dark. In fact, the color-preferences proper, as distinguished from the cases involving ultra-violet rays, are scarcely marked enough to allow one to conclude from the experiments that the fish tested had the power of discriminating colors.

The subject of the following study was a female of the common species, Semotilus atromaculatus, the creek chub or horned dace. Our general plan upon beginning the investigation was to test color-discrimination by establishing, if possible, an association between a certain color and food. This method has a two-fold advantage over that employed by GRABER. First, it is a true test of discrimination as distinguished from preference; and, second, involving, as it does, "associative memory," the truly psychic nature of the phenomena resulting will be admitted by the most conservative biologists, whereas the "preference" method, which involves reaction to present stimulation only, establishes the existence merely of a tropism which may or may not have a mental aspect. Of course, in the case of fish, where intelligence has been shown to exist, by the experiments of MÖBIUS, THORNDIKE, TRIPLETT and others,[1] the presumption would be for consciousness.

The fish was kept throughout the experiments in a circular glass tank 50 cm. in diameter and 45 cm. deep. The apparatus used for feeding it consisted of two like pairs of dissecting forceps which were faced on the outer surfaces with four-cornered strips

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[1] Zeitschr. d. gesammt. Naturwiss., Bd. 42, p. 89; Amer. Naturalist, Vol. 33, p. 923; Am. Jour. of Psych., Vol. 12, p. 354.

of wood 5 x 5 mm. across and 70 mm. long. In all the earlier experiments the strips of wood attached to one pair of forceps were painted red, while those attached to the other pair were green of a shade—to the experimenter's eye—somewhat brighter than the red. The strips were fastened to the forceps by small rubber bands and projected in both cases about 5 to 10 mm. beyond the metallic points. The first attempt to apply our general method may be described as follows:

I. The Method of Inhibition.—When the fish reached a certain position at the bottom of the tank, a young live grasshopper, held in one of the two pairs of forceps, was quickly thrust under the surface of the water. *The fish was allowed to take the food from the red forceps, but when it snapped at the green pair the food was quickly withdrawn.* For one day, the red forceps only were used and for the succeeding four days (six feedings) the red and green were used in irregular sequence. One of us applied the stimulus while the other recorded, by means of a stop-watch, the time of reaction—from the instant the food touched the water till it was snapped at by the fish. At the second red-green feeding, we noticed that the reactions seemed, at times, to be prematurely released by the sight of the approaching hand that held the forceps. In order to eliminate the possibility of reaction to a warning signal, the side of the tank next the experimenter was enveloped with a black cloth screen and half the top was covered with heavy gray cardboard. In the subsequent tests, the baited forceps were slipped over the edge of the cardboard top and directly into the water at the center of the tank. In this way, the fish saw no movement until the object appeared at the surface of the water.

The recorded times were, of course, too inaccurate to be considered as "reaction times"; but it was not with reaction times that we were primarily concerned, but rather with the discrimination of color-tones. It seemed probable, however, that a discrimination of red and green—if it occurred—might be expected to lead, in time, to an inhibition, or at least to a retardation, of the green (unsuccessful) reaction.

In the last four days (six feedings) one hundred and thirty-one trials were made, sixty-two with red and sixty-nine with green. The longest reaction was five seconds, and one hundred and thirteen of the whole number fell within one to three seconds. The average time for red and for green was the same, 1.4 seconds.

The total times for the first ten tests were red, fourteen seconds, green, thirteen seconds; and for the last ten, red, ten seconds, green, eleven seconds.

Neither the times nor the observed behavior of the fish indicated any constant difference in the response to the two colors used. The results do not, however, prove a lack of color-discrimination. They are inconclusive. They simply show that even if color-vision existed and if colors were "associated" with success or failure in procuring food, the discrimination and the "association" were insufficient to cause an inhibition of the "green reaction." The outcome is not unaccountable, since brook fish have, at least during a part of the year, a varied diet, and they may therefore be expected to react positively and persistently to a wide range of objects that offer the possibility of food.

Although the result of the inhibition experiments was, for our purposes, largely negative, the method was valuable both because it made us acquainted at first hand with the behavior of our subject and because it suggested a second method which offered a *choice* of stimuli without, at the same time, demanding the actual inhibition of an old and firmly-rooted mode of response to stimulation.

II. The Method of Choice.—In the second set of experiments, *both pairs of forceps were presented at the same time, the red baited and the green empty.* In order still further to eliminate movement of the stimulus the tank was divided by a thin wooden partition into two like compartments. An opening about three inches wide was left at either side of the partition, allowing the fish to swim freely around the tank. These openings could be closed by wooden gates, thus making it possible to confine the fish in either half of the tank. With the subject in compartment A, the forceps were suspended side by side in the middle of compartment B and about two inches from the partition. They were held in place by being slipped vertically into narrow grooves sawed in a horizontal strip which ran across the tank just above the surface of the water, parallel with, and attached to, the upper edge of the partition. After the forceps had been set into position, one of the gates, right or left, was opened and the fish allowed to swim to compartment B and to secure the food from the forceps.

The procedure involves two constant errors of space, one of position of stimulus and one of direction of movement. The first was eliminated by setting the red forceps as often on the right as on the left of the green, and the second was canceled by using both gates and allowing the subject to enter half the time on the same side as the bait and half the time on the opposite side. Both of these compensatory changes occurred in irregular sequence, but an equal number of "right" and "left," of "same" and "opposite" settings were taken at each feeding. The following sample protocol for a series of experiments will serve to make this clear. "Right" and "Left" refer to the position of the forceps in the horizontal support; "Same" means that the fish was allowed to enter compartment B on the same side as the forceps with food in it, and "Opposite" means that it entered on the opposite side from the baited forceps. "R" and "G" refer to the red and green forceps, respectively.

RIGHT.		LEFT.
G.	Same	R.
R.	Same	G.
R.	Opposite	G.
G.	Opposite	R.
G.	Same	R.
R.	Opposite	G.
R.	Same	G.
G.	Opposite	R.
R.	Opposite	G.
G.	Same	R.

In all these experiments, numbering two hundred and twenty-six exclusive of trials without bait, the red forceps held the food and the green forceps were empty. After August 3 mealworms were used for bait instead of grasshoppers, on account of their greater uniformity of appearance. In each case record was made of the forceps at which the fish *first* bit. The accompanying table (I) shows the results in the columns headed "Food." It will be seen that in the first series, of fifteen experiments (food), made on July 31, the fish bit first at the red eleven times and four times at the green; that in the second series of ten experiments it bit eight times at the red and twice at the green, and that after this point biting at the green was very infrequent; in the last seventy-four experiments, from August 5 on, the green was bitten at only once, on which occasion, as our notes show, the fish was ravenously hungry and chancing to come straight against the green forceps on entering, snapped at them. The exceptional results of August 3, where the fish touched the green first three times and the red first five times, should be accompanied by the statements that the

TABLE I. FOOD IN RED FORCEPS.

Date.	No. Exp.	Food.		No Food.		Remarks.
		Dk. Red.	Green.	Lt. Red.	Green.	
July 31	16	11	4	1		Grasshoppers.
Aug. 1	12	8	2	1	1	
Aug. 1	14	10		4		Partition added.
Aug. 2	16	11	1	3	1	Space errors corrected.
Aug. 2	12	9	1	2		
Aug. 3	8	5	3			
Aug. 3	12	10		2		
Aug. 4	14	10		4		Mealworms.
Aug. 4	14	10		4		Light red sticks on green forceps.
Aug. 5	16	11	1	4		Grasshoppers and mealworms. Sluggish.
Aug. 5	14	12		2		Grasshoppers and mealworms. Sluggish.
Aug. 6	16	12		4		Mealworms.
Aug. 6	7	7				Red, daubed with green, and green with red. Sluggish.
Aug. 7	10	10				Not feeding well. Grasshoppers and mealworms.
Aug. 8	16	11	1	4		Ravenous. Grasshoppers and mealworms.
Aug. 8	15	12		3		Mealworms.
Aug. 9	14	10		4		
Totals	226	169	13	42	2	
		Dk. Red.	Blue.	Lt. Red.	Blue.	Blue strips substituted for green.
Aug. 10		7		2		
Aug. 10		3				
Aug. 11		10		4		
Aug. 12		10		4		
Totals		30		10		

subject was in an abnormal condition on that day, languid and sluggish, and that two of the green "bites" were the merest touches with the nose. The fish's indifference to food on this day was so marked that only eight experiments could be made, as it wholly refused to rise after the eighth.

The obvious source of error which would wholly invalidate the results if they stood alone is that food was actually in the red forceps and not in the green, so that both sight and smell might have led the fish in the right direction. It demanded some care to eliminate this error, for, on the one hand, it was impossible, with the forceps fixed in the support, to have them both baited and, at the same time, to prevent the fish's getting food from the green as well as from the red pair; and, on the other hand, we could not perform a large number of tests where neither fork should be baited without weakening the association between red and food. We adopted the plan of performing each day a certain number of experiments, usually eight or ten, with the red fork baited and then making two tests with both forks empty. If the fish's appetite was good, we would give it two more tests with the baited fork and finish with two "unbaited" tests, again. In this way, without greatly weakening the association, we accumulated forty-four experiments where both forks were empty. In two only of these did our subject bite at the green. These two occurred in the first four days of experimenting, and in the second case the fish merely touched the green, then swam to the red and bit vigorously. The results thus show that the sight of the red forceps came to be connected with the impulse to bite, quite independently of the sight of the food. As a matter of fact, the fish's behavior throughout indicated that the sight of the food played little part in setting off the biting impulse. It seldom bit directly at the food, but nearly always at the ends or sides of the sticks, and if by accident the food became detached and floated in the water half an inch or so away, the chub still ignored the morsel and bit persistently at the stick.

The possibility that the smell of the food might have guided the subject remained uneliminated by merely testing the animal with unbaited forceps; for, since food was so often in the red pair and never in the green, the odor of the food might be supposed to linger about the former. Further, we still had the brightness error to deal with. It was possible that the fish distinguished between the red and the green forceps not as different in color but as different in brightness. To avoid this, we took a suggestion from GRABER, and prepared a pair of sticks exactly like the others in size but painted a light red, of the same color-tone as the previous red—so far as our discrimination went—but considerably brighter to ordinary vision than the green, which was, it will be remembered itself a little brighter than the red hitherto used. In all the unbaited test experiments made on and later than the afternoon of August 4, the following procedure was adopted: While the dark red sticks were still used on the baited forceps in the experiments where the fish was fed, when it was tested without bait we removed the dark red sticks and substituted for them the green sticks on the same forceps, using the same rubber bands that had previously fastened the dark red ones. Thus all the apparatus that could have the odor of food about it was now attached to the green sticks. On the forceps that had previously carried the green sticks were fastened, with the rubber bands that had been used for the green, the pair of light red sticks. When the forceps thus arranged were put into position, the fish had the choice between two unbaited forks, one, the green, having about it whatever food odor was present, the other, the light red, having in common with the pair from which it was usually fed only shape, size and color, not smell or brightness. If, then, the creature persisted in biting first at the red pair, it would show that the impulse to bite was "associated" with the color red, not with smell or brightness. It will be seen from the table that in the twenty-five tests made under these conditions the subject never once failed to bite first at the red.

One last, very remote possibility of error lay in the chance that the green and red paints might have had different odors. Inasmuch as the sticks were all covered with the same varnish, the chance was slight, but it was guarded against by putting, where they would not show, daubs of green paint on the red sticks and daubs of red paint on the green sticks. The results were wholly unaffected by this precaution.

In the work from August 10 to August 12 inclusive, comprising forty experiments in all, we substituted for the green sticks on the empty forceps a pair painted a light blue, lighter than the green and approximately equal in brightness to the light red. The last-named were still used and the forceps exchanged as before in the unbaited test experiments, and food was placed in the forceps carrying the dark red sticks in the ordinary feeding experiments. The fish made not a single error in distinguishing either dark or light red from blue, invariably biting first at the red (Table I).

How firmly rooted the association between the color red and the biting impulse was by this time we learned when from August 16 to August 18, in a series of about seventy experiments, we undertook to break it up and form a new association between food and green. The same procedure in every respect was employed as before, except that in the feeding experiments the food was always placed in the green forceps. Dark red was still used on the other pair, in these experiments, and light red in the unbaited tests, and the forceps were again exchanged in such a way as to eliminate error from smell. Because of the light which its behavior threw on the strength of the acquired impulse, we allowed the fish to bite as many times as it would at the red (empty) forks and recorded the number and order of the bites, in each experiment. In the preceding series, the single experiment practically never lasted beyond two or three bites, for if the fish bit first at the red it usually got the food, and in the few cases where it bit first at the green it bit but once and then either went down to the bottom of the tank or swam over to the red. Not so in these final series. The first time the subject entered compartment B, when the food was in the green forceps, it bit fourteen times in succession at the empty red sticks. It then bit once at the green, but not hard enough to get the food, and, returning to the red, bit thirteen more times at it. The fish then tried the green once more, came back to the red for four bites, and then, when it went down to the bottom of the tank, we considered the experiment over. At the second test, the fish bit three times at the red, then went to the green and got the bait at the third bite. In the next test, it bit ten times at the red, then twice at the green, getting the food on the second bite. At the fourth trial, the subject bit four times, but feebly, at the red, came up once from the bottom between the two forceps, "hesitated" and went down again, then came up, bit at the green and got the food. In the fifth test, it came up toward the red, seemed to look at it, swam to the green, nibbled, bit, and got the bait. The sixth time, it bit first at the green but failed to seize the food, turned to the red and bit once, then to the green and got the mealworm in two bites. The seventh time, the chub bit only at the green, taking four bites to obtain the food. The eighth time, it bit first at the red, then at the green, securing the bait in two bites. We then made two tests with unbaited forks, the usual arrangement of apparatus being maintained. The first of these rather indicated that, in this new order of things, the fish was being somewhat influenced by the sight or smell of the food, for in the absence of food it relapsed and bit ten times at the red before it tried the green. In the second "no-food" test, however, the subject barely touched the red, swam to the green and bit three times. And in three more baited experiments it bit first every time at the green; while in the first of the final two tests without food the subject swam past the red, turning away from it, snapped at a small object floating in the water near the red, then at the red, and then, more vigorously, at the green; and in the last unbaited test it bit first at the green, then at the red, then twice more at the green. The fish's behavior throughout this entire series was of the utmost interest as illustrating the process of animal learning. On the following day, the older habit reasserted itself, at the first trial, and the fish bit three times, vigorously, at the red before it tried the green; the second time, it swam straight as an arrow to the green, although it entered on the opposite side and had to pass the red. From this time on, with occasional rather marked relapses, the new "association" between green and the biting impulse shows growth, until in the last series, made on August 18, and consisting of eight experiments with food and four without, our subject bit first at the green every time, except in the first experiment of the series. The following table (II) shows, like the preceding one, the color first bitten at in each test.

We had some difficulty, in this latter part of our work, on account of the fish's diminishing appetite. The confinement of its life undoubtedly told upon its digestive powers. The series of August 14 and 15 were, for this reason, incomplete, and after that we attempted only one feeding a day, instead of a morning and an afternoon feeding as had been our custom. The "no-food" experiments of August 16 and 17 again furnished some indication that the sight of the food in the green forceps had partly influenced the fish in the feeding experiments and that when both forceps were empty it had a tendency to relapse into the old "red-food" habit. On August 16, after six feeding experiments in which the animal had only once bitten first at the red, when confronted with the two pairs of empty forceps, it bit nine times at the red, went down to the bottom of the tank, rose, and bit five more times at the red, sank, rose to the red without biting, and went down again. And on August 17 there still remained a tendency to bite first at the red when both forceps were empty. Also, we observed, at this time, that the biting movements were made less at random than before, that they were aimed less at the sticks and more definitely at the bait; that there was, in other words, a more precise and delicate adjustment to the food-situation.

TABLE II. FOOD IN GREEN FORCEPS.

DATE.	No. EXP.	FOOD.		NO FOOD.		REMARKS.
		Dk. Red.	Green.	Lt. Red.	Green.	
Aug. 13	15	5	6	2	2	
Aug. 14	6	3	3			Sluggish; refuses to bite.
Aug. 15	7	4	3			
Aug. 15	1		1			Refuses to bite after first exp.
Aug. 16	14	3	7	3	1	
Aug. 17	14	2	8	3	1	
Aug. 18	12	1	7		4	
Totals	69	18	35	8	8	

Another factor, without perceptible effect when the connection between a given color and the impulse to bite was fully established, seems to have had some influence, for a time, during the breaking up of the association, "red-food," and the formation of the association, "green-food." This influence, which appeared about the middle of the process, when we may suppose the tendencies to have been about equally balanced, consisted in the position of the fork with reference to the fish's entrance. If these "food-in-green" experiments be divided into three groups, with regard to the temporal order of their performance, the proportion of right cases, *i. e.*, where the green was bitten at first, is for the first third, comprising twenty-three experiments, 52 per cent. The wrong cases are 48 per cent., of the total number. Of the right cases, 58 per cent. occurred when the fish came up on the same side as the correct fork; 42 per cent. when it came up on the opposite side. Of the wrong cases, 45 per cent. occurred when it came up on the same side, 45 per cent. for the opposite side, and in 10 per cent.

it rose from straight below, midway between the forks. In the first third, then, the position of the forks seems to have made little difference with the results.

In the second third, the percentages of right and wrong cases were as before, 52 per cent. and 48 per cent. But 75 per cent. of the right cases happened when the fish was on the same side as the green fork, and only 25 per cent when it was on the opposite side; while of the wrong cases 64 per cent. occurred when the subject was on the opposite side, 18 per cent. when it was on the same side, and 18 per cent. when it rose from below, between the two forks. In the last third of the experiments, 81 per cent. were right and 19 per cent. wrong. Of the right cases, 50 per cent. were from the same side and 50 per cent. from the opposite side; of the wrong cases, 50 per cent. were from the same side, 25 per cent. from the opposite side and 25 per cent. from the middle. In the previous experiments, where the food was in the red fork, the association was pretty well established before the final method was adopted, which allowed the place of the fish's entrance and the position of the forks to be regularly varied. Of the few errors that occurred after the adoption of this method, half were made when the fish entered on the same side as the red fork, and half when it entered from the opposite side; while, of the right cases, 50½ per cent. happened when the fish was on the same and 49½ per cent. when it was on the opposite side. It looks, then, as if the association once formed was wholly independent of the subject's position, but that, at a critical period, when the animal was not strongly drawn to either fork, the fact that it happened to come upon one of them first was in some degree an influence leading it to bite at that one.

In summary, the experiments indicate the following conclusions:

1. Semotilus atromaculatus distinguishes red from green and from blue pigments, the discrimination being independent of the relative brightness of the colors. It must be borne in mind that owing to the great physical complexity of pigment colors, the existence of specific visual qualities in the fish's consciousness cannot be inferred with as great certainty as if pure (homogeneous) colors had been used.

2. An individual of this species is capable of forming with considerable rapidity an "association" between the impulse to

bite and an object of a particular color, thus displaying in the service of the nutritive instinct a fair degree of "intelligence."

3. Experience involving pleasurable consequences in connection with one object and the absence of such consequences in connection with another object may be powerful enough to guide an animal in the performance of an instinctive action, but not powerful enough to suppress the performance of such an action.

4. An influence, such as the actual presence of food in one pair of forceps, or the fact that the fish entered the compartment on the side nearest a particular pair of forceps, may be completely swamped when the association between a color and the biting impulse is fully formed, but may have some effect while the association is non-existent or incomplete.

One or two comments may be added. The rapidity with which the fish learned was a surprise to us. In general, it may be prophesied that the more deep-rooted and essential the instinct appealed to by the "experience" to which an animal is subjected, the more rapidly will the animal profit by that experience. It is quite probable that the maximal "intelligence" of which such a fish as Semotilus is capable is enlisted in the service of the feeding instinct. The third conclusion seems to us of great interest. When we began the experiments by the Method of Choice we were impressed with the probability that the fish's previous experience by the Method of Inhibition, though it had failed to influence the animal's behavior under that method, was making itself felt in the very rapid learning to choose rightly between red and green. Although this cannot be dogmatically asserted as a fact, yet the speed of the creature's acquisition in this case, together with its apparent entire failure to learn by the other method, affords a very pretty illustration of the truth that the chief function of experience is to guide rather than to inhibit instinct.

THE HABITS OF CERTAIN TORTOISES.

BY

H. H. NEWMAN.

(*Contributions from the Zoölogical Laboratory of the University of Michigan, No. 104.*)

CONTENTS.

INTRODUCTORY REMARKS.

Methods of Study.—In order to understand an animal one must live with it, must spend long hours, quiet days, in thoughtful observation of it, as it pursues its daily round of occupations. This I have had an opportunity of doing, and I now feel that I have a really personal acquaintance with at least five species of tortoises. I believe that I am able to diagnose their dispositions and comparative intelligence—their character.

Not only is there a species character but a sex character and even an individual character. For example, males are, as a rule, more timid than females, and specimens of the same sex and age often show marked individual differences in disposition.

Studies of this sort should, I believe, precede experimental studies, for sometimes shyness or wariness might be mistaken for stupidity, and sullenness for sluggishness in reaction. As a rule the more highly organized and alert species of tortoises display, when in captivity, the greatest degree of sullenness and hence their actions in confinement very poorly represent their true character. The species, on the other hand, that are less highly organized are the species that act more nearly normally when in captivity; but these naturally stupid forms furnish the less interesting psychologic data. Captivity inhibits normal activity in nearly all tortoises; consequently I abandoned at an early stage of my work the observation of specimens in confinement and devoted myself to long-continued, and at times tedious, observation of the various species as they live in their native environment.

Description of the Environment of Species Studied.—The work was done at Lake Maxinkuckee in northern Indiana. This lake is nearly circular and measures 2.7 miles at its greatest diameter. Its depth is on the average not great, at no point more than eighty-four feet. The shores are low and, as a rule, slope gradually. The bottom is for the most part muddy and rather soft except in regions that are covered with stones. The water supply of the lake is mainly artesian and is very rich in all the mineral salts necessary for animal and plant life. The lake bottom is almost everywhere covered with a dense forest-like growth of vegetation, that affords a retreat for mollusca, crustacea and fish of all sorts, and a hunting and browsing ground for the various species of tortoises. On the northeastern shore of the lake there are several artificial lagoons that are freely connected with the main body of water. These lagoons furnish unusual facilities for observation as the water is always quiet.

List of Species Studied and their Relative Abundance.—When I first visited Lake Maxinkuckee in the fall of 1900, I was immediately struck by the abundance and the variety of species of tortoises there, but not until nearly two years afterward did I begin a systematic study of their habits.

The species that occur in the lake are as follows:[1]

1. Aspidonectes spinifer.
2. Chelydra serpentina.
3. Aromochelys odorata.
4. Graptemys geographica.
5. Chrysemys marginata.
6. Nannemys guttata.
7. Terrapene carolina.

The most characteristic and abundant species is Graptemys geographica, outnumbering many times any other species found in the lake. The other species occur in abundance in the follow-

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[1] The nomenclature and order is that found in JORDAN's Manual of the Vertebrates.

ing order: Chrysemys marginata, Aspidonectes spinifer, Chelydra serpentina, Aromochelys odorata, Nannemys guttata, and Terrapene carolina. The first five species were sufficiently abundant for purposes of habit study and it is with these only that I deal in this paper. The first on the list, Aspidonectes spinifer, was found to be the most interesting and instructive, and its habits are here described as fully as observations permit. The other species studied will be dealt with more briefly, attention being directed chiefly to the differences in behavior displayed by the various forms. In brief, the treatment will be comparative.

CLASSIFIED ACTIVITIES.

1. *Aspidonectes spinifer (the Common Soft-Shelled Tortoise of our Lakes and Rivers).*

This species is, in many respects, the most highly organized and specialized of our tortoises. In point of intelligence, alertness, swiftness on land and in the water, and in general capability it ranks first of the species studied. A classified account of the activities of this species will serve to lead up to a general conception of its disposition and character.

Seasonal Activities.—These tortoises are first seen early in April and seem to be in a very weak condition after their winter's dormancy. I have frequently picked them up from the sandy beaches where they lay with head, neck and legs extended to the full, apparently stupified by their first exposure to the sun's warmth. At these times it is an easy matter to walk up and capture them, for when seized they make only a feeble effort to escape. A coating of mud on limbs and carapace is circumstantial evidence that they have wintered in the mud on the lake bottom. It is possible that only much weakened specimens find it necessary to crawl out on shore for a preliminary warming up. After the first few warm days in April they are no longer to be seen basking on the sand, but seem to devote themselves to very active feeding. Mating must take place during April or May but I have not had an opportunity to observe it.

Aspidonectes nests rather later than the other species, as a rule not earlier than the middle of June. Nesting continues until the middle of July, and in rare cases considerably later.

As the water becomes colder in late fall they are less often seen swimming about on the surface, but spend much of their time resting half-buried in the mud. I had an excellent opportunity of observing this preparation for the winter in the case of two large females that were confined within a lattice enclosure in a lagoon. They buried themselves in a peculiar way—by rocking the body from side to side and throwing the mud up in such a way that it settled on the carapace and covered them quickly from sight. By continuing this movement they sunk deeper and deeper, leaving only the snout protruding from the mud.

A few days later the water of the lagoon froze over and I could still see the snouts of the tortoises, but when the ice extended to the very bottom they must have withdrawn deeper into the mud. It was a matter of some surprise to find both of these animals alive when the ice thawed out. After a day or two, however, they died and examination showed that they had suffered from frost. This, then, could not be considered as a normal case, as under natural conditions the animals would be able to bury themselves below the frost line. The observation shows, however, that they are capable of living through the winter without the use of air or water for respiration.

Resting and Basking.—Under ordinary conditions Aspidonectes basks in the open air less frequently than do other species. Occasionally I have seen isolated specimens basking in company with a number of Graptemys on floating objects at a safe distance from shore. On my approach they have invariably been the first to slide off into the water.

This quickness to escape is facilitated by a characteristic habit of turning around so as to face the water, whenever they climb out upon a floating object or upon the shore. Thus no time is lost in turning around when danger approaches. The same trait I have observed in other parts of the country—notably in the rivers of northern Illinois. Here the animals basking on the somewhat precipitous river banks had their heads down so that they could swim away without loss of time or equilibrium.

Their favorite method of warming up—a process that seems to be a physiologic necessity for reptiles in general—is to lie in very shallow water. When seen under these conditions they are always rather thinly coated with mud which they throw up by the use of the rocking or careening movement previously described. Sometimes the snout is protruded above the surface of the water but more often the head is withdrawn into the carapace and only occasionally extended to the surface.

This method of warming up is practicable only in regions where the banks slope gradually and afford shallow water. Where the banks are steep and no shallows are available they come out upon logs, and even upon the shores and bask in the regular chelonian fashion, but they are extremely alert and cannot be taken unawares while out of the water.

Methods of Locomotion.—Aspidonectes is exceptionally swift, whether on land or in the water. It is almost impossible to overtake them in boat or canoe, while other species are easily captured in this way. When pursued, they immediately head for deep water, swimming with powerful and rapid strokes.

On land they move in a manner that belies their name "tortoise." I have seen them scramble down a bank and into the water faster than I could follow, while on a level piece of road they can move nearly as fast for a short distance. Although essentially aquatic they climb steep railway embankments with considerable ease, in order to reach a sand pit some fifty yards from the water.

Methods of Self-Defense.—Although their ability to elude pursuit furnishes them with a most efficient method of defense, they are not limited to this alone. Their bite is vicious in the extreme. When captured they hiss violently and thrust out the head, snapping vigorously with a sudden precise darting movement. Their aim is accurate and if the objective point is within reach they seldom miss. One learns to grasp them by the tail, as this is about the only part of their body that is beyond the reach of their fierce jaws.

Unlike other species they keep the eyes uppermost when snapping at objects back of them. They refuse also to retire into the carapace when captured, but continue to struggle violently for some time. After an exhausting struggle, however, they seem to become discouraged and lie quietly as long as they are watched. If confined in a room they never wander around, but remain in some dark corner, watching one's actions with an alertness quite characteristic.

When first captured there exudes from the inguinal glands a thick yellow semi-fluid excretion resembling in appearance the yolk of an egg. This substance has no perceptible odor, but is undoubtedly homologous with the emission of the inguinal glands of the musk and snapping tortoises, that has such a nauseating odor. Of course it is problematical that even this malodorous excretion serves a protective function, but it at least tends to disgust a captor.

Feeding Habits.—Aspidonectes is voracious and carnivorous, feeding principally upon crayfish and the larvæ of large insects. From the vantage ground of a high bank it was possible on still days to observe individuals as they captured their prey. They crawl or swim along the bottom, thrusting their snouts under stones and into masses of aquatic vegetation, occasionally snapping up a crayfish or larva that they have succeeded in dislodging. They do not tear up their food, but swallow it whole, using the fore-feet to assist in forcing it down.

The stomachs of three specimens, opened during the latter part of June, contained the following:

1. A large female contained nine medium-sized crayfish, only slightly digested.
2. A medium-sized female contained four crayfish and twenty-two dragon-fly larvæ.
3. A large male contained nine dragon-fly larvæ and a few plant buds, probably taken by accident when snapping up the larvæ.

The professional fishermen of Lake Maxinkuckee claim that where "soft-shells" are seen swimming about, large-mouth black bass are not far away. The reason for this became apparent as I watched a group of Aspidonectes feeding. Two large specimens were seen prowling about in a somewhat random fashion, while three large bass accompanied them. Occasionally a fish darted after some object near the tortoises, and once I saw both fish and tortoise aim at the same object. Although I could not distinguish the objects of their search I concluded that the bass were accompanying the tortoises in order to profit by the fact that the latter dislodged many animals that they were unable to capture. The stomach contents of both fish and tortoises are identical and this is further evidence of the reality of their habitual association.

Professor JACOB REIGHARD has noticed minnows of various sorts following soft-shelled tortoises and picking up food, and suggests that the bass might be feeding upon them rather than upon crayfish. The matter might be settled definitely by the examination of a large number of stomachs.

Breeding Habits.—Aspidonectes begins to lay as early as June 10, somewhat later than other species. The females are very wary in their choice of times and places for laying. At one place near the lake shore men are accustomed to harvest hay early in July or late in June. The shore near the hay fields is sandy and sloping and affords an ideal nesting ground for "soft-shells." They will not approach the shore, however, until the men leave for the noon-day meal. Then they crawl out cautiously, dig their nests and deposit their eggs before the return of the harvesters.

They also frequent a sandy road that runs for nearly a mile along the water's edge. A new road has been made farther back from the shore, leaving the "old road" almost without traffic. This abandoned road affords a sequestered retreat for the female "soft-shells," and they nest there in large numbers. So many use this place for nesting that regular run-ways are worn through the tall grass that occupies the strip of land between the road and the shore. One can sometimes detect the presence of tortoises by the waving of the grass and this is often a useful signal for the observer to seek concealment and watch developments.

One soon learns to expect the females to seek a nesting place during the warmest part of the day, as they seem to avoid leaving the water in the cool of the morning or evening.

The female "soft-shells" come to the surface many yards from shore and seem carefully to reconnoiter before coming ashore. They then swim shoreward beneath the surface, coming up at intervals to see if the coast is clear. On reaching the shore they crawl out upon the sand and, before proceeding further, they extend the head to its full height and remain motionless for some time, the very embodiment of alertness. At this time the slightest movement or sound of a suspicious character alarms them and they dash back into the water. If undisturbed, however, they proceed slowly and cautiously to the nesting ground and begin operations without delay, working more rapidly than other species.

The following was jotted down in my field note book as I watched one specimen nesting:

June 22, 1903, 11.10 A. M.—A warm sun-shiny day. Place: the "old road" about ten feet from the water's edge and concealed from view on one side by tall grass. A large female Aspidonectes has just emerged from the grass and is commencing to make a nest. No time is lost in selecting a spot.

She scratches out footholds for the fore-feet and begins to excavate with the hind-feet, using right and left feet alternately with a circular gouging movement. At intervals she pushes aside the accumulated earth with the hind-feet. As the hole becomes deeper it is necessary for her to raise the anterior part of the body to its full height in order to give a more nearly perpendicular thrust with the hind-feet.

In less than forty minutes the nest is completed and she has commenced to lay her eggs, letting the tail down into the narrow hole as far as possible. After depositing several eggs she arranges them with the hind-feet and then rakes in some earth previously wet up with water from the accessory bladders. The earth is gently packed in before any more eggs are laid. The remainder of the eggs are deposited and the hole is filled up with earth and tramped down quite firmly with the knuckles of the hind-feet, right and left feet being used alternately. This treading movement continues for some minutes and seems to be quite thorough. Although not in any way disturbed, the tortoise left without attempting to cover up the traces of scratching feet, and anyone who is familiar with the appearance of a tortoise nest would have no difficulty in detecting this one. At 12.25 she turned and started for the water but was captured with a landing net. The nest was examined and found to be flask-shaped with a narrow neck only an inch and a half in diameter. The depth of the nest was a trifle over six inches and the diameter at the bottom about three inches.

The nest contained eighteen rather large spherical eggs of a delicate pink color and with a very thin brittle shell.

The above account is typical and differs only in minor details from the other cases observed.

Considering their high order of intelligence, they show little or no judgment in the selection of nesting places. The character of the soil seems to be immaterial so long as it is near the water's edge. Nests were found in clay so hard packed that one could scarcely break it with the fingers. One nest was made in a rock pile, the eggs being dropped into crevices between rocks, and sand packed around them. Several nests were made among the smaller roots of a tree growing on the sandy beach, the eggs being deposited between and under the roots in a very irregular fashion. The majority of nests, however, were found in soft beach sand not over six feet from the water.

AGASSIZ says that tortoises while laying or making their nests cannot be frightened away. This statement does not seem to apply to Aspidonectes. Whether or not they leave their task seems to depend somewhat upon the degree of completion of the nest. My observations lead me to believe that they will leave on the first sign of danger if surprised before the actual laying process begins, but will wait to cover up the eggs more or less completely if surprised after laying or during the process.

The suddenness of their dash for the water seems to depend on whether or not they feel that they have been exposed to view. I have frequently passed within a few feet of tortoises that lay hidden in the grass without causing them to take alarm. Had these been in the open they would almost certainly have hastened to make their escape. On one occasion as I was returning after walking to the southern end of the "old road" in search of nesting tortoises I caught sight of a huge female almost hidden in the grass. As soon as she caught my eye she made a dash for the water and escaped. From the fact that she had almost completed her nest I knew that she must have been in the same place when I passed a few minutes before, but was aware that she had escaped detection.

On another occasion I discovered a large female lying very flat on a narrow shelf-like ledge of railway embankment. She evidently saw me immediately as she stretched up her head in the usual alert fashion. For a few moments she remained perfectly still eyeing me closely, and, as I made no hostile move, she continued her work, which proved to be the filling in of a nest. After the completion of this task she remained motionless for some time. Then, as I turned my head slightly to look at an approaching boat, she turned quickly and scrambled down the embankment and into the lake before I could overtake her.

That females may abandon their nests even when engaged in laying is shown by the fact that on one occasion I found a nest of large size containing only seven large eggs that were not covered up. From the fact that the nest was within a few feet of the railway track, I concluded that the tortoise had been unable to control its fright at the sight of a rapidly approaching train and had beaten a hasty and ignominious retreat.

A discussion of breeding habits would not be complete without some account of the character and number of eggs laid, about which there has been a considerable diversity of statement. Some observers claim that as many as sixty, others as many as forty, are laid by one female at one time. This I believe to be an error due to two incorrect observations. One source of error is the counting of ovarian eggs not in the oviducts. It is well known that these are destined for the following two or three seasons. Only the eggs actually in the oviducts are destined for the current season. The other source of error arises from considering all the eggs in one nest as the deposit of one female. Frequently in small sandy areas such large numbers of tortoises lay their eggs that nests are in contact or overlap. I have found as many as forty eggs together but have been able to distinguish the eggs of one nest from those of another by the size, shape and stage of development of the different sets.

By counting the eggs in many isolated nests and in the oviducts of many females caught before nesting or while excavating their nests, I have been able to determine that the number of eggs laid at one time varies from nine to about twenty-four, averaging about eighteen.

On one occasion I found on the "old road" a nest containing nine small ellipsoidal eggs and contiguous with these twenty-three large spherical eggs of much fresher color and evidently more recently laid. This nest was unquestionably a double one made by a very large specimen over or overlapping that of a very small specimen. It is interesting to note that the youngest females lay the fewest and smallest eggs, and that such eggs have a tendency to be ellipsoidal in shape. Another interesting fact is that the eggs are so delicately oriented that they fail to develop if turned over after they are laid.

Behavior in Captivity.—Extreme sullenness characterizes the behavior of Aspidonectes while in confinement. If kept in a room they hide behind the furniture and remain motionless for hours and almost days. When put in aquatic enclosures they immediately bury themselves in the mud and seem to remain there for months. Nothing will induce them to eat or to take any interest in their surroundings. If caught while making their nest, they are sometimes forced to lay the eggs, but never make a nest in confinement. The eggs are simply dropped about on land or in the water and are usually crushed when found. None of their normal characteristics are in evidence and it would be a waste of time to attempt to draw conclusions about their disposition or intelligence from their actions in captivity.

Behavior of the Young.—In many respects the behavior of young and half-grown specimens shows marked differences from that of the adults. They are not likely to display when captured the fierce and sullen traits so characteristic of adults. On two occasions I succeeded in taming specimens four or five inches in carapace length so that they would allow their heads to be scratched without snapping. They will also lie quietly in the hand, apparently enjoying its warmth.

On several occasions I found recently hatched young lying in water an inch or less in depth and partially covered with sand or mud. Their protective coloration was so perfect that only the keenest scrutiny could detect their presence. This protective measure is quite a necessary one, as a young Aspidonectes would furnish a tender morsel for fish or other tortoises, if it were at all conspicuous. This I found to my dismay when I tried to keep several young Aspidonectes in an aquarium with adult Armochelys and Chrysemys.

Summary.—The following brief diagnosis of the character or disposition of Aspidonectes may now be attempted:

The adults are characterized by remarkable swiftness, alertness, wariness and fearlessness when in natural conditions.

In captivity they are sullen in the extreme and show marked depression of spirit.

The young acquire gradually the characteristics of the adult.

2. *Graptemys geographica (the Map Tortoise).*

Of the three species of the family Emydidæ, that occur in Lake Maxinkuckee, Graptemys geographica is the most markedly aquatic, never wandering about on land except during the nesting season. Owing to the abundance of this species and its easily observed activities it seems best to introduce a study of its habits in this place instead of following the order of systematic affinities.

Seasonal Activities.—Graptemys appears earlier in the season than any of the other species studied, a few specimens coming to view as early as the tenth of April. They are first seen basking on the banks of the lagoons, where the water warms up many days earlier than in the open lake. On first emerging from the water they are so thickly coated with mud that they are apt to be mistaken for stones.

At this time they are less wary than usual and may be captured with a dip-net, if a cautious approach be made. A week or so later, however, they become so sensitive to terrestrial vibrations that, even if one takes every precaution to remain in concealment, it is almost impossible to approach nearer than some fifty feet, without causing them to take alarm.

During the month of April they spend all the sunny portion of the day basking in the sun, but on the approach of warm weather they leave the lagoons in large numbers, presumably in search of their particular food, which is far from abundant in the muddy waters of the lagoons. From the middle to the end of May the lagoons are almost free of Graptemys, large specimens being especially scarce there.

Nesting takes place throughout almost the entire month of June, but it is at its height from the sixth to the twentieth of that month.

After the nesting season they resume their regular vegetative activities, swimming, feeding and basking. Even as late as the last week in November I have seen them swimming about near the surface and occasionally resting on shore. Frequently young specimens, while basking on shore at this season of the year, become benumbed with the cold and, in consequence of their inability to return to the water, are left stranded on the shores after the ice has formed. One can easily pick up dozens that have met such a fate.

Graptemys displays a decided reluctance to retire into the mud for the winter. It is a familiar sight to observe individuals swimming about or resting openly on the bottom even after the lake has frozen over for the first time. On one occasion, after a sudden severe frost, a large pile of Graptemys of all sizes was observed on the lake bottom in about six feet of water. They lay perfectly dormant, showing no signs of life. It occurred to me that they had huddled up in that fashion for warmth, instead of burying themselves in the mud; or had been taken unawares by the suddenness of the cold spell and were too benumbed with cold to dig their way into the sand of the lake bottom. Very large numbers of Graptemys winter in the soft mud of the lagoons, which afford ideal conditions for them.

Resting and Basking.—These tortoises are in evidence during the summer months to a greater extent than other native species. Basking seems to be their principal occupation. On warm days they literally line the shores of the lake at certain favorable places. Scarcely a floating board or pier lacks its quota of occupants. In some places where the trees overhang the water or have fallen in from lack of support, the smaller specimens of Graptemys mount among the branches to heights of six or seven feet.

When basking they are decidedly gregarious, collecting in such numbers on certain sheltered ledges that it becomes necessary for them to pile up two or even three layers deep, the smaller ones perching high on the backs of the larger ones. Every member of these groups is on the alert and, at the slightest indication of danger, there is a general scramble for the water. The imitative instinct seems to be highly developed. If one animal scents danger and topples over into the water his neighbors quickly follow suit. I have seen all the tortoises within a hundred yards of shore line follow the lead of one that had become alarmed. So acute is their sense of danger that almost any slight divergence from normal conditions serves to give the alarm. A startled bird flying from the grass along the shore or a frog jumping into the water is sufficient cause for a general commotion among the basking tortoises.

By concealing myself in the long grass across the lagoon from a favorite basking place, I was able to note their behavior. After the initial alarm caused by my approach, they regained confidence and cautiously came to the surface. After reconnoitering carefully and seeing nothing suspicious, they proceeded to crawl out upon the narrow ledge where they habitually congregated. One after another they crawled out, the last ones, for lack of room, upon the backs of the first occupants, until, on a ledge scarcely twenty feet long and averaging less than two feet in width, there were crowded over sixty tortoises. In a few minutes one of them took alarm at something that escaped my observation and slid precipitately into the water. All the others, with one exception, followed the lead and in about four seconds the ledge was in possession of one unusually large female, that, for some reason or other, whether from superior experience or unusual sluggishness, refused to leave the vantage ground.[1] In a few minutes the ledge was again crowded and the previous performance was repeated. During the first forty-five minutes of observation the ledge was vacated seven times.

As they lay basking they were continually snapping at passing insects and wriggling their feet, upon which flies and mosquitos were crawling, their actions reminding one of those of a dog tormented by flies. When undisturbed by pests, however, they stretch themselves out to the fullest extent, the hind legs being extended backward so that the soles of the feet are in contact.

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[1] I have repeatedly noticed such cases of marked individuality among tortoises of several species and am inclined to believe that one must admit that there is as marked a degree of individuality in character in this order of reptiles as is acknowledged for much higher animals.

This love for warmth and relaxation seems to be one of the most pronounced traits of Graptemys and must be considered as one of the potent factors governing its behavior. Other species show the same traits to a less marked degree.

Methods of Locomotion and Defense.—Graptemys, as its large, strongly-webbed feet would indicate, is a good swimmer; but not nearly so swift as Aspidonectes, since the stroke is less rapid and the lines of the body less well adapted for speed.

On land Graptemys is not a good traveler. Its movements are slow but not especially laborious. During its search for a suitable nesting place it sometimes goes as much as a quarter of a mile inland, and to do this it must needs be a fairly good walker.

Apart from the possession of a very efficient armor, Graptemys seems to be defenseless, unless a very complete protective coloration be considered in this category. This coloration, however, is clear and distinct only in very young specimens and becomes more and more vague with advancing age. It is most in evidence when most needed.

When captured they hiss and struggle, but very quickly quiet down and retire into the shell. If one thrusts a finger very close to the beak they attempt to bite but they never advance the head or snap. Their head and neck movement is always slow and deliberate and they seize an object firmly but without haste. This slowness of movement may be due to the fact that they do not capture active prey.

Graptemys, more than any other species with which I am acquainted, seeks concealment amidst the vegetation of the lake bottom. If individuals are pursued in boat or canoe they immediately seek out some burrow or tunnel in the thick masses of water weeds. If one approaches a shore where dozens of Graptemys are basking he may search in vain for any trace of tortoises among the weeds, so quickly do they find concealment.

When in the open, however, they depend entirely upon their speed to escape pursuit. But they are easily captured from boats or canoes with the aid of a long-handled dip-net. As a rule, they give one a brief but exciting chase and then stop and retire into the shell, either through exhaustion or in reliance upon the efficiency of their armor.

Feeding Habits.—Graptemys feeds exclusively upon the flesh of a species of viviparous gastropod that abounds in Lake Maxinkuckee.[1] The stomachs of all that I have examined (over twenty specimens) contained the bodies and opercula of these molluscs. When kept in aquaria the opercula are very numerous in the excreta. Adult specimens feed on adult molluscs and young specimens on young molluscs.

Two methods of feeding prevail. The favorite method seems to be to capture the mollusc when the foot and gills are well out of the shell, to bite off the soft parts and leave the hard shell. To do this the final closure of the jaws must be quite sudden. If they fail to secure the body of the snail in this way they adopt the crushing method. The hard shell is easily crushed between the broad flat jaws and the broken pieces of shell are picked out with the aid of the claws. When in search of food they prowl about the bottom, often underneath the dense vegetation. The heavy growth of Chara or Nitella is tunneled in every direction with passageways made by foraging Graptemys.

It is impossible to induce them to partake of any food other than that mentioned above. Specimens kept nine months in an aquarium never fed, while other species were eager for any kind of animal food.

Breeding Habits.—Graptemys begins to lay very early in June, somewhat earlier than other species observed. The females are apt to wander some distance from the water for nesting, seeming to prefer soft plowed soil or clear dry sand away from the beaches. They wander about for hours in search of a suitable place for nesting. One specimen started five nests before she was satisfied with the condition of the soil. Two were rejected on account of the presence of stones and one because the sand caved in too readily. The other two appeared to me to be suitable in every way and I was unable to explain why she abandoned them.

If one expects to see the first stages of nest-making it behooves him to be astir before sunrise. Over half of the females found nesting were encountered before eight o'clock. They work slowly and seem to prefer the quiet hours of the day, probably because they are less likely to be disturbed.

Apart from the slowness and deliberateness of their movements, they work much after the fashion adopted by Aspidonectes, except that they never work the fore-feet so as to secure a foothold.

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[1] This species has been identified for me as Paludina vivipara.

The nests are of somewhat smaller dimensions and the flask-shaped expansion is more symmetrically placed, scarcely more bulged on one side than on the other. Two layers of eggs are deposited in the flasklike expansion but the last two or three eggs are placed in the narrow neck, the uppermost egg being sometimes only about two inches from the surface.

It is difficult to frighten them away after they have once decided upon a nesting place. When surprised they stop work but soon resume it and continue it to the end, even while the observer is in plain view. The nest of Graptemys is a finished product, all traces of nest-making being obliterated. This is accomplished by dragging the smooth plastron back and forth across the small area that had been disturbed by nesting.

The eggs are ellipsoidal in shape, of a dull white color, and have a rather soft, easily indented shell. The number laid by one female at one time varies from eleven to fourteen.

The eggs hatch, as a rule, late in August or early in September, the young burrowing to the surface through the sand. When they emerge they are covered with sand that adheres for some time. Their instinct directs them unerringly toward the water and they frequently have to travel almost incredible distances before reaching the lake or a tributary stream. On two occasions I have found recently hatched Graptemys, at a distance of about a quarter of a mile from the water, traveling steadily and in an approximately correct direction toward the lake. At the observed rate of progress they would reach the lake in about two days.

For some time I was greatly puzzled by the frequent discovery of newly-hatched Graptemys during the months of May and June. Farmers in the vicinity frequently plowed up nests of eggs that were nearly ready to hatch.

These facts have been explained by the observation of occasional specimens nesting during the latter part of July. Eggs laid at that time would have only about five or six weeks of steadily warm weather in which to develop, and would be retarded by the chilling of the ground in October. Thus the well advanced embryos must pass the winter in a condition of dormancy analogous to that observed in hibernating adults.

On no occasion have I caught a female nesting whose carapace length was less than nineteen centimeters and whose age was less than fourteen years—according to the age record afforded by the annual growth rings on the scutes.

Graptemys refuses to mate in captivity and I have been unable to obtain any data as to mating in nature.

Behavior in Captivity.—When confined in aquatic enclosures with access to land, they spend most of their time wandering about seeking a way of escape. Deep paths are worn along the edges of the enclosures by this continual patrol. They do not become accustomed to their captivity within a year, but will invariably seek the water on the approach of a human being.

Owing to the fact that they will not feed in captivity, it is impossible to keep them longer than about sixteen months, since they become weakened by disease and slowly lose vitality. When near death they seem to commit suicide by filling the lungs with water and breathing it until life is extinct. I have occasionally attempted to rescue them from drowning by putting them on floating boards, but, even if too weak to crawl off they usually manage to immerse the head so as to continue the respiration of water. This apparent suicide is probably brought about by extreme weakness and the consequent inability to come to the surface for air. When once the lungs become filled with water it would be impossible for them to breathe air and the inhibition of respiration caused by removing them from water no doubt stimulates their failing energies to the resumption of water breathing.

Behavior of the Young.—The young bask in more exposed places than the adults and in many ways show a decided lack of wariness. They are less disturbed by capture and retire less readily into the shell. They are also found in shallower water and less frequently swim about on the surface than do the adults. In other respects there is no marked difference in behavior between young and old specimens.

Difference in Disposition of the Sexes.—The males are much smaller and weaker than the females and are much more timid and less fierce when captured, showing a decided gentleness when handled. They are also more retiring and are consequently found in smaller numbers. The disposition of the male Graptemys is much like that of the species Nannemys guttata.

Summary.—Graptemys geographica is a very typical water tortoise. Its disposition or character is not extreme in any particular except that it has become highly specialized in its food. It is neither remarkably timid nor aggressively courageous. It is very fond of basking, but cannot be accused of marked sluggishness. It is active in the water and a fair traveler on land, but in neither element does it equal Aspidonectes. Graptemys might be chosen as a norm to which other species could be referred for comparison.

3. Chrysemys marginata (the Western Painted Tortoise).

This species closely resembles the well-known Chrysemys picta, described at some length by AGASSIZ. The family Emydidæ, to which Graptemys, Chrysemys, Nannemys, etc., belong, shows a gradual advance from a purely aquatic to an almost exclusively terrestrial mode of life. Graptemys is thoroughly aquatic, Chrysemys less so. The other members of the family will not be considered in this account. It will be of interest, however, to note the tendency toward a terrestrial life displayed by Chrysemys.

Chrysemys appears a little later in the spring and hibernates a little earlier in the fall than Graptemys.

The two species are found closely associated during all of the warm months, but Chrysemys is very much in the minority, being only about one-tenth as numerous in Lake Maxinkuckee as Graptemys. In other bodies of water in the vicinity the proportion is reversed or in some cases Graptemys is entirely absent.

The nesting season of Chrysemys corresponds closely to that of Graptemys and the methods of hibernation, so far as I have been able to observe, are identical.

They prefer the stagnant lagoons and quiet bays to the waters of the open lake and consequently are to be found basking only in these places. They are often seen in company with Graptemys on the ledges bordering the lagoons. It is characteristic of Chrysemys to bask with the posterior portion of the carapace submerged. It is not uncommon to see them basking high and dry on the shores and ledges, but the other habit is more frequent. This trait results in a curious growth of algæ on the posterior rim of the carapace in very many specimens. Those that spend long periods entirely out of the water seldom show growths of algæ. Here we have another interesting case of individuality in habit.

It seems that certain specimens habitually bask in one way, while others adopt the other method exclusively. They also are frequently found resting among masses of floating vegetation, such as pond scums, lily pads, etc., by which they are buoyed up and at the same time afforded an effective concealment.

As swimmers they compare favorably with Graptemys, no marked difference in speed being evident. They spend much more time wandering about on land than any species thus far described, traveling even further for nesting purposes than Graptemys. This tendency to terrestrial life is, however, not restricted to nesting females. I have found young and middle-aged specimens of both sexes traveling about on land, either between the railway tracks or on the open roads. On some occasions I have picked them up at a distance of from a quarter to half a mile from water.

It was a common experience to find small specimens of both sexes huddled up against the hot steel rails of the railway. This intense love of warmth seems to be a marked trait in tortoises. Gadow describes a similar state of affairs in connection with Clemmys leprosa. Speaking of their behavior in captivity, he says: "They showed an irresistible love for the hot-water pipes, huddling together by the dozens, so that the pipes had to be screened off to prevent the creatures getting burnt. Until this precaution was taken they heated themselves so much that the shields and even the bones of the plastron were injured." I have observed that Chrysemys when kept in a steam-heated room will invariably congregate under the radiator and will lie as nearly in contact with the hot steam pipes as possible.

When captured, Chrysemys is less fierce and sullen than Graptemys, but is more apt to attempt to bite. The bite however, is not at all severe, since the jaws are comparatively weak. If irritated, they retire into the shell and remain quiet for some time.

Chrysemys is not restricted in its diet, but makes use of any sort of animal food that comes its way. I have observed individuals feeding on dead fish, dead clams, decaying tortoises, worms, meat, and aquatic insects. They even capture the soft and defenseless young of Aspidonectes

They tear their food to pieces with the jaws and the long, sharp claws of the fore-feet and occasionally engage in an exciting tugof-war over the possession of food. In seizing their food the head darts out rather speedily but the movement could scarcely be termed "snapping."

The method of nest-making is essentially like that described for Graptemys, but the flasklike enlargement is much less pronounced. This may be due to the much smaller number of eggs laid and the consequent economy of space. The nesting season is about the same as for Graptemys and the choice of nesting places about the same. They lay only four to eight eggs that are strikingly like those of Graptemys in color, shape and character of shell. In size, however, they are somewhat smaller.

Like Graptemys, the broods are sometimes belated in hatching, so that a forced hibernation of embryos results. Many just-hatched young were found during the months of May and June.

Unlike Graptemys, Chrysemys is capable of domestication, feeding greedily after a few days of captivity and remaining active and reasonably contented in an aquarium for years. After some months of confinement my specimens fed from the fingers without any show of alarm.

I have noticed no marked differences in behavior between young and adult specimens, except that the young tend to be less wary and more timid.

Summary.—Chrysemys is a bright, intelligent little tortoise, showing, when captured, little of the sullenness displayed by other species thus far studied. They are not so wary or suspicious of danger as Graptemys and in consequence are more easily captured. It is a curious fact that, with an increasing tendency toward a terrestrial life, the various genera of Emydidæ exhibit a decreasing wariness and sullenness in captivity.

For experimental work Chrysemys is the best form I know, because it is almost perfectly normal in captivity after a lapse of a few weeks.

4. *Aromochelys odorata (the Musk Tortoise).*

This is the smallest, most sluggish and least intelligent tortoise I have studied, but in many respects the most interesting. Although very decidedly aquatic, preferring the deeper and cooler waters, it by no means refrains from excursions on land. Its general structure—domelike carapace, hinged plastron, small, poorly-webbed feet, etc.—seem to point to a terrestrial ancestry, while its large head, its body covered with papillæ instead of scales, its dull color, combined with striped neck, and its love for cold water relate it directly to an aquatic environment. I am inclined to believe that Aromochelys is secondarily aquatic, having been driven, through competition, to seek its food in the water.

During the latter part of April they are seen in large numbers resting amidst the algæ at the bottom of the lagoon. They are very inconspicuous when at rest, partly because of their immobility and partly because of their dull color. One learns to detect them by the yellow stripe on the sides of the head and neck.

Later in the season they come to the surface on warm days and float among the pond scums, remaining for hours in apparent stupor.

When the water of the lagoons warms up in May, they seek the deeper and cooler portions of the lake and are not seen in the lagoons again until late in the fall, when they return in large numbers to hibernate in the soft mud.

The nesting season begins early in June and lasts nearly the entire month.

Adult Aromochelys never, so far as my observations go, bask openly out of the water. The nearest approach to true basking is seen when they float on the surface supported and protected from view by pond scums. Even in captivity they never crawl out on objects above the water, except when seeking to escape from an enclosure. The young, however, frequently bask on stones and boards after the manner of other tortoises.

Aromochelys is a slow, weak swimmer, seldom attempting to swim free from the bottom, but as a rule adopting a compromise between crawling and swimming. The heavy, compact body is evidently a decided hindrance to rapid aquatic locomotion. If startled while at the surface, they drop suddenly to the bottom and use their best efforts to escape. Although their gait on land is unsteady and clumsy in the extreme, they are addicted to more or less extensive journeys on shore. I have caught them at dusk, crawling about in the grass and have seen them catching and eating slugs. On one occasion during a heavy rain I picked up seven full grown Aromochelys along the railway tracks, of which four were males. They were wandering along between the rails, apparently unable to escape. On many other occasions I have caught Aromochelys of all sizes on the roads and between the tracks.

In certain mossy woods near the southern end of the lake it is possible during the month of June to find specimens wandering about over the moss, rooting it up with their snouts and capturing the insects that abound there. They spend so long periods wandering about in this way that the skin of neck and legs becomes dry and wrinkled and the weight of the body is greatly reduced. They seem to be able to endure a greater degree of desiccation than other species studied.

When first captured they emit a very strong musky odor that is extremely nauseating. This odor proceeds from an exudation of the inguinal glands and probably serves as an efficient protection. Their inconspicuous color, heightened by the dense growth of algæ on the carapace, may also serve a protective function. If seized, they hiss and open the jaws widely giving an impression of fierceness that a further acquaintance belies, for they will seldom bite if given the opportunity. Even when they do bite, they do little damage.

As an additional threatening measure they stretch the head back over the carapace somewhat after the fashion adopted by Aspidonectes, but the eyes are directed down instead of up. When the head is stretched backward in this way one can readily seize them by the jaws and hold the head extended from the body. The open mouth and fierce attitude what might very readily deceive one unless he had become acquainted with their truly inoffensive and non-pugnacious character.

They are the scavengers of the lake, feeding on all sorts of material, from dead molluscs to kitchen refuse. They refuse nothing that could be construed as edible. If food is placed in the midst of a group, they fight over it like so many puppies over a rag, pulling and jerking to the best of their ability.

Their appetite is insatiable and indiscriminate. On one occasion I put a living rat in an aquarium containing several musk tortoises. Almost immediately three of them seized it by the feet and pulled it under, thus drowning it. Before it had ceased to struggle they proceeded to disembowel it and succeeded in making a fairly good skeleton of it in a few hours.

On only one occasion did I have the good fortune to observe Aromochelys in the process of nesting. When I first encountered the little tortoise she was digging in some soft soil, using all four feet and her snout. On my approach she abandoned her work and wandered about for fully an hour trying different places. Finally she selected for nesting a decayed stump that had rotted down level with the ground. She dug with fore-feet and hind-feet a shallow hole about two inches wide and of about the same depth, and deposited two eggs therein. After covering these eggs with the excavated débris, she went her way. The form and workmanship of this little nest were of an inferior order as compared with those of other species of tortoises I have observed.

Specimens were captured on land with eggs in the oviducts, ready to be laid, on the following dates: June 11, 16, 20, 22, 23 and 25. In no case did I find more than three eggs in the oviducts. These were elliptical in form and nearly as large as the eggs of Chrysemys. The shell is hard and of a china-like consistency, brittle but capable of withstanding considerable pressure.

AGASSIZ states positively that tortoises do not mate in confinement, but this phenomenon is not uncommon in the case of Aromochelys. They mate even when large numbers are crowded together in limited space and when people are moving about in plain view. I have been able to observe the process of mating in no other species.[1]

Confinement seems to have little inhibiting effect on the normal activities of Aromochelys. They feed and mate quite normally. But when captured with eggs in the oviducts they do not make nests, being satisfied to drop the eggs at random.

When kept in aquaria they frequently stand for long periods on the hind legs, protruding the snout above the surface of the water. In no case have I observed them leaving the water in order to bask on the bricks and boards provided for this purpose. They soon learn to swim toward the person who feeds them and will take food from the fingers.

The young do not differ materially from the adults in general behavior, except that they are often seen basking on shore during the first two or three seasons. They assume the same threatening attitude, when captured, as do the adults, their mock fierceness giving them a decidedly ludicrous appearance.

Summary.—Aromochelys possesses a shy and retiring disposition, living during a large part of its life on the dark weedy lake bottom, rather than in the warmer and shallower waters. These

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[1] Professor JACOB REIGHARD informs me that he has seen Chelydra mating in a small box.

tortoises combine in a peculiar way the traits of aquatic and terrestrial forms. Their mock fierceness may be the relic of a fierce ancestry. After the first attempts to escape they become quite docile and cease to resent their captivity. The species presents an odd mixture of traits that could probably be reconciled by a more complete knowledge of its phylogenetic history.

5. *Chelydra serpentina (the Snapping Tortoise).*

The habits of this species are quite generally known and have been referred to in a more or less fragmentary way by several authors. My observations on the subject are less complete than those given for the preceding species, yet for the sake of comparison it seems advisable to set down in systematic form the available facts.

Chelydra seems to appear and disappear along with Graptemys and it is certain that hibernation takes place in the mud of the pools, swamps and streams of the neighborhood. I am informed on reliable authority that it is possible at almost any time in the winter to secure "snappers" from the mud of the stream bottoms by breaking the ice and grappling in the mud with sharp hooks attached to stout poles.

During the early spring "snappers" frequent the land, leaving the pools probably in search of food. Later in the season, however, they seem to remain constantly in the water, either floating near the surface with the tip of the snout protruded or buried in the mud at the bottom.

Their nesting season corresponds closely with that of Graptemys.

Chelydra basks occasionally in the open, but is much more apt to resort to warm shallow waters, where it buries itself in the mud, leaving only the head free. The head is very inconspicuous on account of its dull gray color and rough warty appearance. The young are not so careful about concealing the body with mud. In shallow pools at the margins of swamps they may be seen in considerable numbers, lying exposed to full view.

Chelydra is a slow and clumsy swimmer, progress through the water being aided as a rule by walking along the bottom. On land they walk slowly, with a peculiarly elephantine gait, yet succeed in covering considerable distances, often going from one body of water to another. I have found both males and females on land at least half a mile from water.

If brought to bay on land large specimens will make a bold advance to the attack. Seldom will they retreat as do other species. When one approaches close enough they lunge forward with a movement that might almost be termed a leap, snapping savagely at the offender. Their lunge frequently results in a loss of equilibrium and gives them an aspect of impotent fury. When seized by the tail they snap blindly without any apparent objective point. This aimless snapping seems to be an expression of something akin to anger. Like Aromochelys, they reach back over the carapace with eyes directed downward.

Like Aromochelys, too, they emit a musky secretion from the inguinal glands that, although not so nauseating as the emission of the musk tortoise, is decidedly unpleasant. Their habit of burying the body in the mud and the general inconspicuousness of carapace, head and limbs, might be cited as factors in their equipment for self defense.

Chelydra either stalks its prey or lies in wait for it. In the former case it approaches a resting tadpole or frog with movements so slow as to be almost imperceptible. The head is thrust out stiff and is kept very steady and when within easy reach of its prey the fierce jaws are suddenly opened and closed with a snap that leaves no hope of escape for the victim. In the latter case it lies buried in the mud at the bottom, allowing only the head to protrude. The long wormlike tongue is thrust out, probably as a lure for unwary fish. When the prey comes within reach it is suddenly snapped up.

Chelydra captures large animals, such as young ducks, by seizing them by the feet and dragging them beneath the surface. I have seen several such tragedies. Whole strings of fish, left hanging over the side of the boat by inexperienced fishermen have been stolen by voracious "snappers." It is not uncommon for fishermen to lose their tackle when a "snapper" takes their bated hook. Their weight and strength are too much for any but the heaviest tackle. The young feed upon the larvæ of insects that are found by burrowing in the mud.

Only in one instance have I observed the female Chelydra during the nesting process. On this occasion the nest was more than half completed when I first caught sight of her. Although she stopped work and showed signs of preparing for a retreat, she concluded the filling-in process in a somewhat slovenly manner and then retreated. The filling-in process was the same as that observed for Graptemys and Aspidonectes.

The nest was in gravelly sand on the side of a railway embankment, separating the lake from a swamp. An examination of the nest revealed a broad funnel-shaped depression, about a foot in diameter, at the apex of which a tunnel, about four inches in diameter, led diagonally into a wider expansion of irregular shape and about a foot beneath the general ground surface. The tunnel was obstructed by a stout stick and was consequently turned somewhat to one side. In the expansion and communicating tunnel were thirty-three eggs scattered irregularly in a double layer. On the whole it was a decidedly untidy and primitive sort of nest.

At about the same time of the month (June 15) several half-finished nests were found in the same railway embankment and all had the same general characteristics as the one described. I am told by the engineers on the railroad that the females are often seen at work and that they leave precipitately on the approach of the early morning train.

The eggs are spherical with one hemisphere white and the other pinkish. The shell is very tough, so that the eggs, if thrown on hard ground, will rebound several inches without breaking. The eggs laid on June fifteenth hatched during the last week in August.

Large specimens captured on land and put into aquatic enclosures immediately buried themselves deep in the mud and were not seen again until dug out with a hoe months afterward.

One large specimen, weighing nearly fifteen pounds was tethered out in a lagoon by means of a long dog-chain attached to the carapace. It went the full length of the chain and then buried itself at least a foot deep. It is difficult to do anything with beasts so sullen as Chelydra. When kept in captivity on land they are extremely ill-natured, snapping at and injuring one another if they happen to meet. I have never observed a tendency to combativeness in other species.

If kept for some months even the largest specimens of Chelydra accept food eagerly.

If eggs that are near hatching are opened, the young Chelydra snap in a characteristic, though somewhat feeble, manner. Snapping with them seems to be a sort of reflex and may be more or less so in adults. Young specimens lack the fierceness and sullenness of adults, being capable of domestication. They will feed from the hand and seem to enjoy being scratched under the jaws.

Summary.—Chelydra possesses a very "ugly" disposition. It is vicious and intractable, displaying a blind impotent rage when brought to bay. In temperament it is extremely slow and sluggish, preferring to lie in wait for its prey rather than actively to search for it. Sometimes, however, it summons sufficient energy to stalk the prey.

GENERAL SUMMARY.

It will be noted that certain traits and habits are common to all of the species studied and, since the principal groups of tortoises are represented, these may well be considered as chelonian characters. Certain traits stand out more prominently than others and these should be emphasized.

1. The love of warmth and repose seems to be one of the few dominant factors in tortoise life. In some cases they seek warmth to their injury. On the other hand, lack of heat is more apt to cause death than any other factor.

2. Extreme wariness when basking is noticeable in all species that habitually bask.

3. There is a marked variation in the degree of fierceness or timidity exhibited by different species. These characters seem to run parallel with an aquatic or a terrestrial habitat, aquatic species being fiercer than those with a tendency toward a terrestrial life.

4. Naturally enough, it is possible to domesticate the less fierce and less sullen species, while captivity inhibits normal activities in the fiercer and more sullen species.

No general summary of vegetative or reproductive activities is necessary here. The writer, conscious of the incompleteness of his data concerning certain activities, intended to devote another season to the work, but as it seems advisable to publish the facts now as they stand, he hopes to supplement and interpret them on another occasion.

THE INCREASE IN THE NUMBER AND SIZE OF THE MEDULLATED FIBERS IN THE OCULOMOTOR NERVE OF THE WHITE RAT AND OF THE CAT AT DIFFERENT AGES.

BY

THOMAS HARRIS BOUGHTON.

(*From the Neurological Laboratory of the University of Chicago.*)

WITH THREE FIGURES.

INTRODUCTION.

The present investigation is an attempt to determine the rate of development and increase in the diameter of the medullated fibers in a typical cerebral motor nerve of the white rat, and to compare this development, on the one hand, with that of the spinal motor roots of the same animal, and on the other, with the development of the same nerve in an animal of a different species (cat).

SCHILLER ('89) states that the oculomotor nerve of the cat is practically complete at birth, and that the number of medullated fibers increases only 3.2 per cent. between birth and eighteen months. The number of fibers in the oculomotor nerve of the cat according to SCHILLER's enumeration is as follows:

New born (3 cases)	2942
Eighteen months (1 case)	3035

This is quite at variance with what other investigators have found as to the development of other motor nerves, *e. g.*, the spinal motor roots in the frog and rat. Dr. HATAI ('03) working in this laboratory, found that the number of medullated fibers in the ventral roots of the spinal nerves in the white rat increases about 170 per cent. in rats ranging in body-weight between 10.3 grams and 264.3 grams, and that the increase is practically the same in the cervical, thoracic and lumbar nerves. BIRGE ('82) counted in the frog (R. esculenta), the medullated fibers in the roots of all the spinal nerves on one side, and found an average increase of 72 per cent. in the ventral roots between the body-weights of 1.5 grams and 111 grams. HARDESTY ('00), working in this laboratory, counted the number of medullated fibers in the ventral roots of the sixth spinal nerve in the frog (R. virescens), and found an increase of 53 per cent. between body-weights of 7.16 grams and 60.9 grams.

On comparing the results obtained by SCHILLER with those of the other investigations here cited, the question at once arises: Is this discrepancy due to a fundamental difference in the manner of development between the cerebral motor nerves, and the spinal motor roots, or does the cat represent a manner of development different from that of the rat and the frog? In this paper we shall offer a partial answer to the above questions by following the increase in the number of medullated fibers in the oculomotor nerve of the white rat and of the cat.

PART I. THE WHITE RAT.

Material and Technique.

White rats were used, ten males and three females, ranging in weight from 11 grams (eleven days old) to 414 grams (about two years old). Observations were begun at eleven days because at birth none of the fibers is medullated, and it is not until eleven days that the medullation is appreciable. The rats were killed with chloroform, and the nerves immediately removed, and fixed in 1 per cent. osmic acid. They were then washed in water, passed through the graded alcohols and xylol, and imbedded in paraffin (m. p. 56° C.). Sections were made near the origin of the nerve, but after the fila had come together into a single trunk, and were cut in several thicknesses, but those of 4μ were found to be the best, and were chiefly used. The fibers were counted by the photographic method described by HARDESTY ('99) except in the case of the smallest nerve, which could not be photographed satisfactorily. This was counted by using a net and an automatic counting machine.

It was noticed that a fairly sharp distinction could be made between the largest fibers at any age, and the other fibers. In this paper the word "large" is used to indicate the *largest fibers found at given age*, and the word "small" is used to indicate the other fibers. The photographic apparatus used gave a magnifi-

FIG. I.

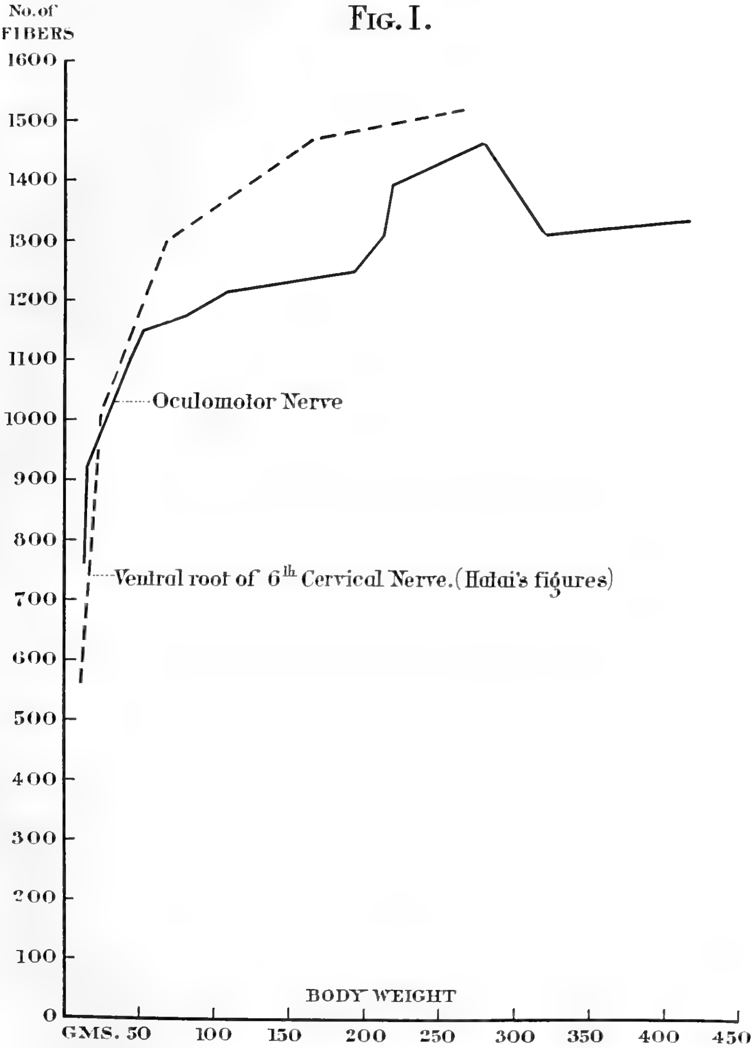

Fig. 1. The increase in the number of medullated fibers in oculomotor nerve and in the ventral root of the sixth cervical nerve of the white rat.

cation of about 600 diameters. Under these conditions the "small" fibers could not be seen very distinctly. To distinguish "large" from "small" fibers at any age, the following method was employed: First, the total number of fibers as shown in the photograph was counted, identifying each by reference to the original section, viewed through a microscope, and then the plainly visible, "large," fibers were counted without referring to the microscope. The difference between these two results was taken as the number of "small" fibers. The rat of two years may be taken as

FIG. II.

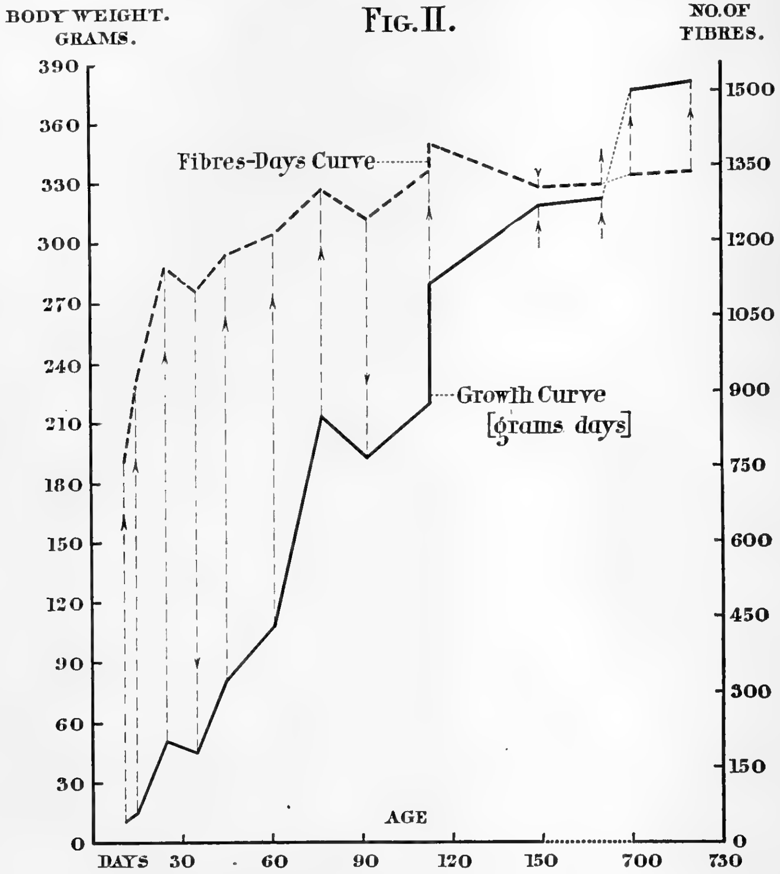

Fig. 2. Showing the relation between the growth curve (grams-days) and the fibers-days curve (oculomotor nerve) in the white rat.

Observations.

TABLE I.

The Increase in the Number of Medullated Fibers in the Oculomotor Nerve in the White Rat.

BODY WEIGHT IN GRAMS.	AGE IN DAYS.	SEX.	NUMBER OF FIBERS.			PER CENT. OF TOTAL INCREASE.
			"Large."	"Small."	Total.	
11	11	M.	764	...	764	..
14	15	M.	880	38	918	20
44	35	M.	885	220	1105	45
51	25	F.	926	227	1153	51
80	45	F.	887	290	1177	54
109	61	F.	888	329	1217	59
192	92	M.	932	316	1248	63
213	77	M.	925	383	1308	71
218	113	M.	926	471	1397	83
278	113	M.	901	566	1467	92
318	149	M.	930	379	1309	71
414	730	M.	928	408	1336	75
172	?	M.	882	465	1347	76

TABLE II.

Increase in Diameters of "Large" and "Small" Fibers.

WEIGHT IN GRAMS.	AGE IN DAYS.	AVERAGE DIAMETER OF "LARGE" FIBERS IN μ	AVERAGE DIAMETER OF LARGEST FIVE FIBERS IN μ	INCREASE IN DIAMETER OVER "14 GRAM" FIBERS. PER CENT.	DIAMETER OF LARGEST "SMALL" FIBER IN μ	PER CENT. OF INCREASE IN DIAMETER. "SMALL" FIBERS.
11	11	1.8	2.2	...	...	...
14	15	3.0	4.3	...	1.4	...
51	25	4.3	6.4	49	2.5	79
109	61	6.5	8.0	86	2.7	92
213	77	7.0	9.3	116	3.0	114
218	113	7.8	10.2	137	4.0	186
318	142	7.6	10.8	151	4.0	186
414	730	8.1	13.4	211	4.3	207

Increase in "largest" fibers between 11 grams and 414 grams = 504 per cent.

representing an age at which increase in the number of fibers practically ceases.

An inspection of these tables and figures shows the following points:

1. There is a nearly regular increase in the number of medullated fibers in rats while growing from 11 grams to 414 grams in body-weight. This increase is most rapid in young rats, and becomes slower as they get older; after sixty days (= 100 grams) it is very slow. The increase between the limits here given (eleven days to two years) amounts to 75 per cent. of the total number of fibers. (After the age of fifteen days the increase in the number of "large" fibers probably is not significant. The relation between the "large" and "small" fibers will be discussed later.) Hence this cerebral motor nerve is more mature in a rat weighing 11 grams than are the spinal motor roots, and it develops more slowly during after life. As already stated, Dr. HATAI ('03) found in rats having body-weights between 10.3 grams and 264.3 grams an increase of 170 per cent. in the ventral roots of the spinal nerves. A curve based on his enumerations is plotted for comparison with my curve in Fig. 1.

TABLE III.

Ratios Between the Areas of Sheath and Axone.

WEIGHT IN GRAMS.	AGE IN DAYS.	AVERAGE DIAMETER IN μ OF TEN WELL DEVELOPED FIBERS.		PERCENTAGE BY WHICH THE AREA OF THE SHEATH DIFFERS FROM HALF THE AREA OF THE ENTIRE FIBER.
		Entire Fiber.	Axone.	
14	15	4.1	2.9	−0.1
80	45	7.3	5.2	−1.5
414	730	8.5	5.9	+3.5

2. The increase in the number of medullated fibers is correlated with the weight rather than with the age of the animal, for the curve relating the number of fibers to the body-weight (solid line, Fig. 1) is smoother, in general, than one based on the age (broken line, Fig. 2), although two rats (both one hundred and thirteen days old) show an unusually large number of fibers.

The fact that the weight- (solid line, Fig. 1) and age- (broken line, Fig. 2) curves do not differ very much is readily explained by a glance at the growth curve (solid line, Fig. 2), which does not show unusual individual variations. The growth curve (solid line, Fig. 2) and the "fibers-days" curve (broken line, Fig. 2) show about the same degree of fluctuation. Moreover, segment for segment, they are approximately parallel (with the single exception of the second from the last segment), so that any variation in the number of fibers is matched by a corresponding increase or decrease in the body-weight. This shows very clearly the intimate relation between the number of fibers and the body-weight. This dependence of the number of medullated fibers upon the weight of the animal (irrespective of the age) gives us a suggestion as to one of the differences existing between large and small individuals of the same species. It should be stated, however, that the above relation holds good only when all the rats compared are reared under the same conditions, for one rat (body-weight, 172 grams; age, unknown), not represented in the curves, but entered last in Table I, and raised under less favorable conditions than the others, had a body-weight much lower than normal, but the number of fibers usually found in rats weighing more than 200 grams.

3. The younger fibers which grow into the nerve, for the most part, do not attain the size of the older ones, although all continue to increase in size during the life of the animal. This is shown by the fact that the "large" fibers can always be readily distinguished from the "small" fibers. The constancy in the number of "large" fibers indicates, probably, that they constitute a special group which medullates early, while the "small" fibers have grown in subsequently. The sudden increase from 764 "large" fibers to 880 between eleven days and fifteen days probably indicates that all the fibers really belonging to this group had not become medullated at the earlier date. Table II shows the increase in the diameters of the "large" and "small" fibers. The first column shows the average diameter of the "large" fibers. The figures were obtained by taking the average of five "large" fibers that seemed to be of about the average size. The second column shows the average diameter of the largest five fibers in the sections measured. The fourth column shows the diameters of the best developed of the "small" fibers. It is shown in this table that the largest of the "small" fibers does not, during two years, attain

so great a size as the largest of the "large" fibers does during the first fifteen days, or, indeed, so great as most of the "large" fibers do during the first twenty-five days. Between the limits here given, the largest of the "large" fibers increase 504 per cent. in diameter, but between fifteen days and two years it increases only 211 per cent., while the largest of the "small" fibers, during the same period (fifteen days to two years) increases 207 per cent. This indicates very clearly that the reason the "small" fibers never attain the size of the "large" is that they come in after the period of most rapid growth. Furthermore, it will be noticed that, in general, the percentage of increase in diameter over the fibers in the 14-gram rat is nearly the same at any given age for the "large" and for the "small" fibers. Hence the rate of growth of a particular fiber does not depend upon the size which it has attained, but upon the age of the animal.

4. At any age, the area of the sheath in the fully medullated fiber is nearly equal to the area of the axone. Table III shows this relation. The figures were obtained by measuring, at each age, both the entire fiber and axone of ten well-developed fibers in two diameters, and averaging all the diameters obtained for the entire fibre and for the axone. This result corresponds exactly with the results found by DONALDSON and HOKE ('05) in a series of vertebrates comprising twenty-six species.

CONCLUSIONS.

1. In white rats having body-weights between 11 grams and 414 grams, there is a nearly regular increase in the number of medullated fibers in the oculomotor nerve. This increase amounts to 75 per cent.

2. This cerebral nerve is more nearly complete in the 11 gram rat than are the motor roots of the spinal nerves in the same animal. (For the latter HATAI found an increase of 170 per cent. between body-weights of 10.3 grams and 264.3 grams.) Hence the subsequent rate of development of this cerebral motor nerve is much slower than that of the spinal motor roots.

3. The number of medullated fibers is more closely correlated with the increase in the body-weight than with the increase in the age.

4. All the medullated fibers continue to increase in size during

the life of the animal, but the newer fibers, classed as "small," and first recognized at fifteen days, never attain the size of the older ones, and, indeed, at two years of age they are not so large as some of the older fibers were at fifteen days. This appears to be due to the fact that they come in after the period of most rapid growth.

5. At any age at which the two groups of "large" and "small" fibers can be distinguished, all the fibers are increasing in diameter at the same rate.

6. At any age, the area of the sheath in the fully medullated fiber is nearly equal to the area of the axone.

PART II. THE CAT.

In this part of the investigation, the oculomotor nerves from six cats (a mother and her five kittens) were used. There were three males and three females, ranging in weight from 112 grams (one day) to 2893 grams (thirteen years). The technical methods used were the same as in the case of the rats (*q. v.*) and the conclusions drawn were almost identical.

An inspection of the tables and figures brings out the following points:

1. There is a nearly regular increase in the number of medullated fibers in the oculomotor nerves of cats increasing in body-weight from 112 grams (one day) to 2804 grams (six months). In the case of the 2893 gram cat (thirteen years old) there is a falling off in the number of fibers, due, probably, to senile changes. The single irregularity in the curve (the cat of 223 grams body-weight) is probably not significant, being merely an individual variation. The increase between the limits here given (one day to six months) amounts to 157 per cent. (The increase in the case of the rats, between much wider limits, was only 75 per cent.) The medullation in the cat at one day is about as far advanced as that in the cat at ten days, so that a direct comparison between the two series just as they stand is not misleading. The oculomotor nerve in the cat, then, develops more rapidly during life than that of the rat, and this may be related to the greater functional importance of the eye in the cat. It will be noticed that the number of fibers in SCHILLER'S cases (about 3000) corresponds roughly with the number of "large" fibers which I obtained, although still

somewhat lower than my figures. The great disparity between my results and those obtained by Schiller is probably due to the less perfect technical methods at his command.

2. The number of cases is too small to make a reliable comparison between the relations of age and of body-weight, respectively, to the increase in the number of fibers.

Fig. III.

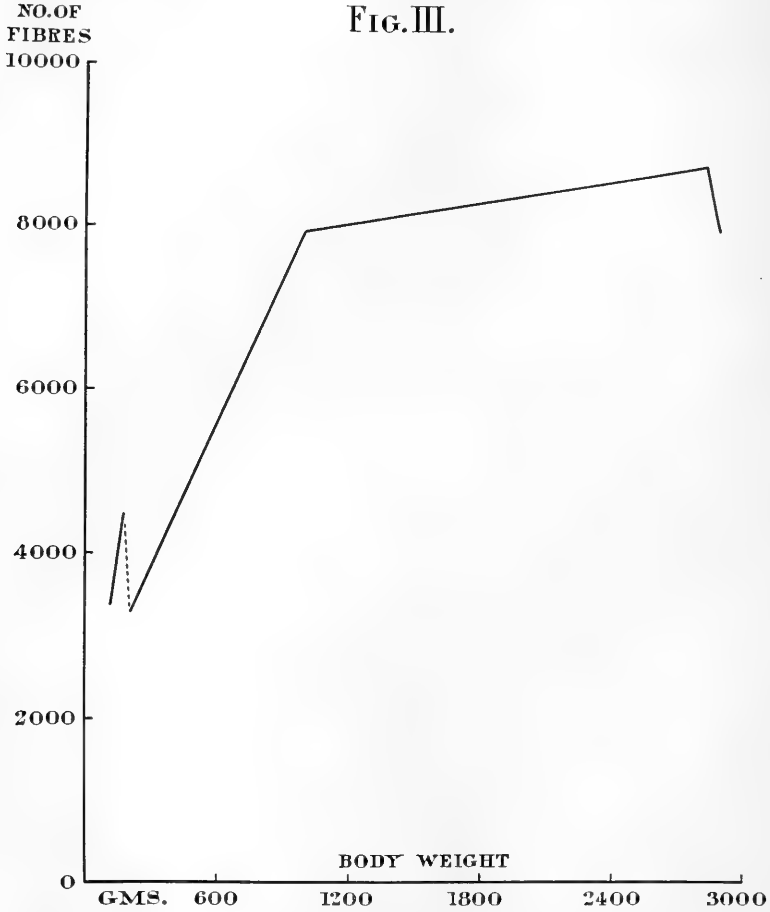

Fig. 3. The increase in the number of medullated fibers in the oculomotor nerve of the cat.

3. Although we do not observe in this series the same degree of constancy in the number of "large" fibers that we observe in the

Observations.

TABLE IV.

The Increase in the Number of Fibers in the Oculomotor Nerve of the Cat.

WEIGHT IN GRAMS.	AGE IN DAYS.	SEX.	NUMBER OF FIBERS.			PER CENT. OF INCREASE.
			"Large."	"Small."	Total.	
112	1	M.	2964	424	3388	....
169	3	F.	3761	752	4513	33
223	10	F.	2785	470	3255	(—4)
984	56	M.	3612	4308	7920	134
2804	182	M.	3212	5493	8705	157
2893	13 years.	F.	3024	4892	7916	133

Average of "large" fibers = 3409.

TABLE V.

Increase in Diameters of "Large" and "Small" Fibers.

WEIGHT IN GRAMS.	"LARGE" FIBERS.		"SMALL" FIBERS.	
	Average Diameter in μ	Per Cent. of Increase.	Average Diameter in μ	Per Cent. of Increase.
112	2.7	...	1.4	...
168	3.5	30	1.8	28
223	4.0	48	2.2	57
984	7.6	182	4.0	186
2804	12.0	344	6.8	386
2893	13.5	400	7.2	414

TABLE VI.

Ratio Between Areas of Sheath and Axone.

WEIGHT IN GRAMS.	AGE IN DAYS.	AVERAGE DIAMETER IN μ OF TEN WELL DEVELOPED FIBRES.		PERCENTAGE BY WHICH AREA OF SHEATH DIFFERS FROM HALF THE AREA OF THE ENTIRE FIBER.
		Entire Fiber.	Axone.	
168	3	3.4	2.4	+ .3
984	56	7.2	5.2	−4.1
2804	182	11.3	7.9	+2.3

case of the rats, the interpretation is doubtless the same: The "large" fibers constitute a special group which medullates early, while the "small" fibers have grown in subsequently. Table V shows also that most of the "large" fibers have attained a greater size in two months (body-weight 984 grams) than any "small" fiber attains in thirteen years. The explanation previously given is here applicable: The small fibers have come in after the period of most rapid growth, and so never "catch up." By comparing the percentage of increase in the diameters of "large" and of "small" fibers at different ages (as shown in Table V) it will be seen that the increase in diameter is not dependent upon the size which the fiber has attained, but that after the early period of rapid growth, when the "large" fibers are differentiated, the increase in diameter progresses at the same rate for both "large" and "small" fibers; thus leaving the two classes always clearly distinguished.

4. Table VI shows that, as in the case of the rats, the area of the sheath in the fully medullated fiber is nearly equal to the area of the axone.

CONCLUSIONS.

1. In cats between the ages of one day and six months there is a nearly regular increase in the number of medullated fibers in the oculomotor nerve. This increase amounts to 157 per cent.

The conclusion of Schiller that nearly all the medullated fibers found in the oculomotor nerve of the cat at maturity are present in the nerve at birth, is therefore not correct.

2. After the oculomotor nerves in the cat and in the rat have reached the same stage of medullation (the cat of one day corresponding to the rat of ten days), the addition of medullated fibers during subsequent growth in the case of the cat is relatively twice as great as in the case of the rat.

3. The medullated fibers continue to increase in size during the life of the animal, but the newer fibers, classed as "small," never attain the size of the older ones. This is due to the fact that they come in after the period of most rapid growth.

4. After the age at which the two groups of "large" and "small" fibers can be distinguished, all the fibers are increasing in diameter at the same rate.

5. At any age the area of the sheath in the fully medullated fiber is nearly equal to the area of the axone.

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CORRESPONDENCE.

To the Editor, Journal of Comparative Neurology and Psychology:

DEAR SIR:—I have read with great interest the article of Mr. YERKES on the sense of hearing in frogs, in No. 4, of last year.

Mr. YERKES concludes that the frogs observed by him did not hear, but that the receptions transmitted by the *Acusticus* influenced their movements; "but the use of the term audition in connection with these reactions has not been justified" (p. 301). The behavior of the frogs in freedom as well as in confinement—noises do not cause them to flee—justifies his conclusion. I am well acquainted with the brain of the frog. No connection at present traceable—certainly not a larger one, which could not have escaped our notice—exists between the cerebrum and the acoustic terminal stations in the domain of the mid-brain. The auditory nerve terminates essentially in the medulla oblongata. Even this circumstance alone gives rise to the presumption, that irritations transmitted by the eighth nerve are not turned to account in the same manner by frogs as by higher vertebrates; we cannot, therefore, conclude that hearing is lacking merely on account of the absence of expected movements of flight. Movements alone reveal to us that which is induced by a sensory reception; but it should not necessarily be denied that there are receptions which do not lead to movements. For instance, an animal may hear, without the noise causing it to move.

It is no doubt true, that Mr. YERKES' very clever arrangement of experimentation shows that noises irritate the auditory nerve and that they influence the animal's movements, even though in a different way than expected. But those experiments do not allow us to say "the frog does not hear." All we may say is: "the frog does not respond to auditory impressions like a higher animal."

There are experiences that argue in favor of the assumption that the apparatus for the reception of sound, which in the frog is so clearly present and especially constructed, must allow the possibility of hearing also in the sense of our anthropocentric psychology. When one frog in a pond, for instance raises his voice, on a warm summer evening, another one answers first and gradually others join in, until finally a general croaking extends all over the pond.

In answer to an inquiry on my part Prof. BOETTCHER, probably the best informed authority of the present day on amphibian life, the editor of the volume Amphibia in BREHM'S "Thierleben" (Animal Life), writes as follows:

"We can readily agree with Mr. YERKES' statement regarding 'The Sense of Hearing in Frogs' but we must repel the idea that the conclusions which the author draws from his experiments, should be *generalized.*

"His experiments may be correct as far as Rana clamata Daud (clamitans Merr.) and the allied R. catesbiana Shaw, also R. halecina Kalm are concerned, and even for our European kinds R. esculenta L. and R. temporaria L.; but they do not apply to all 'Anura Batrachians.' It is very easy to prove that the sentence, *loc. cit.*, p. 303: 'When given alone a sound never causes a motor reaction' is especially wrong as regards Hyla arborea L. and likely all tree-frogs. Not only myself, but numbers of my friends have observed dozens of times, that tree-frogs in confinement react with croaking on certain definite sounds, even with the promptness of the release of an irritation. Even a loud human voice may induce the male tree-frog to answer; this succeeds with absolute certainty when I pound with a pestle in a brass mortar. This capacity is not very wonderful. For most of the Hyla kinds live by themselves and often widely disseminated over bushes and trees. I may well assume that their loud voice serves the purpose first of all to allure the female during mating time. This also agrees well with YERKES' observation, who discovered (*loc. cit.*, p. 304), at least with experiments conducted in winter, that the reaction on auditory irritations was greater in the female of Rana than in the male."

Mr. YERKES' fine work will in many respects lead to discussion and to reflection. It appears to me that we have not yet sufficiently laid down, in a precise manner, fundamental definitions for the phenomena that take place in the *central* apparatus, for instance, such as occur in course of impressions of special sense, of sensation or of motion, that we are still entirely too much influenced by expressions and categories derived from the physiology of the mammalians. There must be, for instance, an essential difference between the receptions and their effects when an animal possesses only the nuclear apparatus, which receives the nerve of special sense, and when it has tracts leading from the nuclear end to the mid-brain (likely always the case) or when it possesses communications between the primary apparatus of receptions and the thalamus. It must, finally, make a tremendous difference whether the receptions reach a cerebral cortex or not, and how the latter is constituted.

Animals possessing apparatus of association in a well-developed cortex will be able to convert their sensory receptions into sensory perceptions. All these postulates are inferred from the greater or lesser complications of the structure as revealed by anatomy.

Psychology will gradually be able to clear them up, when it is furnished with more treatises of the same exactness as the one which I have here the honor to discuss.

I am, dear sir,
Yours truly,
DR. EDINGER

Senckenberg Neurologisches Institut,
Frankfurt am Main, Germany.

Statements in Reply to Dr. Edinger.

In fairness to Dr. EDINGER and myself certain statements concerning his criticisms should be made at once.

I do not conclude, as Dr. EDINGER states, that the frogs observed by me do not hear; on the contrary I conclude and distinctly state in several places (pp. 287, 300, 303) that the use of the word hearing is justified by my experiments. The sentence quoted in the criticism, "but the use of the term audition in connection with these reactions has not been justified," when taken from its context means just the opposite of what I intended. What I proceeded to say after that statement was that the previous experiments had not excluded the possibility of the reactions in question being due to the stimulation of cutaneous or other sense organs than the auditory. Experiments described in the remainder of the paper proved to my satisfaction "that the reactions with which we have to deal in this investigation are due to stimulation of certain sense organs of the ear, and that the use of the word hearing in connection with them is appropriate."

Dr. EDINGER's criticisms call attention to several important neurological facts which must be taken into account by the student of animal behavior, and suggest possible striking differences in the sense processes of animals. Despite the misunderstanding of my conclusions, I greatly appreciate and have profited much by Dr. EDINGER's kindly criticism and general approval of my work.

With reference to Prof. BOETTCHER's comments I wish to say that the statements of my paper were meant to apply only to the three species of frog studied R. clamitans, R. catesbiana and R. pipiens. I, too, can confirm his observations concerning the reactions of tree-frogs, but I have still to see or hear of locomotor reactions by frogs in response to sounds. I do not doubt, however, that they occur in many species, and I hope observations of such reactions may soon be put on record.

ROBERT M. YERKES

LITERARY NOTICES.

Carpenter, F. W. The Development of the Oculomotor Nerve, the Ciliary Ganglion and the Abducent Nerve in the Chick. *Bul. Mus. Comp. Zoölogy, Harvard Col.*, Vol. 48, No. 2. Jan. 1906.

After a minute description of the adult relations of these nerves in the fowl, the details of development are given, followed by a discussion of the results. The literature is well digested. The two motor nerves in question develop as fibrous processes of neuroblasts which remain within the neural tube. They are followed by "indifferent" cells which migrate out from the medullary tube, accompany the fibrous processes and finally invest them to form the sheath of Schwann. Some of the indifferent cells, however, become directly transformed into cells of the ciliary ganglion. This ganglion contains also other and smaller cells which migrate into it along the ophthalmic branch of the trigeminal nerve from the Gasserian ganglion. The latter are undoubtedly sympathetic in character. The significance of the former group, which comprises the larger part of the ciliary ganglion remains problematical. C. J. H.

Flechsig, Paul. Einige Bemerkungen über die Untersuchungsmethoden der Grosshirninde, insbesondere des Menschen. Dem Zentralkomitee für Hirnforschung vorgelegt. *Berichte über die Verhandlungen der königlich Sächsischen Gesellschaft der Wissenschaften zu Leipzig.* Math.-Phys. Bd. 56, pp. 50–104, 177–248. 1904.

An extended review of the author's own investigations upon the medullated tracts by the embryologic method and an exhaustive critique especially of the works by MONAKOW and DEJERINE with pathologic methods. The results of the two methods are critically compared in many instances. Brief space is given to the purely histologic problem as related to the neurone theory, and to the relation of developing tracts to the external morphology of the brain. G. E. C.

Sterzi, G. Intorno alla divisione della dura madre dall' endocranio. *Monitore zoologico Italiano.* Vol. 13, pp. 17–22. 1902.

Sterzi, G. Recherches sur l'anatomie comparée et sur l'ontogenèse des méninges. *Archives italiennes de Biologie,* Vol. 37, pp. 3–15. 1902. *Atti del R. Instituto Veneto di Sc., Lett. ed Arti.* Vol. 60, pp. 1101–1372. 1900–1901.

A layer of embryonic connective tissue which surrounds the cord first divides to form the internal periosteum of the vertebræ and a *méninge primitive.* The latter divides later to form the dura mater and an internal layer which subsequently separates into arachnoid and pia. In cyclostomes, fishes and urodeles the *méninge primitive* alone exists. In Anura, reptiles and birds, there is a dura mater and a *méninge secondaire.* In mammals, alone, does the latter become differentiated into two distinct membranes. G. E. C.

Frohlich, Alfred. Beitrag zur Kenntnis des intraspinalen Faserverlaufes einzelner hinterer Ruckenmarkswurzeln. *Arbeiten aus dem Neurologischen Institute an der Wiener Universität.* Bd. 11 pp. 378–384. 1904.

Experimental degeneration in Macacus rhesus, of fifth, sixth, seventh cervical and first and second thoracic dorsal roots of the left side, and of the right, the sixth, seventh and eighth cervical and first thoracic. G. E. C.

Locy, William A. On a newly recognized Nerve connected with the Fore-brain of Selachians. *Anat. Anz.*, Bd. 26, pp. 33–63, 111–123. 1905.

This paper describes the nerve, its ganglion and root, as found in twenty genera and twenty-seven species of selachians, and its embryonic history in Squalus acanthias. In the adult the nerve enters the dorsal surface of the brain in some species; in others, it enters the ventral surface. In the embryo it is primarily connected with the lamina terminalis. It is therefore called the nervus terminalis. It precedes the olfactory nerve in development and probably arises from the ganglionic crest. It contains medullated and nonmedullated fibers and it distributed to the olfactory epithelium. Its peripheral arrangement has certain resemblances to branchial nerves. Locy considers the nerve homologous with the preoptic ventral nerve of Protopterus and Amia.

G. E. C.

de Vries, E. Over het Ganglion Vomeronasale. *Koninklijke Akademie van Wetenschappen te Amsterdam*, Afdeeling van 22 April, 1905. (Also, Note on the Ganglion Vomeronasale, *Ibid.*, *Proceedings of the Section of Sciences*, Vol. 7, Part 2, July, 1905.)

Demonstration in the human embryo of a dorsal olfactory nerve in addition to the ventral well-known olfactory nerve. The new nerve connects with the ganglion vomeronasale and Jacobson's organ and is regarded as related to Locy's new nervus terminalis of selachians. C. J. H.

Norris, H. W. The so-called Dorsotrachealis Branch of the Seventh Cranial Nerve in Amphiuma. *Proc. Iowa Acad. Sci.*, Vol. 11, 95–102. 1904.

A description of the nerve from serial sections, with especial reference to Kingsley's recent work on the cranial nerves of Amphiuma (*Tufts College Studies*, 1902). G. E. C.

Mathews, A. P. The Nature of Chemical and Electrical Stimulation. I. The Physiological Action of an Ion Depends upon Its Electrical State and Its Electrical Stability. *Amer. Jour. Physiol.*, Vol. XI, pp. 455–496. 1904.

The results of Mathew's important study of the nature of stimulation can best be stated by means of quotations from his summary.

1. The stimulation of the sciatic nerve of the frog, which is produced by nearly all electrolytes and nonelectrolytes having an osmotic pressure of about fourteen atmospheres, "is probably due to the extraction of water setting up a definite change in the colloids of the nerve, rendering the protoplasmic hydrosol unstable."

2. Electrolytes which are too dilute to extract water act through the electrical condition of the solution. "All anions have a stimulating action; all cations a depressing action."

3. "The physiological action of any ion depends (1) on its concentration; (2) on the sign of its electrical charge; (3) on its electrical stability or ionic potential. Its action is also modified by its velocity and weight; the faster it moves the more powerful it is; the heavier it is, the less powerful."

4. "Physiological action is hence dependent upon the electrical state and stability of the ion and is independent of chemical composition, except as the chemical composition may influence its velocity and weight."

5. Whether any salt stimulates or depresses, depends upon the relative efficiency of its anion and cation. If the anion markedly predominates, as in hydrates, the salt stimulates; if the cation predominates, the salt depresses.

6. Chemical stimulation is thus shown to be electrical and dependent upon the electrical charges of the ions. Electrical stimulation is produced by modifying the distribution of ions in the nerve and thus altering their concentration as NERNST suggested. R. M. Y.

Baird, John Wallace. The Color Sensitivity of the Peripheral Retina. *Published by the Carnegie Institution of Washington*, May, 1905. 80 pp.

This paper presents a valuable historical sketch of the study of the functions of the peripheral retina in addition to a statement of the results of experiments by Dr. BAIRD.

The object of the experiments was to determine: (1) the chromatic character of the sensation aroused when a constant color stimulus is applied successively to different regions of the retina; (2) the relative extension of the different retinal areas within which the tones of the different color stimuli are correctly recognized.

The results agree with those of most earlier investigations in indicating the existence of three retinal zones: (1) an extreme peripheral zone on which stimuli appear colorless; (2) an intermediate zone where they appear yellow or blue, and (3) a central zone where they may appear red, green, yellow or blue.

The limits of these color zones may be varied by changing the retinal adaptation, background, magnitude of visual angle, condition of optical refraction, brightness and saturation of the stimulus, etc.

"Of all possible colors, there are four and only four which undergo no change of tone in indirect vision. These are a purplish-red (non-spectral), a yellow (about $570\mu\mu$), bluish-green (about $490\mu\mu$), and a blue (about $460\mu\mu$)."

The after-effects of retinal stimulation are surprisingly persistent, and in the opinion of Dr. BAIRD they have invalidated the results of many studies in color vision.

All of the results of this investigation are interpreted by the author as in agreement with the HERING and FRANKLIN theories of color vision. R. M. Y.

Stern, Richard. Die Pseudomotorische Funktion der Hirnrinde. *Leipzig, F. Deuticke*, pp. 27. 1905.

This paper is purely speculative and proposes the theory that all nervous currents are centripetal. Muscles lose none of their contractility by being isolated from the nerves that are ordinarily supposed entirely to govern their contractions. Contractility is a vital function of muscle; "and we must in all earnestness ask ourselves whether it is not possible that muscle contractions normally take place without any innervation coming to them from the central nervous system." According to present conceptions of sensory and motor currents, although the ganglion cells are closely similar in the two kinds of nerve, "the motor cell has to generate energy, while the sensory cell simply receives it. Morphologically similar structures should thus seem to have diametrically opposite functions." Is it not possible that all nervous currents move centripetally?

Muscular contraction would be explained in this way: the ganglion cells of motor nerves possess a spontaneous power of change; perhaps this is an ameboid motion, or perhaps it is a change merely of conductivity. In this latter case, for instance, if the conduction is greater in the ganglion of the motor nerve, more heat is conducted away from the muscle thereto attached, and this muscle contracts. If the resistance is raised, less heat is conducted and the muscle relaxes. In the former case more, and in the latter case less, nervous energy is simultaneously conducted to the brain. A similar activity goes on in the cerebral neurones, but here when the resistance is raised the energy that passes through is transformed, the author seems to mean, into consciousness; just as a highly resisting wire transforms electricity into heat. A lower resistance in the cerebral neurones allows more energy to pass through while less is allowed to contribute to consciousness. The author says that the cerebral cells "do mostly not function to conduct the energy which flows to them and to send it on to stations beyond; but they are themselves end-stations in which 'sensation' is produced." The author says, however, "Yet there is a large variety of phenomena in human consciousness which points to the fact that a cell which just now meditated a sensation, may in the next moment assume a wholly different function; that is, in many cases it is not at all the duty of a sensory cell to feel, but rather to 'conduct.' We have only to call to mind our 'subcortical' activities." The author then goes on through the rest of the paper, amidst a host of assertions that the physiologist must account hazardous, to say the least, to develop his theory of all-centripetal nervous impulses. The main value of these speculations probably lies in the emphasis given to probable changes in the conducting power of the neurones that mediate consciousness, for which indeed there seems to be considerable empirical evidence. The author seems quite to follow Professor OSTWALD's view that consciousness is a form of energy. He offers no explanation for the spontaneous powers ascribed to the spinal and cerebral ganglion cells. It seems probable that this would be his physiologic explanation of free will.

E. B. H.

Piper, H. Beobachtungen an einem Fall von totaler Farbenblindheit des Netzhautzentrums im einen und von Violettblindheit des anderen Auges. *Zeitschrift f. Psychologie u. Physiologie der Sinnesorgane*, Bd. 38, pp. 155–188. 1905.

In the present case PIPER found violet color blindness in the fovea of the left eye and total color blindness in that of the right eye. For the left eye a match for every monochromatic light of the spectrum could be found either in other unmixed monochromatic lights or in mixtures of two, one of short wave-length (500$\mu\mu$) and the other of longer wave length (650$\mu\mu$). The curves for the relative quantities of all such lights, necessary to match the successively presented monochromatic lights, correspond closely to the first two curves (red and green) for normal vision; the third normal curve is wholly lacking. The case is, therefore, one of violet color-blindness, and is easily explicable by HELMHOLTZ's triple-component theory.

In the totally color-blind right fovea the distribution of brightness in the spectrum tallied with that for normal "day-vision" (brightest in orange-yellow), but, for the whole eye, when dark-adapted, with that for normal "twilight-vision" (brightest in green). This is the first time that this difference in central and peripheral brightness-distribution has been observed in the same eye, undisturbed by the presence of color vision, and it supports in a striking way v. KRIES's "Duplizitätstheorie"; *i. e.*, that the cones mediate colorless sensation in "day-vision" and the rods in "twilight-vision." The facts are incompatible with HERING's assumption of the specific brightness of colors, because that cannot be present when the colors are absent, and yet HERING introduced the conception to explain this very difference between "day" and "twilight" vision. The phenomena are, however, reconcilable with HERING's general theory if specific brightness is dropped. They also may be made to fit HELMHOLTZ's theory if one supposes, following suggestions of FICK and KÖNIG, that total color-blindness is not due to the absence of all three components but rather to a modification in their relative excitability so that their curves coincide. The resulting curve would then take the course of that for the brightness values in "day vision."

R. P. ANGIER.

Piper, H. Ueber die Functionen der Stäbchen und Zapfen und über die physiologische Bedeutung des Sehpurpurs. *Medizinische Klinik*, Nos. 25 and 26, pp. 1–19. 1905.

The author here gives an excellent review of the facts that support what v. KRIES has called the "*Duplizitätstheorie*," according to which the cones of the retina mediate color sensation and when the light intensities are relatively high, colorless sensation, the so-called "day vision," whereas the rods give us merely colorless sensation, and that, moreover, only when adapted to the dark and stimulated by light of low intensity, "twilight vision." Particularly interesting are certain parallels drawn from physics and a summary of the facts which show that the curve for the absorption power of visual purple for the various monochromatic lights corresponds closely to that for the distribution of brightness-values in the spectrum (highest point in green) for the dark-adapted human eye—under exclusive functioning of the rods. Similar curves are also obtained for the relative bleaching effects of monochromatic lights on visual purple and for the action-currents which they produce in the retinas of night-seeing birds.

R. P. ANGIER.

Maxwell, S. S. The Effect of Salt-solutions on Ciliary Activity. *Amer. Jour. Physiol.*, Vol. 13, pp. 154–170. 1905.

An investigation of the relations of salt solutions to prolongation of life and preservation of power to do mechanical work in the ciliated epithelium of the esophagus of the frog.

R. M. Y.

Smith, Grant. The Effect of Pigment-migration on the Phototropism of Gammarus annulatus S. I. Smith. *Amer. Jour. Physiol.*, Vol. 13, pp. 205–216. 1905.

The author has shown that retinal pigment-migration in part determines the phototropism of Gammarus. When the eyes are dark-adapted the phototropism is indifferent, slightly negative or slightly positive; when they are light-adapted, it is strongly positive.

R. M. Y.

Carlson, A. J. The Nature of Cardiac Inhibition with Special Reference to the Heart of Limulus. *Amer. Jour. Physiol.*, Vol. 13, pp. 217–240. 1905.

The most important conclusion adduced by Dr. CARLSON from his study of the nature of cardiac inhibition in Limulus is that there can be no doubt that it "falls within the category of inhibition of automatic or reflex neural processes in the central nervous system." In Limulus, as in the vertebrates, inhibition of the heart results from the action of inhibitory nerves on the ganglia of the heart instead of on the heart muscle.

R. M. Y.

Lyon, E. P. Rheotropism in Fishes. *Amer. Jour. of Physiol.*, Vol. 12, pp. 149–161. 1904.

By a series of very simple experiments the author has proved that the orientation of fishes in currents of water is due to a great extent to visual stimuli, and far less than is usually supposed to cutaneous stimulation. "I am convinced," writes Dr. Lyon, "that with the fishes experimented with orientation in currents of fairly uniform velocity is usually an optical reflex. The current does not directly stimulate. Indirectly it does, by tending to move the fish away from the fixed points of its environment."

Experiments with fish in stationary vessels about which the environment was moved, and with blinded fish prove conclusively that sight is of heretofore unsuspected importance in the so-called rheotropic reactions. Contact with solids influences the reaction, but the author believes that "pressure results from orientation; it does not produce it."

The paper is a valuable contribution to the literature on tropisms.

R. M. Y.

Towle, Elizabeth W. A Study of the Effects of Certain Stimuli, Single and Combined, upon Paramecium. *Amer. Jour. of Physiol.*, Vol. 12, pp. 220–236. 1904.

This investigation of the effects of stimuli upon the form and condition of Paramecium serves chiefly to emphasize, as the writer points out, the importance of the large number of unknown factors with which we deal in all our studies of animal reaction. The facts indicated in the paper cannot be summarized easily, but perhaps the following sentence will indicate its trend and content: "Finally we are, I think, forced to the conclusion that the terms 'coagulation' and 'liquefaction' at present serve largely to cover our ignorance, for they express only in the vaguest way the processes that take place in living organisms in response to different stimuli. The retarding influence of lowered temperature, the secondary effects which take place in certain reagents, and the appearance of new phenomena when mixtures of subfatal solutions are used . . . point to the occurrence in the protoplasm of extensive changes which we cannot now fully analyze."

R. M. Y.

Thauziès, A. L'Orientation du pigeon voyageur. *Revue Scientifique*, 5 Sér., Vol. 2, pp. 417–420. 1904.

As a lifelong student of the carrier pigeon, Thauziès rejects the theory of E. de Cyon (L'Orientation chez le pigeon voyageur, Revue Scientifique, 4 Ser., Vol. 12, pp. 353–357, 1900) that nasal sensations partially condition distance orientation, stating that the sense of odor is undeveloped in pigeons. This misinterprets the author in question, for he says explicitly that he is not thinking of olfactory sensations, but of others arising from the stimulation of the mucous membrane by the wind. Thauziès heartily agrees with him, however, in appealing, also, to certain higher physical acts as factors in the process (local memory, choice, etc.), and states that his long experience shows the animal to be of considerable mental development; he believes even that it "observes, compares, reasons, reflects."

J. E. R.

Roy et Juquelier. Aphasie motrice a répétition chez une morphinomane. *Journ. de psychol. norm. et pathol.*, Vol. 2, pp. 1–15. 1905.

This is an interesting account of a transitory aphasia occurring during the progress of treatment for morphinism. The patient had taken morphin for a period of twenty-eight years, and during the slow demorphinization developed a motor aphasia. She could read aloud, recognized the use of objects, understood what was said to her, but could not write her name spontaneously, and could not name objects. Two months later there was a complete recovery. This attack had been preceded by four similar attacks under similar conditions. At present, so far as it can be determined, this is another case in which there is a functional derangement without a corresponding anatomic change.

S. I. F.

Mayer, André. Influences des images sur les secretions. *Journ. de psychol. norm. et pathol.*, Vol. 1, pp. 255–264. 1904.

In this article MAYER calls attention of psychologists to numerous physiologic articles by PAWLOW and his pupils, and by many French investigators, on the effect of mental states upon secretions—particularly of the digestive glands. The sight of food is sufficient to produce a glandular secretion and the food which is most liked produces most abundantly the digestive juices. The author remarks that it is the emotion, the pleasure, that puts into play the organic reaction, the secretions, and that the emotions do not follow the reaction—a fact which would be adverse to the JAMES-LANGE theory of the emotions. There are, however, other conditions equally important in which the secretions precede the emotional condition.

S. I. F.

Lepine, R. Sur un cas d'agnosie. *Journ. de psychol. norm. et pathol.*, Vol. 1, pp. 163–165. 1904.

A report of a case in which at most times there was complete inability to recognize even the most common objects. On certain days the patient could recognize almost every object. This recovery was particularly noticeable on one day when there was a slight fever, which probably increased the irritability of the cerebrum. The author found no visual or auditory defect, and concludes that the inability of recognition is due to loss of mental images.

S. I. F.

Kahn, Paul, et Carteron, Emile. Expériences de dynamométrie. *Journ. de psychol. norm. et pathol.*, Vol. 1, pp. 462–464. 1904.

Conclusions from experiments with the dynamometer and ergograph.

1. Dynamometric force increases from morning to afternoon and then diminishes again, although higher at end of the day than at the beginning.
2. There is a dynamogenic effect from visual stimulation by colored lights, but the results are not constant for the different colors.
3. Pain decreases the dynamometric force.
4. Intellectual work decreases muscular power.

S. I. F.

Weber, Ernst. Ursachen und Folgen der Rechtshändigkeit. *Marhold, Halle.* Pp. 116. 1905.

Dr. Weber, after reviewing the facts of right-handedness and left-handedness in animals, children, primitive and civilized races, discusses in turn the following theories which have been advanced in explanation of the phenomena: 1. Asymmetry of blood supply. 2. Position of the fetus. 3. Position of the center of gravity in the body. 4. Chance. 5. Position of the organs of the body, as indirect cause. The first four of these so-called causes of right-handedness the author shows to his satisfaction to be results rather than causes of the phenomenon under consideration; the last-named theory he plausibly defends.

A second portion of the book deals especially with the consequences of right-handedness. This also is chiefly historic. Most attention is given to the effects of right-handedness on the brain, and of writing as a cause of the unilaterally developed speech center.

The book is of value primarily because it brings together many interesting and important facts concerning the subject, as well as a list of references.

R. M. Y.

BOOKS AND PAMPHLETS RECEIVED.

Warren, John. The Development of the Paraphysis and the Pineal Region in Necturus maculatus. Reprinted from *The American Journal of Anatomy*, Vol. 5, No. 1, Dec. 1905.

Harper, E. H. Reactions to Light and Mechanical Stimuli in the Earthworm, Perichæta bermudensis (Beddard). Reprinted from *Biol. Bulletin*, Vol. 10, No. 1, Dec. 1905.

Watson, George A. The Mammalian Cerebral Cortex, with Special Reference to its Comparative Histology. I. Order Insectivora. Preliminary Communication. Reprinted from the *Proceedings of the Royal Soc., London.* Read December 14, 1905.

Johnston, J. B. The Cranial Nerve Components of Petromyzon. Reprinted from *Morph. Jarbuch* Vol. 34, No. 2. 1905.

Mills, Charles K. and Weisenburg, T. H. Word-blindness, with the Record of a Case due to a Lesion in the Right Cerebral Hemisphere in a Right-handed Man; with some Discussion of the Treatment of Visual Aphasia. Reprinted from *Medicine*, Nov. 1905.

Berger, E. W. Habits and Distribution of the Pseudoscorpionidæ, principally Chelanops oblongus, Say. Reprinted from *Ohio Naturalist*, Vol. 6, Dec. 1905.

Schofield. The Management of a Nerve Patient. *Philadelphia: P. Blakiston's Son & Co.* 1906.

Banchi, A. Di un Nucleo non Descritto del Rombencefalo (Nucleo Superiore del Corpo Restiforme). Reprinted from *Rivista di Pat. Nerv. e Ment.*, Vol. 10, fasc. 9, Sept. 1905.

Bancroft, Frank W. On the Validity of Pflüger's Law for the Galvanotropic Reactions of Paramecium. (Translated from *Pflüger's Archiv*, Bd. 107, S. 535-556.) *University of California Publications, Physiology*, Vol. 2, No. 19, Nov. 1905.

Wilson, J. G. The Structure and Function of the Taste-buds of the Larynx. Reprinted from *Brain*, Part 110, pp. 339-351. 1905.

Esterly, C. O. Some Observations on the Nervous System of Copepoda. *University of California Publications, Zoölogy*, Vol. 3, No. 1, Jan. 1906.

Bradley, O. Charnock. On the Development of the Hindbrain of the Pig. Reprinted from *Journ. Anat. and Physiol.*, Vol. 40. 1906.

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THE MIXED CEREBRAL NERVES IN MAMMALS.

BY
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(*From the Embryological Laboratory, Harvard Medical School.*)

WITH PLATE XVII.

The occasion for this note is the difficulty of presenting the embryology of the cerebral nerves to medical students in such a way that it shall not be an added burden, but shall facilitate the learning of human adult conditions. This difficulty may be partially met by the adoption of a consistent nomenclature free from synonyms, and by the use of such diagrams as are to be considered presently.

The "Nomina anatomica" (N. A.) adopted by the German society of anatomists should be the basis for future anatomical terms.[1] Its great advantages are the elimination of synonyms and the substitution of descriptive for personal names. Since the numbers applied to the cerebral nerves are synonymous with the descriptive names, and lead to the erroneous idea that there are twelve pairs of comparable nerves connected with the brain, it is preferable to employ the names rather than the numbers. Four of the cerebral nerves are mixed, consisting of a dorsal (sensory) root and a lateral (motor) root. Naming these for their dorsal portions they are the trigeminus, the intermedius, the glossopharyngeus, and the vagus. Their lateral portions may be called respectively the portio minor trigemini, portio facialis intermedii, portio motoria glossopharyngei, and portio accessoria vagi.

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[1] Die anatomische nomenclatur. *Arch. f. Anat. u. Entw.*, Supplement-Band, 1895. This nomenclature is accessible to students in *Barker's* Laboratory Manual of Anatomy, *J. B. Lippincott Co.*, 1904.

It is believed that such names are more in accord with embryological knowledge than those of the German society in 1895, whereby the motor portion of the trigeminus was named, as above, the portio minor; the motor part of the glossopharyngeus received no name; but the corresponding parts of the intermedius and vagus were counted as separate nerves, the facial and the accessory. The change proposed is, however, so easily understood as scarcely to require explanation. It is a slight change, but by its adoption attention is drawn to the fundamental morphological similarity between these four mixed nerves.

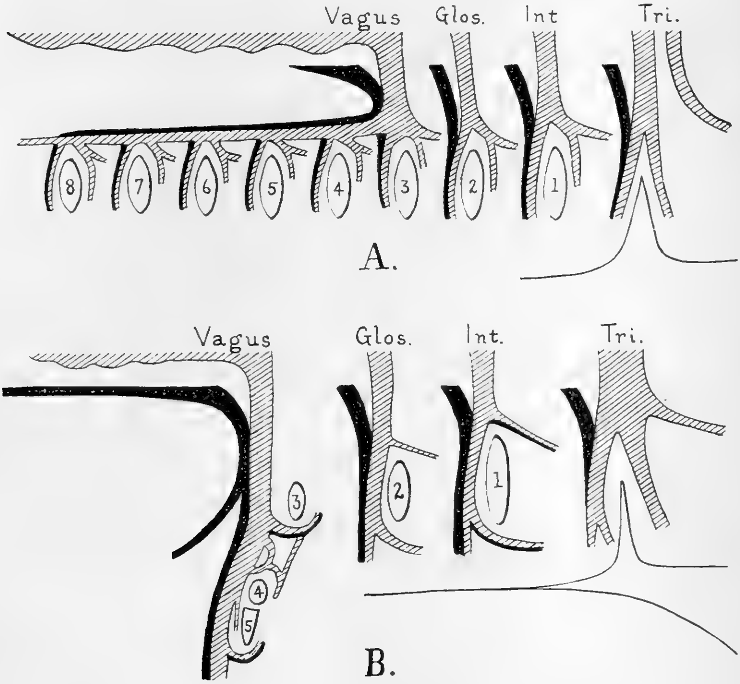

Fig. 1. Diagrams of the trigeminus, *Tri.;* the intermedius, *Int.;* the glossopharyngeus, *Glos.*; and the vagus nerves, showing their sensory portions shaded, and their motor portions in solid black. The somatic sensory branches have been omitted. The numbers indicate the gill clefts counting the spiracle as the first; 5, in B, marks the postbranchial body. A, a generalized diagram based chiefly upon Petromyzon, after Johnston. B, a diagram following closely the conditions in a pig embryo of 12 mm.

The branches of these nerves can best be understood by considering them first in the lower vertebrates. They are shown in

Fig. 1, A, a modification of JOHNSTON's diagram based chiefly upon Petromyzon.[1] The trigeminus is here represented by two separate nerves, the ophthalmic in front, and the maxillo-mandibular behind. The latter divides into the maxillary branch, in front of the oral cleft, and the mandibular branch, posterior to the cleft. The ophthalmic nerve is purely sensory. The maxillo-mandibular is mixed; its minor portion, in fishes generally, accompanies the mandibular branch exclusively.[2]

The intermedius, after uniting with its facial portion, divides into three branches. The post branchial passes down behind the first branchial or spiracular cleft, in the hyoid arch. The suprabranchial runs forward above the cleft toward the palatal region. From it the third or præbranchial branch passes down in front of the first cleft, in the mandibular arch. Of these three branches the suprabranchial and præbranchial are sensory and the postbranchial is mixed.

The glossopharyngeus is similarly related to the second cleft. It also has sensory suprabranchial and præbranchial divisions, and a mixed postbranchial. The same is true of the vagus, but this nerve supplies not only the third cleft but all those which follow it. It is assumed that each of these once had its separate nerve. By the formation of a collecting commissure along the brain, and of a distributing commissure above the branchial clefts, and by the disappearance of such portions of the nerves as extended between these commissures, the posterior branchial nerves have become a part of the vagus. This process would lead to such a vagus as is shown in the diagram.

In mammals the branches of the mixed cerebral nerves have been carefully studied by FRORIEP,[3] in cow embryos. A reconstruction of a 12 mm. pig, from which the diagram, Fig. 1, B, has been drawn, agrees closely with his figures. The trigeminus in these mammals shows no evidence of its double origin, the ophthalmic nerve having fused completely with the maxillo-mandibular. All of the motor fibers go with the mandibular

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[1] JOHNSTON, J. B., *Journ. of Comp. Neurology,* 1905, Vol. 15, pp. 175-275, Pl. 4.

[2] In Bdellostoma some motor fibers enter the maxillary nerve (WORTHINGTON, J., *Quart. Journ. of Mic. Science,* 1905, Vol. 49, p. 168) and in Petromyzon a large part of this nerve is motor (JOHNSTON, J. B., *Morph. Jahrb.,* 1905, Vol. 34, p. 156).

[3] FRORIEP, A., *Arch. f. Anat. u. Entw.* 1885, pp. 1-55.

branch, which is beginning to divide into the inferior alveolar and the lingual nerves.

The intermedius joins the facial portion and divides into a suprabranchial branch (large superficial petrosal nerve) and a postbranchial branch. The latter forks to form the chorda tympani in front and the facial nerve behind. Although the petrosal nerve and chorda tympani are predominantly sensory and the facial nerve is chiefly motor, WEIGNER[1] has shown that all three branches contain some fibers of both sorts.

The glossopharyngeus has a suprabranchial branch (tympanic nerve) and a postbranchial branch which divides to form the lingual ramus in front and the pharyngeal ramus behind. The tympanic nerve and the lingual ramus are chiefly sensory and the pharyngeal ramus is mixed.

Neither the intermedius nor the glossopharyngeus possesses in mammals a præbranchial branch, but both of them have subbranchial branches which have not been described in fishes. These are the chorda tympani and the lingual ramus respectively.

The vagus has neither a suprabranchial nor a præbranchial branch in relation with the third cleft. The postbranchial nerve for this cleft has been identified by FRORIEP as the superior laryngeal nerve. In the pig of 12 mm. there is a small plexus between the third and fourth pouches, in which a præbranchial branch for the fourth pouch may be represented. There is no nerve passing between the fourth pouch and the postbranchial body, which by some authorities is counted a fifth pouch, although a small nerve runs beside the postbranchial body. This may be what FRORIEP (*loc. cit.*, p. 16) described as a postbranchial branch for the fourth pouch. In cow embryos it was a small nerve which disappeared in later stages. Behind the postbranchial body and the pulmonary aortic arch, the vagus sends out the recurrent nerve, a large branch which may represent a fusion of nerves for pharyngeal pouches which fail to develop.

The course of the ramus externus, which contains accessoria fibers for the trapezius and sternomastoid muscles has not been satisfactorily explained.

The sensory portions of the intermedius, glossopharyngeus and vagus thus far described supply the splanchnic structures only.

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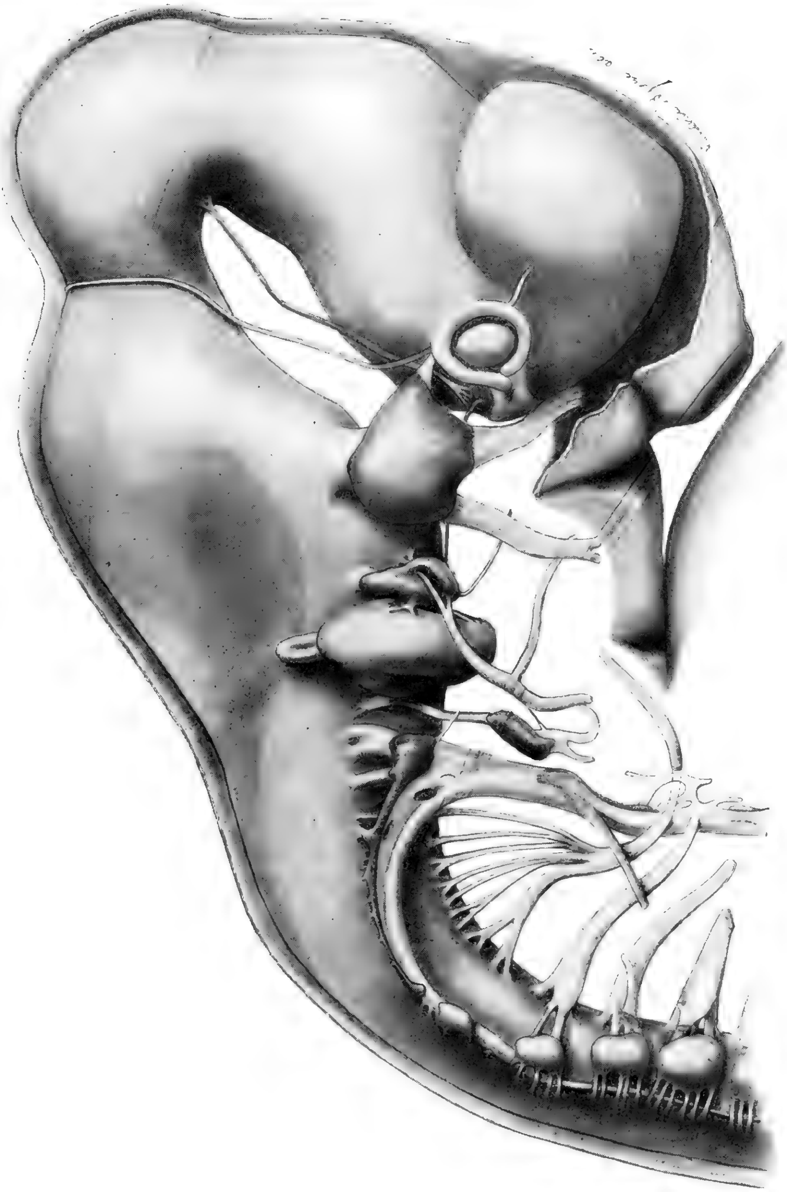
[1] WEIGNER, K., *Anat. Hefte*, 1905, Vol. 29, pp. 97-162.



A somatic sensory branch leaves the vagus just below its jugular ganglion to supply the external acoustic meatus and the back part of the auricle. This is the auricular branch of the vagus, which may be joined by a similar branch from the glossopharyngeus.

That the acoustic nerve should be considered a highly developed special somatic portion of the intermedius, with which it is closely connected in mammalian embryos, is regarded as probable by some authorities. The entire separation of the acoustic elements from the other cerebral nerves, as recorded by WORTHINGTON (*loc. cit.*, p. 170) in Bdellostoma is considered unique, and not fundamental.

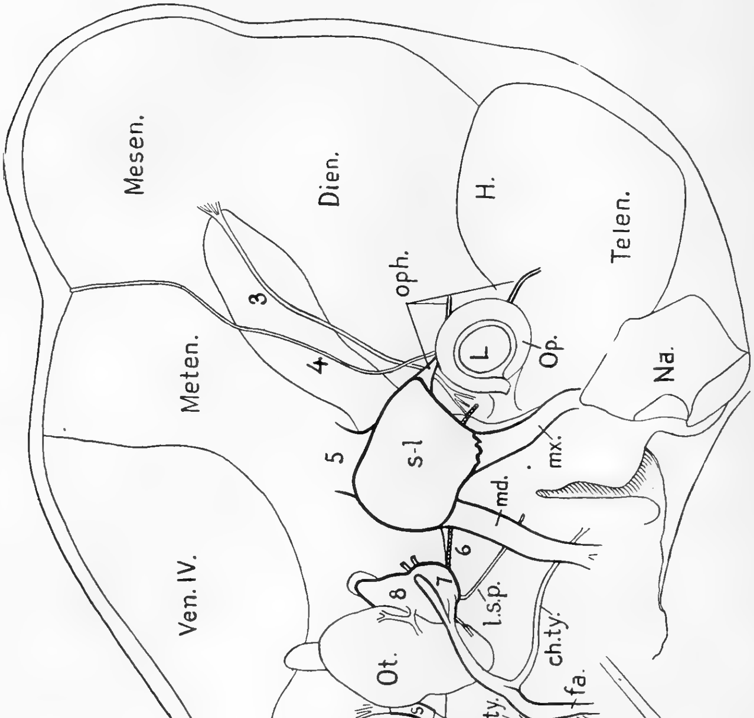
All of the nerves and branches to which reference has been made are shown in the following reconstruction (Plate XVII) of the 12 mm. pig, a revision of that published in the *American Journal of Anatomy*, 1903, vol. 2, following p. 225. In the new figure the superior ganglion is more definitely outlined, and the large superficial petrosal, the tympanic and the auricular nerves have been added. The lettering is more consistent and complete.

EXPLANATION OF PLATE XVII.

Reconstruction of the brain and cerebral nerves in a 12 mm. pig embryo.

Nerves.—3, Oculomotor. *4*, Trochlear. *5*, Trigeminal, with its semilunar ganglion, *s-l.*, and three branches—*oph.*, ophthalmic; *mx.*, maxillary; *md.*, mandibular. The motor portion which goes with the mandibular nerve is concealed in this view by the sensory portion. *6*, Abducens. *7*, Geniculate ganglion of the intermedius. Fibers from this ganglion mix with the motor fibers of the facial portion, and both sorts enter the three branches—*l.s.p.*, large superficial petrosal; *ch.ty.*, chorda tympani; *fa.*, facial. *8*, Acoustic, showing an upper vestibular portion, and a lower cochlear portion. *9*, Glossopharyngeal, showing its superior ganglion, *s*, above; its petrosal ganglion, *p.*, below; and its three branches,—*ty.*, tympanic; *l.r.*, lingual ramus; *ph.r.*, pharyngeal ramus. *10*, Vagus, with its jugular ganglion, *j.*, extending posteriorly as a ganglionic commissure, *com.* Just below the jugular ganglion the auricular branch extends forward. Below this is the ganglion nodosum, *n.* The branches of the vagus here form the laryngeal plexus, with the superior laryngeal nerve above, and the recurrent nerve, *rec.*, below. *11*, Accessory portion of the vagus; *ex.*, its ramus externus. *12*, Hypoglossal. *F.*, Froriep's hypoglossal ganglion. *c.1*, *c.2*, *c.3*, Cervical nerves.

Brain and Sense Organs.—Telen., Telencephalon. *Dien.*, Diencephalon. *Mes.*, Mesencephalon. *Meten.*, Metencephalon. *Myelen.*, Myelencephalon. *H.*, Hemisphere. *Ven. IV*, Roof of the fourth ventricle. *Op.*, Optic cup. *L.*, Lens. *Na.*, Nasal pit. *Ot.*, Otocyst.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PRELIMINARY REPORT ON THE CYTOLOGY OF MOLLUSCAN NERVE CELLS.

BY

W. M. SMALLWOOD.

WITH SEVEN FIGURES IN THE TEXT.

The observations now reported are on the Opisthobranch, Haminea, the Lamellibranch, Venus, and the Pulmonates Planorbis and Limax. In addition to these forms Helix, Littorina, Melantho, Montagua gouldii, Aplysia and others have been worked during the past three years.

Interest in the structure of the cytoplasm not only of the nerve cells of both vertebrata and invertebrata but in gland, epithelial, egg and sperm cells has resulted in the accumulation of a very considerable literature during the past ten years and more especially the last five. (See HOLMGREN, '01; RHODE, '98, '03 a, '03 b, '04 a, '04 b; BERGEN, '04, and others.) Sufficient facts have been advanced by these writers to indicate here are a large and varied number of conditions existing in the nucleus and especially in the cytoplasm of adult cells. My purpose is to refer but briefly at this time to these structures in nerve cells, reserving for the full paper a more extended survey of the literature.

The structures already found in the nerve cells of vertebrata and invertebrata are given a variety of names in part at least due to the theory of their origin and fate. These may be grouped under two headings for convenience in description, although in some instances at least the two classes are interrelated.

1. The *lymph spaces* which have no constancy of form or position in nerve cells, sometimes being found near the nucleus, or in the vicinity of the periphery of the cell, or again having a general distribution. Some writers regard them as artefacts while others maintain that they are normal and essential to the cell activity.

2. In this second class may be placed a large variety of bodies

which are differentiated by osmic acid and the basic stains. SCHNEIDER ('02) designates them in mollusca as NISSL bodies, thereby implying their similarity to the well known NISSL bodies of vertebrate nerve cells. In their distribution in the nerve cell, they are arranged usually in concentric rows around the nucleus, becoming fewer as the cell wall is approached. That such regularly disposed bodies exist in many invertebrate nerve cells there can be no doubt, but there is considerable doubt as to their distribution even in the same family; and as to their significance we possess no generally accepted conclusions.

Closely associated with these regular-shaped and regularly distributed NISSL bodies are some bodies to which the term mitochondrien and chondromiten (RHODE, '04 a) is given. RHODE would include here also the NISSL bodies. The term chondromiten is used when there is a considerable accumulation of a densely-staining substance in the cytoplasm. The collection of several bodies (mitochondrien) gives rise to a mass which is known as chondromiten and conversely the chondromiten may break up into a number of small bodies known as mitochondrien. RHODE makes a great deal of these various combinations in which he tries to establish a genetic continuity. The result is that he advances a hypothesis of elementary organisms for the cell which is a modification of ALTMANN's bioplastic hypothesis.

In general it may be said that HOLMGREN and his followers look on these structures as the expression of an activity in the cell and that under different physiological conditions the cytoplasm reveals different structural states.

After spending considerable time on the cytology of nerve cells in mollusca, I became convinced that, unless the cause of these remarkable structures could be resolved, not only was all theorizing futile, but also a correct interpretation of the facts as well. In the further work which is now well under way on this and kindred topics Dr. C. G. ROGERS will be associated with me and it is our purpose to follow careful physiological experiments by cytological observations.

Haminea solitaria.—Concerning the question as to whether the lymph spaces have a definite wall other than would be formed by the granules of cytoplasm, I do not wish at this time to make any statements for or against the contentions of HOLMGREN, RHODE and BERGEN.

There are located in the cerebral, pleural, pedal and visceral ganglia of most gastropods a few nerve cells much larger than those that make up the bulk of the ganglion. In Helix, Doris, Aplysia and others these are of enormous size. The small nerve cells are too small for a satisfactory study, so one is limited in the main to the few large cells in each ganglion.

All of the text figures were drawn with a camera lucida, the $\frac{1}{12}$ oil immersion and two-inch ocular, Bausch and Lomb.

In Fig. 1, *a* there are two conspicuous lymph spaces and four smaller ones. These are not connected with one another or with the surrounding neuroglia cells. The cytoplasm is quite uniformly granular. The nucleus is sharply defined by a membrane and the larger size of its granules. On the side toward the axone, the nuclear membrane is sharply bent in toward the center of the nucleus and the larger granules assume a radial and beadlike arrangement as if there were some marked physiological activity taking place. In Fig. 1, *b* the lymph spaces are smaller and more evenly distributed. The cytoplasm differs from the conditions in Fig. 1, *a* in that there are several rodlike and granular bodies present. These bodies take the same kind of a stain that the large granules in the nucleus of each cell takes. In one instance the granules of the cytoplasm were arranged radially around one of the rodlike bodies having very much the appearance of a centrosome and sphere. McCLURE ('97) describes similar conditions in gastropod nerve cells and explains them on the ground of the persistence of the centrosome and sphere.

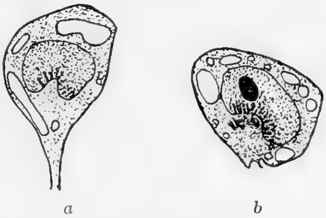
a *b*

Fig. 1.

It is further to be noted that the granules in the nucleus have the same radial, beadlike arrangement around the infolded nuclear membrane. These granules are very noticeable because of their intense reaction to basic stains. The nucleolus is solid and large; a single one is figured in this section, but as many as seven have been counted in some nerve cells of Haminea. These two nerve cells were taken from the same animal which was fixed with picro-acetic (BOVERI) under normal conditions.

Venus.—A large number of preparations of the visceral ganglion of the common market clam were made in the hope that the conditions existing in these cells could be harmonized with other mollusca. Clams just taken from the sea and those that had been transported to Syracuse, N. Y., were used, but no constant difference was found to exist. The tissue was fixed in picric acid-sublimate (Holmgren), as well as sublimate and osmic acid.

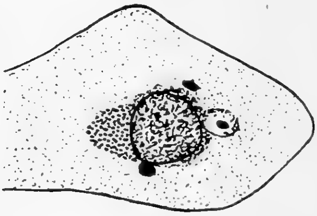

Fig. 2.

In Fig. 2 the cytoplasm is loosely granular, showing many fibers present in the region where the axone arises. The nucleus is limited by a conspicuously staining membrane; the chromatin is pretty generally distributed throughout the nucleus. On one side of the nucleus there is a cone-shaped mass of deeply-staining granules which are much like the usually described Nissl bodies for molluscan nerve cells, but it should be noted that these bodies do not have the general concentric distribution so characteristic of Nissl bodies. In close connection with each other and the nuclear membrane, there are various shaped bodies and granules which occupy the remainder of the space around the nucleus. The smaller of these bodies are indistinguishable from the cytoplasmic granules, while the two larger are more like nucleoli than anything else. On the side of the nucleus opposite to the cone-shaped mass of Nissl granules here is an interesting condition. A number of the cytoplasmic granules have increased slightly in size and form a rather complete boundary to what is evidently a lymph space. In this space there is a solid staining body similar to the two already mentioned. It would seem as if we had an early stage in the formation of the limiting wall.

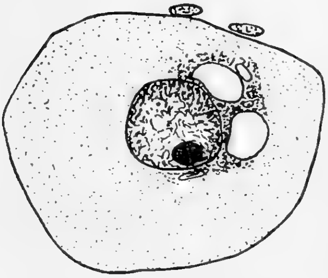

Fig. 3.

Figure 3 reveals one or two additional characteristics. The chromatin shows a tendency to mass around the periphery of the nucleus similar to the condition already described for Haminea. There seems to be an entire absence of Nissl bodies as such. There are two conspicuous lymph spaces sharply limited, apparently empty. Associated with these two are several smaller ones, some likewise empty of stainable substance, others containing one or more bodies. Surrounding these lymph spaces there is a considerable amount of densely staining subtance similar to that described in Fig. 2.

Figure 4 again shows the NISSL bodies rather numerous and completely filling one end of the cell. The nucleus is evidently undergoing division as indicated by the state of the chromatin lying free in the cytoplasm. There are a few lymph spaces near one edge of the cell, close to the cell membrane.

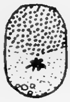
Fig. 4.

Planorbis.—The fresh nerve collar of Planorbis was placed in a 3 per cent. solution of osmic acid for eight days. In hundreds of cells obtained by this method, the conditions were much as shown in Fig. 5. Here there seems to be a nearly typical distribution of NISSL bodies. The appearance of these bodies is more like the usual conditions for the NISSL flakes. When other stains are used a fine granular cytoplasm is then evident. There are scattered in the cytoplasm a number of lymph spaces with no apparent regularity of form or position. Most of the nucleoli contained a central vacuole. Apart from the lymph spaces represented in the drawing this nerve cell would be typical of many of the nerve cells reported by RHODE.

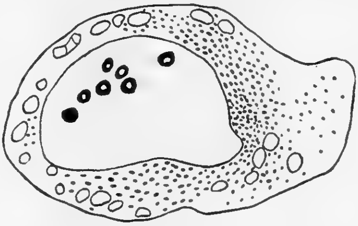
Fig. 5.

Limax.—Collections of Limax were made October 13, 1903, from a brick walk on our campus. A part of the specimens were killed at once in several of the best fixing reagents and the remainder were placed in a dark, moist chamber having plenty of grass. The conditions in Fig. 6 are such as are common in the freshly collected animals, while in Fig. 7, the nerve cells exhibit many unusual structures after being kept in the dark for seventy-two hours with plenty of grass.

In Fig. 6 the lymph spaces are very large and distributed irregularly. The cytoplasm seems to be free from NISSL bodies or other densely-staining granules. In the nucleus there are two large nucleoli. The chromatin is evenly and loosely

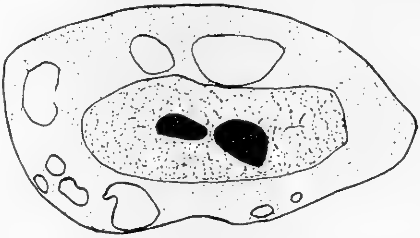
Fig. 6.

distributed. The nuclear membrane is distinct. One would hardly imagine the nerve cells shown in Fig. 7 was from the same species as that represented in Fig. 6. In the axone there are four large lymph spaces containing densely-staining bodies of irregular shape. There are also nine roundish lymph spaces each containing a rodlike or roundish body as well as many small spaces rather evenly distributed. The remaining bodies illustrate very well RHODE's ('04 a) idea of chondromiten and mitochondrien as well as sphere substance. I am inclined to doubt very much the value of his distinctions in regard to the several structures of the cytoplasm. In some instances in the figure these irregular masses lie free in the cytoplasm; while in others, the granules of the cytoplasm are arranging themselves to form a wall which will result in a lymph space. Some of the bodies are quite large and regular shaped, while others are equally irregular and very small.

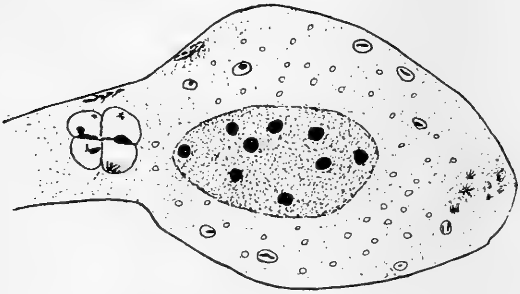

Fig. 7.

The conditions of the cytoplasm and nucleus described above represent several different states. A later paper will attempt to correlate them.

Syracuse University, Department of Zoölogy, May 10, 1905.

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'03 b.—II.—Ueber eigenarte aus der Zelle wandernde "Spharen" und "Centrosomen," ihre entstehung und ihren Zerfall. *Ibid.*, Vol. 75.

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'04 b.—IV. Zum histologischen wert der Zelle. *Ibid.*, Vol. 78.

SCHNEIDER. '02.—Vergleichende Histologie der Tiere.

ON THE CORRELATION BETWEEN INTELLIGENCE AND THE SIZE OF THE HEAD.

BY

RAYMOND PEARL.

On account of the considerable intrinsic interest of the question as to whether or not there is a sensible degree of correlation between intellectual capacity and the size of the brain or of the head it seems desirable to have all the exact and direct evidence on the matter which can be obtained. It has been alternately maintained that such a correlation does exist, and that it does not exist, but until comparatively recently there have been no attempts to obtain by adequate methods any definite quantitative statement regarding this question. It is, I think, perfectly obvious that the only way in which a definite answer may be obtained to the problem is to apply proper methods of reduction to a sufficiently large body of homogeneous statistics which record for each individual some measure of the intellectual ability on the one hand and of the size of the brain or head on the other hand. It is idle to attempt to reach any answer by an examination of individual cases, because, to name one point only, our general experience teaches beyond question that if such a correlation exists at all it is of a low order, and in consequence even its existence, to say nothing of its amount, cannot be determined from individual instances. The important thing to determine first of all is whether, if we take a large sample out of a homogeneous population, the individuals of more than average intellectual ability possess brains or heads above the average in size. It is to get evidence on this direct question of fact that, so far as I understand it, the biometrical work on the problem has been undertaken.

The purpose of this paper is to present the results of the reduction of some new statistics which have been recently published, and which show, for a reasonably homogeneous German population, the relation between the horizontal circumference of the head and intelligence. These admirable statistics were collected by

Dr. G. EYERICH and Dr. L. LOEWENFELD and are published in a memoir by these authors, bearing the title: "Uber die Beziehungen des Kopfumfangs zur Körperlänge und zur Geistigen Entwicklung."[1] The statistics which are given in most complete form in the memoir provide data for 935 Bavarian soldiers in the ordinary two-year service, regarding intelligence and head circumference. The data are recorded in two tables; the first of these gives as one variable the head circumference of the individuals in 0.25 millimeter classes, and as the other variable the "intellektueller Begabung," the individuals being sorted into four classes designated as follows: "I, sehr gut beanlagt"; "IIa, gut beanlagt"; "IIb, normal"; "III, beschränkt." The second table gives the same data with classes IIa, and IIb, of the intelligence scale combined into one, the rubrics then being "sehr gut," "gut," and "schwach." As the only data of a similar kind which have hitherto been analyzed biometrically are those of PEARSON on Cambridge undergraduates[2] and English school children[3], it seemed to me desirable to reduce these German data in order that comparisons might be instituted.

The all-important matter in dealing with data of this character is to know something about the basis of the classification on the intelligence side. If there is any constant bias in the distribution of the individuals into whatever "intelligence" classes are adopted it is clear that the resulting statistics will lose all significance so far as our problem is concerned. In order that as clear an idea as possible may be gained of the nature of this German material in this respect it seems best to quote in full what the authors say in regard to the matter. On page 26 of the memoir referred to is the following statement:

> Um die Verwertung des gesammelten Materials zu vereinfachen, haben wir die untersuchten Personen bezüglich ihrer geistigen Befähigung in 3 Klassen gesondert: insolche von mittlerer, *i. e.*, durchschnittlicher Begabung und in solche, deren Begabung über und unter dem Durchschnitt steht. Die uns vorliegenden Angaben über die geistige Qualifikation der untersuchten Leute ermöglichten jedoch die Trennung der Durchschnittsgruppe in 2 Untergruppen und lassen auch eine solche wünschenswert erscheinen: eine Gruppe, die den über dem Durch-

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[1] Wiesbaden, J. F. Bergmann, 1905, pp. 55.

[2] PEARSON, K. On the Correlation of Intellectual Ability with the Size and Shape of the Head. *Proc. Roy. Soc.*, Vol. 69, pp. 333-342.

[3] LEE, A., LEWENZ, M. A., and PEARSON, K. On the Correlation of the Mental and Physical Characters in Man. Part II. *Proc. Roy. Soc.*, Vol. 71, pp. 106-114.

> schnitt stehenden sich nähert, und eine solche, die mehr an die unter dem Durchschnitte heranrückt. Es entgeht uns hierbei keineswegs, dass die Beobachtungen, auf welche sich unsere Qualifikationen stützen mussten, z. T. unzulänglich und nicht ganz einwandfrei sein mögen. Es konnte nämlich im Allgemeinen neben der auf das dienstliche Verhalten sich beziehenden Qualifikation seitens der militärischen Vorgesetzten zunächst nur ein von den einzelnen Untersuchten geliefertes Elaborat über ihren Lebensgang bis zum Eintritt in die Armee verwertet werden. Das militärische Leben ist begreiflicherweise nicht geeignet, einem Individuum Gelegenheit zur Entfaltung aller seiner geistigen Gaben zu geben, und so mag wohl einmit gewissen, z. B. künstlerischen Talenten Ausgestatteter, militärisch eine schlechte Zensur erhalten. Die Verhältnisse liegen jedoch derart, dass wir für die Beurteilung des allgemeinen Standes der Intelligenz, auf den es uns in erster Linie ankommt,—einseitige Talente kommen sogar bei Schwachsinnigen vor—die militarische Qualifikation als wohl verwertbar ansehen müssen. Die Qualifikation erfolgt nämlich erst nach längerer Beobachtung der in den Dienst eingestellten Individuen. Ein Mensch von mittlerer oder über dem Durchschnitt stehender intellektueller Begabung mag sich bei den dienstlichen Ubungen ungeschickt benehmen, es auch an der notigen Aufmerksamkeit fehlen lassen. Er wird aber dann beim Unterricht seine Fähigkeiten zur Geltung bringen und in seinem Curriculum vitae ebenfalls einen Index für den Stand seiner Intelligenz liefern. Erhebliche Irrtümer bezüglich der geistigen Klassifizierung der Untersuchten, etwa derart, dass ein Beschränkter als wohlbegabt und umgekert angesetzt wurde, scheinen uns daher ausgeschlossen. Wir haben übrigens in einzelnen Fällen, die uns spezieller Aufklärung bedürftig erschienen, es nicht an eingehenderen Nachforschungen über das geistige Verhalten der Betreffenden fehlen lassen.

From this statement I think we may fairly conclude that the statistics were properly collected, and probably give a fair representation of the distribution of this population with respect to general intellectual ability. That there was no significant, constant bias working in the collection of this material seems to me also very probable from the following fact: The conclusion which Drs. EYERICH and LOEWENFELD reach is that there is no definite relationship between intelligence and the size of the head. Hence it seems reasonable to suppose that any subconscious tendency which might have existed toward biasing the returns would have been likely to be operative in the direction of making the statistics show no correlation between these variables. Yet as we shall see later the statistics when subjected to analysis show a slight but very regular and perfectly definite tendency toward the association of more than average intelligence with more than average head circumference. The statistics are, I believe, on the whole trustworthy.

TABLE I.

FÄLLE.	KOPFUMFANG.	I. SEHR GUT BEANLAGT.	II A. GUT BEANLAGT.	II B. NORMAL.	III. BESCHRÄNKT.
1	50.50	—	—	—	1
1	50.75	—	1	—	—
1	51.75	1	—	—	—
2	52.00	—	—	1	1
1	52.25	—	—	—	1
1	52.50	—	1	—	—
1	52.75	—	—	—	1
5	53.00	—	1	1	3
7	53.25	—	1	4	2
12	53.50	2	3	5	2
6	53.75	1	3	1	1
22	54.00	3	5	6	8
21	54.25	2	7	5	7
29	54.50	6	6	11	6
29	54.75	6	11	10	2
55	55.00	11	16	17	11
43	55.25	4	15	15	9
45	55.50	6	13	15	11
36	55.75	6	10	11	9
107	56.00	19	33	40	15
74	56.25	16	18	22	18
57	56.50	13	15	21	8
44	56.75	6	15	18	5
92	57.00	22	31	29	10
40	57.25	8	13	12	7
44	57.50	6	13	16	9
28	57.75	4	7	15	2
49	58.00	12	17	15	5
27	58.25	4	11	8	4
16	58.50	5	3	6	2
9	58.75	1	3	3	2
15	59.00	4	5	5	1
4	59.25	2	2	—	—
6	59.50	1	1	4	—
1	59.75	—	1	—	—
2	60.25	—	1	—	1
1	60.50	—	—	1	—
1	61.00	1	—	—	—
935					

TABLE II.

KOPFUMFANG.	FÄLLE.	KLASSIFIKATION.		
		Sehr gut.	Gut.	Schwach.
50-51	*2*	—	*1*	*1*
		·37	1.28	·35
51-52	*1*	*1*	—	—
		.18	.64	.18
52-53	*5*	—	*2*	*3*
		.92	3.20	.88
53-54	*30*	*3*	*19*	*8*
		5·52	19.21	5·26
54-55	*101*	*17*	*61*	*23*
		18.58	64.70	17.72
55-56	*179*	*27*	*112*	*40*
		32·93	114.67	31.40
56-57	*282*	*54*	*182*	*46*
		51.87	180.65	49·46
57-58	*204*	*40*	*136*	*28*
		37·53	130.68	35·78
58-59	*101*	*22*	*66*	*13*
		18.58	64.70	17.72
59-60	*26*	*7*	*18*	*1*
		4·78	16.66	4·56
60-61	*3*	—	*2*	*1*
		·55	1.92	·53
61-62	*1*	*1*	—	—
	—	.18	.64	.18
	935			

The raw material is given in detail in Tables I and II, which are copies of Tables IV and V of the original memoir. In Table II the observed frequencies are given in italic type: the ordinary figures in each compartment of the table give the proportionate frequency which should fall in that compartment on the basis of independent probability (*cf. infra.*).

In dealing with this material I first applied the contingency method[1] to Table II as it stands. It was apparent as soon as the

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[1] PEARSON, K. Mathematical Contributions to the Theory of Evolution. XIII. On the Theory of Contingency and its Relation to Association and Normal Correlation. *Drapers' Company Research Memoirs, Biometric Series,* I., pp. 1-35, 2 pl., 1904.

independent probability of occurrences for each compartment of the table had been calculated that there were very considerable and regular deviations of the observations from what would be expected if intellectual capacity and head circumference were in no way associated in this sample. If these two characters were entirely independent we should expect the frequency in each compartment of Table II to be, within the limits of error due to random sampling, the same as that given by the ordinary figures. But it is clear that the italic figures and the ordinary ones differ from each other in a definite way and by considerable amounts. Thus, neglecting the arrays of low frequency as too small to be significant, we see that in the left hand column (intelligence above average) individuals with small heads occur in defect of the expected proportions, and those with large heads occur in excess of expectation. The reversed relation holds for the right hand column (intelligence below average).

From Table II as it stands I find the value of the mean square contingency (*cf.* Pearson, *loc. cit.*) to be:

$$\Phi^2 = .0385$$

which leads to a value of the contingency coëfficient of

$$C_1 = .1925$$

Using the method of mean contingency

$$\Psi = .0397$$

whence $C_2 = .13.$

Now, if the variation follows the normal law and the grouping is not too fine, the value of C calculated by the two methods should be equal. This is clearly not the case. Hence, it is necessary to determine whether, by taking a somewhat coarser grouping, these values may not be brought nearer together.[1] Accordingly, a table was formed in which the size of the head circumference classes was doubled, thus reducing the number of rows from twelve to six. This new table then had eighteen compartments with some observed frequency in each. Working from this table I found the following values:

$\Phi^2 = .0203$

$C_1 = .1410$ (mean square contingency coëfficient.)

$\Psi = .0426$

$C_2 = .14$ (mean contingency coëfficient.)

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[1] A full discussion of the effect of too fine grouping on the value of the contingency coëfficient is given in the original memoir on the contingency method, to which the reader is referred.

These values are in very good accord and we may hence conclude that with this grouping

$$C_1 = C_2 = r = 0.14$$

It has been shown by PEARSON that it is likely that the probable error of a contingency coëfficient will be less than

$$2 \times .67449 \frac{1 - C^2}{\sqrt{N}}$$

For C = .1410 and N = 935 the value of the above expression is ± .0432. Assuming that this in any event does not exceed the true value of the probable error we conclude that the data in Table II exhibit a positive correlation between general intelligence and head circumference expressed by a coëfficient of

$$r = .14 \pm .04.$$

In other words, the chance that such a system of frequencies as that given in Table II should arise if, in the population under consideration, there were no correlation between head size and intelligence would be, so far as we can judge, not greater than 1 in 1250. It seems reasonable to conclude, therefore, that this material does show a sensible correlation between these characters.

We may, however, test the matter further. From the data furnished by Table I it is possible to form a fourfold table, and evaluate the coëfficient of correlation directly and with a known probable error by the method given by PEARSON.[1] Such a fourfold table is given as Table III.

TABLE III.

Correlation Between Intelligence and Head Circumference.

Intelligence.

Head Circumference.	BELOW AVERAGE.	ABOVE AVERAGE.	TOTALS.
BELOW 56.50	272	227	499
56.50 AND ABOVE	209	227	436
TOTALS	481	454	935

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[1] *Phil. Trans.*, Vol. 195 A., pp. 1-46.

The division for head circumference was taken as nearly as possible at the mean.[1] From this table I find the following values for the constants:

$$h = .03620, \quad k = .08456,$$

whence $.000635\,\theta^4 - .001409\,\theta^3 - .001531\,\theta^2 + \theta - .103222 = 0$

Accordingly $r = .103 \pm .034.$

Or, the coëfficient of correlation is almost exactly three times its probable error. The chance, then, of such a system of frequencies as that of Table III arising if intelligence and head circumference were not correlated in the population from which the sample is drawn is approximately 1 in 1000. We may reasonably conclude then that there is a sensible correlation between these characters.

There is one further point needing discussion. It will be noted that the coëfficient of contingency deduced from Table II is some-

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[1] The constants for the head circumference distribution as given in Table II were found to be as follows:

Mean = 56.499 ± .031 cm.
Standard Deviation = 1.413 ± .022 cm.
Coëfficient of Variation = 2.501 ± .040 per cent.

These values are in close accord with those obtained from well-known homogeneous series, and point clearly to the very substantial *physical* homogeneity of the present sample. Indeed this fact is so striking that I cannot refrain from reproducing for comparison the following tables of coëfficients of variation for horizontal circumference from MACDONELL's memoir on the skull (*Biometrika*, Vol. 3, p. 223). I insert in the table the coëfficient deduced from the present paper.

AUTHORITY.	RACE.	HORIZONTAL CIRCUMFERENCE.	
		♂	♀
Macdonell	English	2.87	2.92
Pearson	Bavarians	2.86	3.09
Pearson	Modern Badensians	3.02	2.34
Pearson	Row Grave Germans	2.70	2.40
Fawcett	Naqada	2.54	2.27
Eyerich and Loewenfeld (Pearl)	Bavarians (living head)	2.50	——

Actually the present data show the least variability of any of the male series in spite of the fact that the measurements were made with a tape on the living subjects.

what greater than the coëfficient of correlation from Table III while at first thought it might be supposed that according to the theory of contingency they ought to be equal. This, however, does not follow, because the division of the intelligence scale in Tables I and III is different from what it is in Table II on which the contingency coëfficient is based. In Tables I and III the middle class of Table II is divided. Now, I think it will be admitted that there would be far more doubt in the mind of the classifier as to whether a given individual ought to be placed in class IIa or IIb of Table I, than as to whether he should be placed in the "gut" class of Table II. But any errors made in the assorting of individuals into the two middle classes of Table I, will affect the coëfficient of correlation deduced from the fourfold table, while, of course, they would in no way affect the contingency coëfficient. Consequently I am inclined to think that in this case the contingency coëfficient is a truer measure of the real degree of correlation. In any event, the difference between the contingency coëfficient and the correlation coëfficient from the fourfold table is only of the order of the probable error of the latter.

To sum up, then, we find by analyzing fairly copious statistics forming a homogeneous sample of the males in the poorer classes of the Bavarian population that there is a low, but still sensible, positive correlation between the horizontal circumference of the head and general intelligence. This result appears to be of considerable interest. The only previous statistics of a similar nature are PEARSON's data[1] for Cambridge undergraduates, and English school children.

In order to show how these results compare with those of the present paper I have taken the mean of the nine coëfficients for the correlation of absolute head dimensions (length, breadth and auricular height) with intelligence which PEARSON has given. The value is .0736. All of the nine coëfficients are positive.[2] To these values we are now able to add the coëfficient for the

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[1] *Loc. cit.*

[2] I am informed by Professor PEARSON that since the preliminary papers here cited were published, the material on which they were based has been worked over anew by the contingency method. The result has been to give slightly higher values to some of the coëfficients and a generally smoother system. These new values are thus in even better accord with the coëfficient found in the present paper for intelligence and horizontal circumference. As these new values are to be published shortly, it seems undesirable to reproduce in detail the coëfficients given in the preliminary papers.

correlation between intelligence and another head measurement, *viz:* horizontal circumference, with a value of .14 ± .04. While some of the coëfficients given by PEARSON are, when taken by themselves, insignificant in comparison with their probable errors, we must give due weight to the fact that the sign of the correlation when we deal with absolute head measurements and intelligence is in all cases positive.

In general I think the reasonable conclusion to draw is that from the data now available it seems probable that there is a sensible, but *very slight*, positive correlation between intelligence and size of head. It will be understood that any conclusion regarding this matter must for the present be more or less tentative. It is perfectly clear that we are dealing here with a correlation of a very low order, the *general* existence of which cannot be definitely asserted till we have further statistics covering a wide range of social classes of different races. How slight this correlation must in general be is indicated by the fact which has been elsewhere brought out,[1] that what are probably the best series of brain-weight statistics now available give no definite evidence of the existence of a positive correlation between that character and intelligence. The results from the statistics analyzed in the present paper, though the material was drawn from a very different population, essentially confirm PEARSON's conclusion that "there is no *marked* correlation between intelligence and the size or shape of head."

Suppose it be granted that it is a fact that there is, however, a slight, though sensible, correlation between size of head and intelligence, what interpretation are we to put upon the fact? It seems to me that it would be absolutely fallacious to base upon these data any general argument that "men of genius have large heads." I quite agree with Professor PEARSON in his conclusion that: "For practical purposes it seems impossible, either in the case of exceptionally able men or in the bulk of the population, to pass any judgment from size of head to ability or *vice versa.*" If further statistics (of which there is great need) should show that generally there is a just sensible positive correlation between these characters, the correct interpretation of the fact would, it seems to me, probably be physiologic rather than psychologic. That is to say,

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[1] PEARL, R. Biometrical Studies on Man. I. Variation and Correlation in Brain-Weight. *Biometrika*, Vol. IV, pp. 13-104.

the association between vigor in growth processes (leading to a well-developed body) and vigor in mental processes would most probably be the result of the action of good conditions of nurture. Other things being equal groups of men with well-nourished bodies are on the average likely to be more able intellectually than groups in which bad conditions of nutrition prevail. Such an interpretation of the facts seems at present to have much better justification than any which in effect implies that a big brain connotes *per se* an able mind.

Rightly interpreted the facts regarding the correlation between size of head and intelligence seem to me simply to furnish, so far as they go, direct statistical evidence in favor of the adage: *Mens sana in corpore sano.*

DEATH-FEIGNING IN RANATRA.

BY

S. J. HOLMES.

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GENERAL CHARACTERISTICS OF THE DEATH FEINT.

The instinct of feigning death is developed in Ranatra to an unusual degree. If a Ranatra is picked out of the water it usually becomes motionless, either at once, or after a few spasmodic movements. Sometimes, however, the insect will not feign at first, but kicks about with its second and third pairs of legs, at the same time moving its anterior legs up and down so as to produce its characteristic squeaking sound by rubbing the bases of these appendages against the prothorax. When dropped on the table, even while moving, Ranatra usually becomes quiet as soon as it strikes the substratum. The attitude assumed is variable and depends to a great extent upon the position of the legs when the insect is dropped. The anterior legs are generally held close together straight in front of the body. Sometimes the two hinder pairs of legs are held straight backward close to the ventral side of the abdomen where they lie in a depression on either side of the median ventral carina. In this position the insect resembles a straight stick and may very readily be mistaken for one. Frequently both pairs of legs are bent forward and slightly dorsally. All sorts of intermediate attitudes are assumed, and the legs on the two sides are quite commonly held in different positions. This variation in the position of the appendages is in marked contrast to the definite and constant attitude which is assumed during the death feigning of many other insects.

When in the death feint, Ranatra lies motionless for a period varying from a few minutes to several hours. Under ordinary circumstances, however, the feint does not usually last for more than an hour. There is a wide variability in the duration of the feint in different individuals under the same conditions; and different circumstances, as will be described below, influence the result to a very marked degree.

The death feint may be brought about by picking the insect up in the fingers, or, if this does not suffice, by gently stroking the body. If an individual that is picked out of the water persists in moving its legs about in an effort to escape, it may usually be quieted if its legs are bent backward alongside the abdomen and the body gently stroked or rolled about in the fingers. If when beginning to come out of its feint Ranatra is stroked or sometimes even lightly touched it will resume feigning. A breath of air blown upon the insect will frequently produce the same result. When Ranatra is walking about it often happens that, owing to the lack of adequate support by the legs, the body is allowed to touch the table. This contact frequently results in causing the insect suddenly to feign death for several minutes. The death feint may be induced in susceptible individuals by slight contact upon the thorax, legs or abdomen. Contact with the breathing tube, however, is much less likely to produce this result. In handling specimens which I do not wish to throw into the death feint I find that it is best to seize them by the tip of the breathing tube. Specimens may be moved about in this way and still kept in an active condition, whereas they would be pretty certain to feign death if they were seized by any other part of the body. If they can be induced to use their legs and walk off before their body comes in contact with the table they are much less apt to feign. This may be frequently accomplished by dragging them backward over the top of the table so that their claws catch in the wood. The walking reflexes are thus set up and the insect may often be picked up in one place and set down in another without throwing it into a quiescent state.

While in the death feint Ranatra is in a condition of tetanus. The muscles are set so that the body and limbs are in a state of extreme rigidity. All sorts of unnatural positions which the insect may happen to assume in the beginning of the feint are retained for a long period. It may be picked up by the outstretched anterior legs and held out straight, ventral side upwards, for some time without bending the legs. When the weight of the insect finally causes the muscles to relax, the body descends very slowly and in an irregular manner. When an insect which is not feigning is held in this way the body drops down at once. If one of the hinder limbs is outstretched the insect may be seized by the tibia and held out horizontally without causing the least bend in the femoro-tibial joint. When the muscles finally give way the body sinks downward very slowly. When we reflect that the weight of the whole body in this case must be sustained by the minute extensor of a very slender limb acting with a very disadvantageous leverage, it is evident that the muscles must be in a state of extreme contraction. The attempt to bend any of the limbs in an individual that is feigning death will afford proof of the extreme muscular rigidity of the insect in this condition. Ranatras that are feigning may be placed in all sorts of unnatural attitudes which they will retain for from several minutes to over half an hour. In one case an individual which had feigned death with its hinder pairs of legs drawn up dorsally and forward was placed ventral side up so that it was supported only by the tips of its outstretched legs and the extremity of the breathing tube. The vertical distance between the tips of the anterior legs and the top of the table was indicated by a mark on a block placed close to the legs so as to gauge the rapidity of their descent. The abdomen nowhere touched the table, but its tip at the base of the breathing tube lay about a millimeter above the surface. In this position the insect remained without a perceptible movement from 7.57 P. M. to 9.10 P. M. when the tip of the abdomen touched the table. Between 9.10 and 9.20 the tips of the anterior legs sank about two millimeters. At 9.25 they had sunk another millimeter and at 9.28 the insect sank down on its back and began very slowly to move its legs. The position in which the insect was placed was one that could be maintained only through severe muscular strain—both of the leg muscles and the muscles that move the breathing tube. In another case a specimen was placed so that it stood upon its four posterior legs with its head pointing nearly directly downward. After six minutes it bent the left hind leg so as to rest on the knee, after which it remained in this very awkward position for seventeen minutes longer when it toppled partly over on its side where it remained several minutes more before getting up.

A similar condition of muscular rigidity is quite common among insects that feign death. In certain spiders that feign death the condition is described by ROBERTSON[1] as one of "extreme tetanus." In most cases the appendages are drawn up close to the body. In some amphipods and isopods the body is strongly flexed and the legs drawn up into a compact form—a condition that can be maintained only through the exercise of a constant muscular strain. An apparently similar state occurs in the rigid form in which the asp and certain other serpents may be thrown by the proper manipulation. And it is not improbable that the cataleptic stage that sometimes occurs in hypnotized human beings may fall within the same general category of physiological phenomena.

One striking peculiarity of the death feint in Ranatra is the apparent insensibility to pain which is shown. One may perform the most severe mutilations upon an individual that is feigning death without evoking the least manifestation of feeling. This is well illustrated by the following experiment: In a Ranatra that was caused to feign death the four hinder legs were cut off one by one. Not a wince. Both anterior legs were then cut off, and after a slight jerk the insect was as immobile as before. The tip of the abdomen was cut off. No movement. Then the abdomen was cut off next to the thorax. Still no response. Then the body was cut in two across the thorax leaving a short middle piece with the stubs of two pairs of legs and the anterior end of the insect with the stubs of the anterior legs. No movement in either piece. In eight minutes the stubs of the anterior legs began to move in a lively manner. The head piece was then picked up and stroked when it was again thrown into a rigid condition.

DURATION OF SUCCESSIVE DEATH FEINTS.

In experimenting upon the duration of successive death feints in the beetle Scarites, FABRE[2] found that there was a gradual increase in the length of the feint the oftener the insect was compelled to repeat the performance. In the experiment cited the

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[1] ROBERTSON, T. B. On the Sham Death-Reflex in Spiders. *Jour. Physiol.*, Vol. 31, p. 410. 1904.

[2] Souvenirs Entomologiques. 7me. Sér., p. 14.

beetle feigned for seventeen, twenty, twenty-five, thirty-three and fifty minutes in successive trials; and other experiments the details of which are not given were found to yield similar results, although there was very great variability in the lengths of the responses. The insect, however, could not be induced to feign indefinitely; sooner or later all efforts failed to make it fall back into the death feint, as if it found the ruse useless and decided not to persist in it.

My own experiments upon quite a number of unrelated forms have shown that in nearly all cases the duration of the death feint diminishes instead of increases with successive trials. Details of these experiments will appear in a future paper. Ranatra forms no exception to this rule, although there is usually a very great amount of variation in the duration of the first feints. In the experiments whose results are recorded in the following table ten Ranatras were picked up, stroked to about the same degree, and laid down on the table. As soon as a specimen awoke it was immediately picked up and caused to feign again, and its time of awakening recorded. This was continued as long as any of the Ranatras would feign. All of the specimens were exposed to the same amount of light, and the temperature of the room was kept nearly constant. The experiment was begun at 9 A. M. and continued without any interruption until 5 P. M., when the last specimen refused to feign longer.

TABLE SHOWING THE DURATION IN MINUTES OF SUCCESSIVE DEATH FEINTS IN TEN SPECIMENS OF RANATRA.

A	B	C	D	E	F	G	H	I	J
5	6	14	17	26	38	38	115	117	125
13	70	34	37	37	32	56	35	22	35
24	38	30	31	31	15	19	25	43	30
16	31	6	11	19	8	43	10	9	37
41	14	32	73	52	7	11	9	15	31
8	15	6	35	29	4	9	3	2	12
26	5	9	46	79	2	12	16	16	22
29	17	6	48	61	2	9	4	10	20
4	8	24	21	9	3	9	1	15	12
12	10	41	6	15	2	1	1	10	11
2	3	11	13	4	1	16	.5	7	5

Continued on next page.

A	B	C	D	E	F	G	H	I	J
4	2	19	9	6	1	8	0	8	6
4	1	3	8	6	3	3	0	7	8
4	11	5	5	3	2	1	0	6	13
1	14	11	5	2	1	2	.5	6	5
1	4	5	3	3	0	3	0	5	2
2	2	5	2	3	0	3.5	.5	3	1
1.5	3	10	3	1.5	0	1.5	0	3	1
1.5	3	3	3	1	0	2	0	7	2
.5	8	7	3	5.5	0	1	0	2	2
1	3	4	3	4	0	.5	0	1	2
1	4	8	5	9	0	.5	0	2.5	2
1	7	3	6	3	0	.5	0	1	1
2	1	3	7	6	0	.5	0	1.5	.5
1	9	3	2	3	0	1	0	0	2.5
2	8	3.5	3	1	0	0	0	0	1
.5	1.5	2.5	1	1	0	0	0	.5	4
.5	4.5	2	1	2	0	0	0	0	3
.5	8.5	2	1	.5	0	0	0	0	4
0	1	2	2	1.5	0	0	0	0	1
0	5.5	3	4	1	0	0	0	0	.5
.5	1	5	0	2	0	0	0	0	2.5
0	0	2	0	1	—	—	—	0	3
.5	0	1.5	0	0	—	—	—	—	2
0	0	2.5	0	0	—	—	—	—	30
0	0	1	0	0	—	—	—	—	0
0	0	.5	0	0	—	—	—	—	0
0	0	.5	0	0	—	—	—	—	0
0	—	1	—	—	—	—	—	—	0
0	1	—	—	—	—	—	—	—	0
—	—	1.5	—	—	—	—	—	—	0
—	—	2.5	—	—	—	—	—	—	0
—	—	2	—	—	—	—	—	—	—
—	—	.5	—	—	—	—	—	—	—
—	—	0	—	—	—	—	—	—	—
—	—	0	—	—	—	—	—	—	—
—	—	0	—	—	—	—	—	—	—

THE EFFECT OF TEMPERATURE ON THE DURATION OF THE DEATH FEINT.

The duration of the death feint in Ranatra is decreased if the insect is exposed to a higher temperature and increased if the temperature is lowered. The duration of the feint in different individuals is very variable, as may be seen by a glance at the accompanying tables. In all the experiments the insects were subjected as nearly as possible to the same amount of handling, and exposed to light of the same intensity. The Ranatras were picked out of the water, and, after the legs were bent back against the body, the specimens were stroked a certain number of times and laid on the bottom of a glass dish. Each dish was covered by a glass plate and kept partly immersed in water of the desired temperature which was indicated by a thermometer placed in the dish. All of the conditions except temperature to which the different lots of specimens were exposed were made practically the same.

In one experiment nine Ranatras were exposed to a temperature of 35° C., and an equal number kept at the temperature of the room which was 21° C. In the first lot the duration of feints in minutes in different specimens was as follows: 8, 8, 9, 10, 14, 18, 21, 25, and 40—giving an average duration of feint of seventeen minutes. In the lot kept at a temperature of 21° C. all of the specimens, without exception, were still feigning after an hour and five minutes when the experiment was discontinued.

In a second experiment eight specimens were kept at a temperature of 30° C. and eight others at a temperature which varied from 10° C. to 14° C. while they were kept under observation. The duration of the feints in the two cases was as follows:

Specimens Kept at 10° -C.14° C.	Specimens Kept at 30° C.
65	7
145	11
146	13
147	17
147	25
149	52
160	102
168	107
Average 137 minutes.	Average 43 minutes.

In a third experiment one lot of seven specimens was kept at the temperature of the room which was 22° C. while eight other specimens were exposed to a temperature of 34° C. The duration of the feints was as follows:

SPECIMENS KEPT AT 22° C.	SPECIMENS KEPT AT 34° C.
30	9
30	11
34	11
40	16
49	21
83	34
88	39
	41
—	—
Average 50.57 minutes.	Average 22.75 minutes.

The experiments show that heat diminishes and cold increases the duration of the death feint to a very marked degree. This result is similar to that which FABRE obtained in experimenting on the Buprestid beetle, Capnodis tenebrionis Lin. Ordinarily this beetle feigns death for less than an hour. Exposed to cold, its feint continued for over five hours. In Scarites, on the other hand, FABRE[1] found that a slight decrease of temperature caused the death feint to become shorter, a result not improbably due to the shock effect of the transition.

Ranatras transferred from the ordinary temperature of the room to a temperature of from 0° C. to 4° C. often come out of the death feint almost as soon as they touch the cold bottom of the glass dish. The cold acts as a sudden stimulus to them and they react much as if they were laid against a hot surface. If they are kept longer at this temperature they move about very sluggishly as if benumbed, and finally settle down to a comparatively quiet state. This condition is, in great measure no doubt, due to cold rigor, and in the specimens which are not aroused by the sudden chill it is not possible to determine when the death feint terminates, since the insects lie quiet in both of these conditions. Specimens which I had kept for some time in water at 10° C. and then transferred to a glass dish at a temperature of 4° C. continued to feign death without interruption. The transition in this case was not so great and the specimens were not subjected to the sudden shock which they received in the former

[1] Souvenirs Entomologiques. 7me. Sér., p. 14.

experiment. None of these specimens showed any signs of awakening for three hours, and probably they would have remained quiet for a much longer time.

THE EFFECT OF LIGHT ON THE DURATION OF THE DEATH FEINT.

The duration of the death feint in Ranatra is diminished, as a rule, by exposure to bright light. Twelve Ranatras were exposed to the light of a sixteen candle-power electric light at an average distance of about one foot. At the same time another lot of thirteen specimens was exposed to a much dimmer light in another part of the room. The duration of the feints under these conditions was as follows:

Specimens Under Bright Light.	Specimens Under Dim Light.
14	24
23	33
41	41
46	65
70	90
71	105
81	105
88	115
93	139
101	145
108	180
174	210
	255
Average 75.8 minutes.	Average 116 minutes.

Ranatras are roused from their death feint much more quickly if the light is moved about near them than if it is kept stationary. In experimenting on the effects of moving light one lot of specimens was placed under a sixteen candle-power lamp six inches away, a flat dish of water being interposed to cut out the heat rays. Another lot of specimens was exposed in the same way except that the light was kept moving above them at an average distance of about six inches. The duration of the death feints under these conditions was as follows:

EXPERIMENT 1.

UNDER MOVING LIGHT.	UNDER STATIONARY LIGHT.
3	20
4	28
8	40
15	41
26	42
Average 11.2 minutes.	Average 34.2 minutes.

EXPERIMENT 2.

UNDER MOVING LIGHT.	UNDER STATIONARY LIGHT.
	13
3	14
3	15
6	21
11	24
15	38
21	39
21	78
Average 11.4 minutes.	Average 30.2 minutes.

Specimens that have been lying quiet for some time may frequently be aroused very quickly if the light is moved about near them. Each time the light approaches they respond with a twitch which increases in vigor with each repetition until finally they get up and begin to walk around.

DEATH-FEIGNING IN DECAPITATED SPECIMENS.

In cutting off the head of Ranatra close to the body only the supraesophageal ganglion is removed. The subesophageal ganglion lies considerably behind its usual position in the insects and is closely connected with the first ganglion of the thorax so that it cannot easily be destroyed without inflicting injury to the latter organ. In each case the head of the decapitated specimen was examined to make sure that the supraesophageal ganglion (which also lies quite far back) was entirely extirpated.

The shock-effects of decapitation in Ranatra are comparatively very slight. I have kept specimens for several days after this operation and probably could have kept them much longer by observing the proper precautions. In one set of experiments fifteen Ranatras were decapitated with a pair of fine scissors. When liberated most of the specimens were able to walk about in an apparently normal manner soon after the operation. They were much more restless than normal individuals and moved about ceaselessly without any apparent external cause. Those that I took up in my hand soon after decapitation either did not feign death at all or feigned for only a few seconds. Many of them when picked up would spread apart the anterior legs and move them up and down producing their characteristic squeaking sound in the usual way. When placed on their backs they would right themselves as readily as the normal insects. After five hours of restless perambulation all of the individuals operated upon became quiet. They proved, however, to be extraordinarily sensitive to stimuli. Even the disturbance of gently raising the cover of the glass dish in which they were confined caused most of the Ranatras to begin moving around. The others were roused to activity when a very slight breath of air was blown upon them. For over four hours they walked about and clambered over each other in the most restless manner. Should one settle down to rest it would soon be set going again by another individual wandering over it. The specimens paid no attention to the light of the window near which they were placed, and subsequent experiments showed that they were insensitive to much stronger illumination. Ten hours after decapitation all of the specimens were picked up, stroked gently, and then thrown down upon the table. Most of the specimens feigned death in the characteristic manner, but only for a few seconds. Some, however, continued to feign for three or four minutes. In this feint they show the same state of tetanus as normal individuals do under the same conditions. Specimens feigning with the legs drawn up dorsally were found to lie in an inverted position supported only by the tips of the outstretched legs and the caudal end of the body. This certainly gives evidence of a considerable degree of muscular rigidity. When seized by the tips of the anterior legs and held out horizontally with the ventral side upward they maintain themselves in a perfectly rigid attitude for several seconds, and then bend downward very gradually. If a specimen not in the death feint is held out in this manner the body drops down at once.

About three hours later all of the specimens were picked up again, stroked, and dropped on the table as before. None of them feigned as long as a minute, and some started off as soon as they were free. Then the same experiment was repeated three times, and in no case did the feint last more than a minute. At 8.30 the next morning several of the headless specimens were walking restlessly about the dish. Those which were lying quietly on the bottom were roused to activity by the slight current of air caused by slowly waving an object above them. None of the specimens could be induced to feign death for more than a few seconds. In the evening they were again tried with the same result. Restless movements were kept up, with short intervals of quiet, all day, and on the following morning, although a few were dead, most of the individuals were still active. None of these would feign death for more than two minutes.

It is abundantly evident that removal of the supraesophageal ganglion causes a marked diminution of the duration of the death feint. This is, in all probability, due to the heightened irritability which normally follows when the inhibiting influence of this center is no longer exerted. When decapitated specimens are thrown into water they show the same restlessness as in air. They swim about with perfectly coördinated movements of the legs, often for hours at a time. When they come to rest they assume the same attitude as that taken by normal individuals, keeping the tip of the breathing tube exposed at the surface of the water. If two individuals meet they seize each other and struggle for some time before they become disengaged. If an object touches one of the first pair of legs it is usually grabbed at with the claws. When seized by the tip of the breathing tube the headless individual immediately makes strokes with great vigor and rapidity. If this does not enable it to get free the insect has recourse to a remarkably neat and apparently intelligent device. The hind legs are thrown as far back as possible; they are thus able to grasp the breathing tube a short distance behind the body; then by exerting a pull they bend the body ventrally. This soon brings the second pair of legs so that they can reach the offending object when all four legs are employed to push the body away. Several ineffectual attempts may be made to grasp the tube, but as soon as this is accomplished the insect immediately ceases to free itself by swimming and follows up an entirely different series of instinctive acts. The behavior of the decapitated insect in this situation certainly affords an excellent simulation, not only of purposive action, but also of considerable ingenuity in carrying it out.

In one case a decapitated insect was kept in water for six days after being kept in the air a day to enable its wound to heal. During all this time its reactions were essentially the same as they were soon after the operation, except that the insect became gradually weaker and less active. After the fifth day it would remain quiet in the water, but when disturbed would execute the regular swimming movements and would walk in the usual manner when placed on the table, although it would right itself only with extreme difficulty. All of its responses were weak, and it soon gave signs of exhaustion.

REACTIONS OF RANATRAS WITH THE BODY CUT IN TWO ACROSS THE PROTHORAX.

A specimen feigning death was cut in two across the middle of the prothorax. It did not make the least movement when the cut was made. Both parts were placed on the table where they lay perfectly quiet. In nine minutes the forelegs on the anterior piece began to move, and in fifteen minutes when light was passed over the head their movements increased greatly in vigor and the head showed the usual lateral and vertical reflexes. Then the anterior piece was picked up and stroked; the legs became rigid. When the piece was laid down on the table again it gave no signs of movement and when the light was moved about near it the usual head reflexes failed to appear. On continuing the movements of the light for two minutes the head movements began to occur and soon became more decided. Shortly afterward the legs began to move about vigorously, swinging and clutching in all directions. Soon the anterior part of the body showed all the excitement that is manifested by a normal individual when fully aroused to activity. On picking up the anterior part of the body a second time and stroking it, it again became rigid and irresponsive to light. After moving the light around it for about a minute, the head reflexes and leg movements began to appear again, and the part was soon as violently excited as ever. The fore legs were frequently drawn up as they are in a normal Ranatra when it prepares to fly toward the light. The part showed marked responses to light for over an hour.

The posterior portion of this specimen continued to retain its rigidity for some time after it was cut off, but it showed very little movement and died about four hours after the operation. Its original tetanic condition seemed to pass gradually into one of limpness and flaccidity.

A second specimen was cut across the hinder part of the prothorax. Just before the operation when the specimen was taken up in the fingers the fore legs were moving, although the hind part of the body was rigid. When cut across, the insect gave no response except that the fore part of the body became rigid like the rest. Eleven minutes after the operation the head would give no reflexes when the light was moved about near it for over a minute. Five minutes later it would not respond at first, but when the light was moved about over it for nearly a minute the head reflexes began to appear and these were quickly followed by movements of the legs. The part was then taken up, the legs straightened out and stroked, when they became rigid. It was then placed on the table where it remained immobile and insensible to light. When the light was moved around it for over a minute the head reflexes reappeared. The more the light was moved about, the more the excitement of the part increased, until it became very active and vigorous. For three hours and a half the head continued to show reactions to light. The posterior part of the body gradually became less rigid, but showed little independent movement; it died about four hours after it was removed. The same experiment was tried on other specimens with similar results.

The severed posterior portion of the body of Ranatra comes out of the death feint more quickly than the part containing the head. If it is picked up and stroked, it may be thrown back into the death feint again, but it remains in this state for only a comparatively short time. If the nerve cord of Ranatra is cut between the first and second thoracic ganglia, the insect may be kept alive much longer than when cut across the prothorax. The two parts of the body may then be caused to feign death independently. The effect of cutting the nerve cord in the prothorax is greatly to lessen the spontaneous movements of the second and third pairs of legs. The posterior legs may move about when the head and anterior legs are quiet and *vice versa.* When the whole insect is caused to feign the posterior part is usually the first to recover, although it does not always give such evident signs of so doing.

DECEPTIVE QUIET.

It was only after keeping Ranatras for some time that I observed that they manifested the least awareness of my presence. So far as observed these insects never attempt to escape by swimming or walking away, although other aquatic hemiptera, such as Zaithas, water boatmen, etc., make a great ado upon one's approach and scurry away in the most lively manner. So ungainly an insect as Ranatra could seldom effect its escape by swimming, much less by walking, from any enemy large enough to overpower it. And when out of water it apparently never occurs to the poor creature to seek to get away by using its wings, although it could often easily do so. Ranatra seems to be entirely devoid of all instincts to seek safety by flight in every sense of this term. In experimenting on the reactions of these forms to light I have worked with individuals for hours, picking them up here and setting them down there, and subjecting them to a variety of treatment some of which was perhaps not particularly pleasant, yet the creatures seemed stolidly unaware of my existence except when actually handled. Pick up a Ranatra that is bent on going to the light, and if it does not feign death it will travel to the light immediately after being liberated as if impatient of the rude interruption. I have often observed individuals struggle to get to the light even before their release. If its phototactic proclivities are well aroused one may make all sorts of movements in the vicinity of a Ranatra that is seeking the light but the insect will completely ignore them.

Ranatras under natural conditions are nevertheless keenly aware of the events that take place in their neighborhood. They are attracted by small moving objects that may serve for prey, and these they lie in readiness to seize. The appearance of large objects in their field of vision causes a sudden and complete cessation of movement. If one approaches a group of Ranatras when they are swimming about in a dish of water, it will be noticed that most of the individuals cease their movements and lie with outstretched legs. If one remain perfectly still the movements of the Ranatras are soon resumed; if now the hand is passed over the dish, the Ranatras will immediately become as quiet as so many sticks which they so closely resemble. If movements near them are continued, the Ranatras soon cease to respond so readily, and after a time they pay little or no attention to what goes on around them. Specimens that have been kept in the laboratory for several days are much less responsive than those that have been recently brought in.

The question naturally suggests itself, whether or not this state of deceptive quiet has any relation to the immobile condition that occurs in death feigning. So far as could be determined, the two phenomena have little in common beyond a certain superficial resemblance. In an insect that suddenly ceases its movements in the water one may very readily move its legs about with a piece of fine wire. The legs seem relaxed and offer almost no resistance to movement. The attitude of the legs in deceptive quiet is one which is quite constant and which would naturally be assumed if the muscles were relaxed. If a dead and limp specimen is held in the water its legs lie spread apart much as they do in deceptive quiet, although not so symmetrically. These facts indicate that deceptive quiet, instead of being associated with the muscular rigidity that characterizes the death feint, is attended by a relaxation of the muscular system.

The subject of deceptive quiet acquires an interest because of its possible relation to certain aspects of fear. What kind of feelings exist in the consciousness of a Ranatra when it suddenly becomes quiet upon the appearance of a large object is a question upon which it is perhaps not profitable to speculate. Deceptive quiet may have some relation to what is commonly, though somewhat loosely, spoken of as the paralyzing effect of fear in higher animals, but of fear in its more usual manifestations Ranatra shows no sign. Species not distantly related to Ranatra, however, swim about upon one's approach with all the appearance of violent alarm. We may say that these creatures manifest fear, since they exhibit the usual outward and visible signs of that state. Fear has undoubtedly arisen along many independent lines of descent, and in numerous cases has been suffered to disappear again. It leads animals now to lie quiet, and now to seek safety in flight. These two aspects of the fear response are found in different relative degrees of development in different forms. Both are of service in escaping from enemies, although sometimes one is employed to greater advantage than the other. Fear as it occurs in higher animals is a sort of combination of two instinctive tendencies of a very different nature, but whose manifestations are brought about by similar situations. Often these tendencies conflict and there results a state of indecision in which neither finds its natural expression. In some animals only one of these elements usually found in fear phenomena are present; there is only one method of meeting the situation. Ranatra shows only the element of deceptive quiet in the presence of its enemies. Other insects whose reactions I have studied exhibit no trace under any circumstances of the instinct to seek safety in remaining quiet, but always make vigorous efforts to escape by flight. Which of these instinctive responses develops doubtless depends on the general mode of life of the animal and its habitual environment. Where an animal possesses both, as most higher forms do, there is opportunity for meeting different kinds of situations with a more appropriate response.

OBSERVATIONS ON THE COLOR-SENSE OF A CHILD.

BY

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Published observations on the color-sense of young children have not been numerous.[1] Since the accounts, furthermore, are in not a few points contradictory, one may indeed say that our positive knowledge in this subject is still very incomplete and that new observations are greatly needed.

It is obvious, since the psychic life as a whole develops more quickly in some people than in others, that there must be large individual differences in the age at which colors are first correctly named. Whether the actual ability to *distinguish* colors (Farbenunterscheidungsvermögen) likewise shows similar differences may be doubtful; we have, indeed, no indication whatever that there is such a thing as an evolution of the color-sense in the individual, nor does opinion, now-a-days, at all incline toward the assumption of a development of the color-sense from a simpler to a more complex form, or, specifically, from partial color-blindness to normal color-vision.

No one perhaps would now venture to assume, as many for a while believed, that color-blindness could result from the neglect of the color-sense in childhood, although there may be those who think that a "weak color sense" or that which has received the name of "color stupidity" (Farbendummheit) may be traced back to that cause. We must, however, dismiss the thought of such a causal reference, as we learn more and more to see that even these lesser disturbances in the color sense are not, in most cases, to be understood as undefined criteria of a general uncertainty in the power to distinguish colors, but rather as sharply defined types of color vision.

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[1] A bibliography of the various investigations of the color sense of young children is to be found in PREYER's book, "Die Seele des Kindes," 5th edition, edited by K. L. SCHAEFER, Leipzig, 1900.

I shall consider further on the contents of some earlier publications on the color sense of children. I wish here, at the outset, to mention that the aim of my own experiments, of which I treat in the following pages, is not wholly identical with the aims of former authors. It was not my chief concern to determine either how well the child could already distinguish colors, or which color-names he could learn. My prime interest was, rather, to make sure of a diagnosis that would determine whether the child, at two and one-third years of age, showed a normal (trichromatic) color sense, or whether there was any reason to assume the presence of a dichromatic or otherwise abnormal color vision.

The problem was, therefore, similar to that which HIMSTEDT and I[1] had proposed to ourselves in the year 1902 in certain experiments on a dog; at that time, however, we confined ourselves to tests designed to show whether any color sense whatever was present, or whether the animal was totally color blind. This single point was decided by the fact that the dog discriminated between red and blue.[2]

In the investigations on the child, as in those on the dog, one requirement was fulfilled, which, so far as I know, has not been taken into account by any previous investigators with animals or children; I took care, namely, that the two colors that were to be distinguished from each other should be shown simultaneously in several sharply different degrees of brightness. The dog had not to choose between *one* blue and *one* red object, but between five or six of each color. The danger was thus avoided of concluding that the animal had distinguished between two colors whereas in reality he had chosen only according to brightness.

The experiments on the child had to be carried out in the same way, and the results that I obtained therefore furnish a much surer answer to the questions proposed than even PREYER'S fuller experiments could have yielded.

Rather as a by-product of my experiments I obtained answers to the question put by PREYER: From a large number of colored objects, which colors can the child most easily pick out and

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[1] F. HIMSTEDT und W. NAGEL. Versuche über die Reizwirkung verschiedener Strahlenarten auf Menschen- und Tieraugen. *Festschrift der Albert-Ludwigs-Universität* in Freiburg 50 jähr. *Reg. Jubil. d. Grossherzogs Friedrich. Freiburg,* 1902.

[2] HIMSTEDT afterward continued his tests with his dog and found, further, that he could recognize the difference between blue and green and between red and green.

correctly name? Or, in other words, what serial arrangement, according to this method, will he give? Since I confined my tests to a short period of time (two weeks), in order to minimize the effects of "training," I could get no such complete answer to this question as PREYER; yet I feel that I had here, again, a certain advantage in the already mentioned principle of showing the colors in various degrees of brightness, which enabled me to determine with greater certainty than PREYER whether the child, in the given case, discriminated colors or merely differences in brightness.

The child investigated, my older son Gerhard, was two years and four months old when the experiments began. He was physically and, so far as one may conclude, at that age also mentally, well developed. To judge from PREYER's statements, I should say that, especially in physique, but also mentally he was somewhat in advance of PREYER's child, perhaps from three to six months.

In the mother's family (the mother being especially concerned in the hereditary transmission of color blindness) anomalies in color vision are not to be found. Both grandfathers of the child have normal trichromatic color vision; I, his father, as well as one of my two brothers, am deuteranopic (green color blind), the other brother is normal. Two cousins (male), on the father's side, are "anomale" trichromates, and, according to the designation of v. KRIES, "Rotanomale."[1]

I began the systematic investigation of the child in November, 1905. Similar tests had not previously been made; he had been merely occasionally told that such an object was red, such an one blue, etc.

The boy often played with a so-called "game of mosaics," that is, with a system of cubes on which single portions of differently colored pictures were respectively represented. Some of these parts contained a vivid red. One day I showed the child a red spot and said to him, "that is red," which phrase he at once re-

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[1] "We may, indeed, represent the protanopic (red-blind) and the deuteranopic (green-blind) visual organs as originating in a lack of the red and green components (of HELMHOLTZ's theory) respectively, and the Rotanomale and the Grünanomale in a variation in the nature of the red or the green component" (NAGEL's Handbuch der Physiologie des Menschen, *Braunschweig*, 1904, III Band, S. 279).

peated. He then learned, in the course of a few minutes, to point out the red spots on the other cubes, making, however, several errors. It is worthy of note that, in these first experiments, "orange" was often indicated as "red," a confusion which occurred less and less often. I repeated the questions several times the same day and the day following, always carefully avoiding fatigue by making the actual test-period short. Even in later experiments, as well as in these earlier ones, a test seldom lasted more than one or two minutes.

On the third day I showed the child a fairly large number of colored paper squares, usually twenty at once, each square measuring about four centimeters on a side. In the first experiments with these squares I merely asked, "where is red?" At the very beginning the first three or four requests for "red" received correct answers; then, however, fatigue or distraction had set in, and the answers became either quite incorrect or were wholly wanting. I was surprised that the child pointed, not only at brilliant red, but likewise at rather unsaturated strawberry-red ("fraise").

On the following day the results were even more favorable. Each time he was tested he designated *without an error* all the papers in the collection that were red, and surprised me again by including in his choice a fine purple-red and even a very bright pink.

The next four or five days were devoted to a repetition of the same experiments. I showed the child the colors three times daily, on an average, and received in all cases, even when others were present, correct answers to the five or six questions that were necessary to enable him to find all the red pieces of paper. I always took away each piece that he had called red before asking the next question. In these tests there were, among the reds, likewise browns, greens and blues, all in various degrees of brightness and saturation.

From the fact that in answering the several hundred questions which I put to the child during the tests he not once confused red with brown or green, one may with certainty conclude that his was no case of red-green color-blindness. For me, a deuteranope (green-blind), the strawberry-red was only with great difficulty distinguished from a bright brown, and a protanope (red-blind) would have confused it with a somewhat darker shade of brown, which was also to be found among the colors shown. Further, a bright pink cannot be distinguished by either of these dichromates from a bright blue-green. The child was, however, not to be confused. I may, too, at once mention that in his case all further experiments argued against the assumption of a dichromatic and in favor of that of a trichromatic color vision.

After I had continued these experiments for five days, the child was able to point to any reddish portion of any object. He did this at times, too, unasked.

When the boy had thus been taught to heed *one* color, it was easy, as I had supposed, to impress on him the names of others and to teach him to recognize them. It was, indeed, much easier than I had thought. He learned in a few minutes to recognize and to name green, blue, black and white.

In fact, during the whole of the remaining period given to these observations, I never heard him name black or white incorrectly. When I mentioned for the first time the word "schwarz" (black) in his presence, it made a great impression on him. I spoke it in a deep, hollow voice, pointing, at the same time, toward the black piece of paper. I spoke the word "weiss" (white) in a high, clear tone. He imitated the sounds of my voice and recognized the colors easily, although obviously with the assistance of these associations.

I was astonished at the sure feeling which he at once manifested for the term "green." The experience with red was here repeated; I had taught the child the name "green" by showing him several examples of a deep, somewhat dark green, whereupon he at once and unasked pointed to several bright green and even gray-green squares, which he had not been told were green, saying: "those are green, too." From this moment on he knew green just as surely as red, and could find it easily and quickly among reds, browns, blues, grays and violets of the most various shades and hues.

In regard to certain statements of PREYER it is particularly noteworthy that the discrimination between green, on the one hand, and gray and blue, on the other, was made at once and with full certainty. In discriminating green from gray (both colors being presented simultaneously in various degrees of saturation) my son far excelled me, a deuteranope (green-blind), making distinctions that I could not possibly make.

On the following days, also, green was recognized just as certainly as was red; that is, when not fatigued, the child picked out, from any combination of colors whatever, and without error, the various shades of green. I noticed, however, that he showed even greater pleasure in naming and in finding this color.

His treatment of blue was very striking. He had learned, as I said, the term "blue" along with the terms "green," "black," and "white"; that is, within a few minutes. The same day and the one following he designated the blues quite correctly and did not confuse blue with green or violet (the name of which he did not yet know) or with black. A bright sky-blue he called at first green, but only at first, not later.

The two chief desiderata, in the whole series of tests, were to get the child to learn, (1) red, and (2) blue. In showing him blue I *incidentally* mentioned the names "green," "black" and "white." The result was, however, that these latter names remained fixed, whereas "blue" not only lost its hold after two days, but also during this time, showed itself to be insecurely fixed. Even when not fatigued by the experiments, the child said, at times, when blue was shown him, hesitatingly, "red," but more frequently "not red," or, "but that is not red." On the following day he did not at all use the term "blue"; during the whole experimentation period of fourteen days he made use of it, therefore, only on the day when he had first learned it and the next following day.

It would be wrong to assume from this that the child was no longer able to *recognize* blue, *e. g.*, to *differentiate* it from the other colors; on the contrary, he did so frequently with complete certainty. From color-sets containing several blues, variously saturated and of different brightnesses, he picked out the green, red, black and white pieces with assurance, and without once confusing blue with them. Further than that, he could also select the various bright and dark grays, without a single error, from among the greens and blues. But, although he thus knew the blue, he could not point to it when asked to do so; he designated, instead, a red or some other color, mentioning, however, the correct name; or he chose green first and said: "Now that is not blue." But most frequently, when asked for blue, he became embarrassed and tried to turn my attention to something else.

I was curious to know how he would behave toward violet. From the very beginning I had often put violet squares in with the other colors, but had named neither that color nor the colors brown and yellow.

On the ninth day of the tests, three days after his recognition of blue, green, black and white, and one day after he had recognized gray, I showed the child some lively violets among the others and said to him, "that is 'lilla.'" He at once took up the term with great enthusiasm, and showed me other "lillas," among them a very dark one. Here, too, the color sense of the child proved to be much superior to dichromatic color vision since I (deuteranope), as well as the other type of dichromate (the protanope), cannot with certainty distinguish violet from a somewhat unsaturated blue.

A marked difference from his behavior toward blue, which persisted throughout the days following, was that the designation "lilla" was used with evident pleasure and without any hesitation. On the other hand, the limits of the concept lilla were obviously not so sharply drawn as those of "red" or "green," nor even that of the unloved "blue." After the child could correctly pick out violet, he designated, likewise as "lilla," not infrequently a brilliant purple (from the colored papers of ROTHE), and, less frequently, a pure ultramarine blue. If I then immediately afterward showed him the same blue and asked, "is that 'lilla'"? I received invariably as answer an almost indignant "no! that's not lilla."

With the other colors, when the child was not tired, such confusion did not, as I have already mentioned, occur; it occurred only when he was tired or noticeably inattentive. I had the impression, with regard to violet, that the difference between it and blue or purple was not quite surely recognized, or, that the difference, as one might say, was not as great as that between red and green or green and blue.

On the same day that the child had learned violet I pointed to yellow, for the first time, and named it for him. My questioning showed, the next day, that he had retained the term; nor did he ever forget it during the remaining days of the investigation, often using it quite spontaneously. Yet, and that seems to me noteworthy, the term "white" disappeared simultaneously from his vocabulary of spontaneously employed words. It seemed, as it were, to have been crowded out by the term "yellow." Nevertheless, confusion between white and yellow seldom occurred, and between yellow and greenish-yellow, never. Yet, even up to the last day of the investigation, I could not induce the child, on showing him white, to give the correct *name;* he said either "yellow" or, more frequently, nothing—the same attitude, therefore, as toward blue.

I broke off my investigations on the fifteenth day, but intend to renew them somewhat later; until then the child is not, if possible, to be questioned about colors.

In reviewing the experiences of our fifteen days' experimentation the following points appear to me to be worthy of note:

1. In the very first systematic tests the child at once designated as "red," not only the spectral red that he had learned to recognize during the preliminary experiments, but likewise bright and dark as well as unsaturated reds; he included in his choice also pink, purple and, occasionally, orange.
2. Green was learned without much practice and was not afterward forgotten; similarly, a few days later, violet and black.
3. The recognition of gray and blue developed rather more slowly.
4. Blue was forgotten again in two days; that is, the name was not used, although the color was only very infrequently confused with other colors.

The first point is important because it shows that the child grasped the concept "red" forthwith, quite independently of the accidental brightness or saturation of the particular red in connection with which he had at first been taught the name of the color. This fact further clearly demonstrates that red-green color-blindness could not have been present. From the very beginning I had taken care that during the first week such colors as green and gray, and especially brown, which dichromates confuse with red, should be, in numerous variations, amply represented; the opportunity for the typical confusions was therefore constantly present. Such confusion occurred, however, neither at first nor later, when I kept introducing all sorts of combinations of greens, browns, grays and pinks, in order to give him the chance to confuse green too with the other colors, a confusion which not only every dichromate, but likewise many "anomale" trichromates would have fallen into.

At first glance it might appear that the child's behavior toward blue speaks for "tritanopia" (violet color-blindness), or at least indicates a certain degree of weakness of the yellow-blue sense. I believe that to be, however, an error. There is surely no question there of tritanopia. The typical tritanopic confusion between blue and green was not made, although several varieties of green and of blue were often intentionally shown him; nor did any confusion between brown and unsaturated red manifest itself.

The child's disinclination to name blue remains, nevertheless, noteworthy and is not easily to be explained. Among the colored squares some were to be found of a particularly fine and brilliant ultramarine blue; but he paid no attention to them. He showed the same indifference when I gave him, on the tenth day, a game to be played with colored blocks of red, green, blue, yellow, black and white; all the other colors interested him more than the blue. He recognized and named, at least during the first days, the white blocks correctly.

I think that the child's forgetting of the white, toward the end of the period, may be partly due to the fact that I was not enabled, at that time, to concern myself much with him and, in particular, seldom questioned him about white. In addition to this, it may also be that the newly-learned yellow had usurped in interest the place of the white.

With blue, however, the case is quite different. After he had learned the name, on the eighth day, I took quite particular pains to test him for ability to discriminate between blue, violet and green. The child nevertheless used the term "blue," as I have already indicated, only on the eighth and ninth days, avoiding it later altogether. In point of time this change coincided with the acquisition of violet, for which, as well as for green and red, his interest did not flag. Perhaps, therefore, the blue was crowded out by the violet, the two colors having for the child a manifest similarity. It was not a difficulty with the word itself, for he repeated the word easily, when I pronounced it for him, at the same time frequently pointing to some color with the words: "that's surely not blue" or "that may be blue—no, it isn't, either."

It is, too, practically certain that the blue did not look particularly dark or particularly unsaturated to the child's eye; if the absolute stimulus-value had been specially low, if, in other words, the color appeared too dark, there would have been danger of confusing it with black or with dark green; such confusion did not, however, show itself, and, furthermore, the only mistake that I noticed, with regard to black, was that he at times took it for dark green, whereas still darker blues, violets and reds were present.

Had the sensation which resulted from a too weak *saturation* of the blue been the cause of the curious reaction to blue, then at least a confusion would have occasionally occurred between blue and gray; this was, however, not the case, although at least three different brightnesses of blue and the same number of gray were shown together. I can, therefore, merely say that the child's disinclination for blue remains for me quite inexplicable.

I have still to mention that in the second week of the tests, my son introduced, on his own account, a procedure into the experimentation that it had not at first occurred to me to employ. He reacted, namely, to questions like, "where is red?" or, "where is blue?" more and more frequently with answers such as, "that is *not* red" (pointing to blue or green), or (pointing to green), "now this is green." He designated in this way a large number of the colored papers *always* by omitting the color-term about which I had questioned him. He clearly favored, in these responses, the greens, violets and reds, for which he had all along shown an especial fondness.

From the twelfth day on, I could scarcely induce the child, at my behest, to point to three or four varieties of a certain color. He indicated either only one example of the tone I wished, or none at all, picking out, however, with the utmost willingness, all sorts of colors which he knew and could name, with the exception of blue, which he never chose. The first method of investigation was becoming tiresome to him, and I soon felt that an attempt to carry through systematically the earlier procedure could end in nothing but aversion and inattention.

From such experiments as I have here reported one may conclude, if one adopts the same procedure, that a clear answer is hardly to be had to the question which colors the child can discriminate, but that the various interests or the different preferences of the child for the single colors influence his reactions. The solution of the chief problem, the ability of the child to distinguish colors, is thereby made more difficult, and the more so the longer the experiments are continued. During the two weeks of my investigation, I could plainly see that my son generally spoke of that particular color which he had last learned. Only in the case of blue was this not true. Toward the end of the second week the interest for green and black and, secondarily, for violet prevailed over everything else, and during the following weeks, after I had ceased to question him about colors, he would bring me objects, mostly green and black, and gave their names correctly.

As to the question whether an evolution of the color-sense is to be found in the individual and, in particular, whether the young child's color-sense is a different, a simpler one than that of the adult, the observation of a single case gives but qualified information. The experiments that I have reported offer, it must be admitted, positive proof that in this one case the color vision of the son showed itself to be superior to, or more complex than, that of the father, and that at any rate, *for children of this age, the universal prevalence of any form of dichromatic color vision cannot be maintained.* I myself had not expected to obtain so clear a proof of the presence of trichromatic color-vision.

The experiments are also in a certain sense instructive if one considers them in relation to the older ones of PREYER,[1] BALDWIN,[2] etc. My aim was, however, a different one from that of these two authors, and from BALDWIN's my investigation differs, too, markedly in method. To draw from BALDWIN's experiments any conclusions about the ability of the child under investigation to discriminate colors seems to me impossible.

Those of PREYER are decidedly better, and yet I am not quite clear, from his description, what degrees of color-discrimination his child had reached at the respective periods. Some statements awaken the suspicion that PREYER's child had dichromatic (red-blind or green-blind) color vision, but, as I said, that is only suspicion. It must be remembered that his researches were the first in this field, that he had, therefore, the entire method to create.

The most interesting thing in PREYER's report is, according to my judgment, his concluding compilation in which he gives the various per cents. of wrong and right answers that he had received to his questions about the different colors. These are calculated,

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[1] *Loc. cit.*

[2] J. M. BALDWIN, Mental Development in the child and the Race. 1895; German edition, 1898.

it is true, up to the thirty-fourth month. For comparison with my results I here reproduce PREYER's table:

PREYER'S TABLE.

COLOR.	CORRECT ANSWERS.	INCORRECT ANSWERS.
Yellow	96.7	3.3
Brown	90.8	9.2
Red	86.7	13.3
Violet	85.3	14.7
Black	84.8	15.2
Pink, or rose	72.4	27.6
Orange	67.1	32.9
Gray	51.5	48.5
Green	45.1	54.9
Blue	28.8	71.2

It should be mentioned that the number of tests with the separate colors varied.

I cannot, as a result of my experiments, offer a similar table, because they lasted only fifteen days and of this time the first six were occupied in practice with red; the other colors, furthermore, were named and practised for the first time on different days. The aim of my experiments was, however, from the outstart a different one.

At best the only tests of mine that are comparable with PREYER's are those of the last three days. If, according to these, a color-series were to be constructed, in such a way that the colors named correctly and with the most certainty were to stand at the top of the tabulated series and those most uncertainly named at the bottom, it might be represented somewhat as follows:

Green
Violet } About equal in rank in the series.
Red.
Black.
Yellow
White } About equal in rank in the series.
Gray
Blue.

The single point of agreement which stands out prominently in both tables is, as may be easily seen, that blue occupies quite the lowest position, and the most essential variation is the very different positions taken by green. It is the low position of green in PREYER's table that made me suspect color-blindness, just as the normal vision of my child is, on the other hand, particularly well shown by his ability so sharply to discriminate between green and gray, blue and violet, red and brown. The great difference in the reactions of PREYER's child to blue and violet argues, nevertheless, against the supposition of color-blindness.

It seems to me that my experiments mark a certain advance over those of previous authors in that every color was shown, from the very beginning, not in *one* degree of brightness and of saturation only, but in as many as possible; this was markedly the case with the most important colors that dichromates confuse. Correct choosing, on the child's part, of the colors asked for under these conditions, means much more than if each color is presented in but one shade, tint or hue (which seems to have been the procedure of earlier authors) and if orange and pink are regarded as independent colors.

In making use of PREYER's experimental series, it is also to be taken into account that for some of the colors (brown, pink, gray) so small a number of tests was offered, that one may scruple somewhat about including them in the series at all. As an actual error in PREYER's experiments, if I correctly interpret his protocol, I consider his failure to include white and yellow among the colors simultaneously shown. Under such conditions, the reactions of PREYER's child to yellow may well have been simply reactions "to much the brightest color." It is an unfortunate habit of many physiologists and psychologists in such cases, where various colors are offered for comparison, to make use of a yellow of much higher intensity, because it appears brightest in the spectrum, than that of the other colors. It is my belief that, if pigment colors are to be employed, a "brown" should always be given for comparison with the other colors, that is, a dark but saturated yellow with neither a trace of green nor of red; one introduces, otherwise, a quite unintentional complication, namely, the marked difference in brightness and saturation between the yellow and the other colors.

It is, indeed, self-evident that when an adult can discriminate between red-colored and yellow-colored papers, absolutely no conclusions can be drawn with regard to his color-sense; he may equally well be normal, red-blind or green-blind. On the other hand, it needs most certainly a normal color-vision, for one who is quite without practice, to distinguish a red (even when little saturated) from a brown colored paper. I feel compelled especially to emphasize this point because it has been quite disregarded in numberless researches in color-physiology, and because this neglect has bred such great confusion, robbing not only previous observations on the color-sense of children, but also, and especially, those on the color-vision of animals of much of their worth and of their interest.

TABULAR VIEW OF THE EXPERIMENTS.

First day	
Second day	
Third day	
Fourth day	Systematic practice in selection of *red.*
Fifth day	Occasional naming of the term "*green.*"
Sixth day	
Seventh day	Futile attempts to teach "blue"; *green* always correctly recognized and named without further practice. *Blue, black* and *white* now learned.
Eighth day	Blue correctly recognized and named; no confusion of it with violet or green. Occasionally naming of "yellow," which was not, however, retained.
Ninth day	*Violet* now learned.
Tenth day	*Gray* now learned; "blue" no longer called by name.
Eleventh day	The term "*white*" employed more and more seldom; "*yellow*" even oftener and more correctly. *Red, green, violet, gray, black* correctly named; *blue* and *white,* while not often confused with other colors (violet or yellow), nevertheless never spontaneously named. Purple, at first called "*red,*" now usually called "*violet.*"
Twelfth day	
Thirteenth day	
Fourteenth day	
Fifteenth day	

GEORGES BOHN'S STUDIES IN ANIMAL BEHAVIOR.

Of the recent papers by Bohn included in the following bibliographic list the longest and most important ones are marked with an asterisk. In the discussion of the author's work which follows, reference to the various papers is made by the use of their numbers in the list, not by title.

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A general review and discussion of the work of GEORGES BOHN is justified, I believe, by the fact that it is known scarcely at all in America, although much of it is of considerable importance to students of animal behavior. This surprising lack of acquaintance with BOHN's papers in this country is due, no doubt, in large measure, to the fact that many of the most important of them have appeared in the bulletins and memoir of the Psychological Institute of Paris, which, so far as I can learn, are in very few of our libraries.

The general field in which BOHN has worked, as is indicated by the titles of his papers, is that of animal behavior. The problems which he has sought to solve are in the broadest sense biological, for he is interested in the psychology of his subjects as well as in the dynamics of protoplasm. While believing in the legitimacy and value of comparative psychology, he insists, especially in his most recent papers, that subjective terms shall not be used merely to cloak our ignorance of the conditions which determine reaction. Consequently his work is of equal interest to the radical objectivists of the BEER-BETHE-VON UEXKULL-NUEL camp, with their emphatic denials of the possibility of comparative psychology, and to such extreme subjectivists and anthropomorphists as BINET, WASMANN and WEIR. It is apparent from his writings that he has become much more guarded in his use of psychological terms during the last few years than he was earlier in his career.

The striking characteristics of BOHN's experimental work are simplicity and directness; of his writings, a labeled-and-numbered-package method of presentation and repetition. One is likely to underestimate the value of his observations because of the extreme simplicity of his methods and the predominance of qualitative studies. Much of the work seems crude and inexact at first, but careful consideration of the author's purposes and methods of presentation leads me to conclude that it has great value. For BOHN is constantly bringing to light new facts; and if, in the opinion of certain of his readers, these same facts are not always satisfactorily established, his work will at least serve an excellent purpose in stimulating other investigators to further experimentation along the lines which he has indicated. Unhappily, our author is addicted to the publication of brief notes during the progress of his investigations, the substance of which he later brings into a single long paper. This manner of presenting the results of experimental work, which prevails in France because of the custom of publishing full reports of the meetings of academies and societies, is wasteful of the reader's time and patience, for it forces him to look up a number of papers of which only one is of value to him.

The papers which we propose to consider in this review naturally fall into four groups: (1). Studies of the psychic life: Receptive capacity, intelligence, memory, etc., of various animals. In this group belong the papers numbered 2, 11, 12, 14, 15 and 24. (2). Studies of the forms of reaction of various animals. Papers numbered 1, 3, 6 and 7 belong to this group. (3). Studies of the reactions of organisms in relation to light, moisture, gravity etc., and of theories of the tropisms. In this group we may mention numbers 4, 5, 8, 9, 10, 13, 16, 17, 18, 19, 20, 21, 22, 23, 25, 26, 27, 29 and 30. (4). Studies which deal with the problems of all the preceding groups. Numbers 28 and 31 are of this nature.

Concerning the work described in the papers of the first group, it may be said, that were the author to restate his results, there is every reason to believe that he would use objective terms almost exclusively, and that the papers would therefore fall into one of the other groups. In other words, what formerly interested him because of its probable psychological significance, BOHN is now concerned with, because of its value as fact. In the introductory chapter of his memoir on reactions to light (No. 28) he makes clear his present position with reference to the use of subjective terms, and at the same time states his purposes of research. He claims that there is a difference between seeing (a subjective term) and being influenced by light, and that we are not justified in using the word see (*voir*) in connection with the reactions of certain molluscs, since it involves an interpretation of the phenomena observed, which may possibly be false and which is unnecessary. And he continues, (No. 28, p. 5,) "in this memoir, I shall describe the facts without explaining them, and I shall guard myself well against saying that in Littorina, states of consciousness do not exist and do not intervene. I do not know; I affirm nothing, deny nothing." BOHN does not, however, in any of his papers go to the absurd length of trying to avoid entirely subjective terms. The final result of the introductory chapter referred to above in which the author discusses the dangers to biology of anthropomorphism, psychologic, vitalistic and mechanistic errors, is well summed up in his statement of what he has attempted to do in the memoir (No. 28, p. 14). "(1) To limit myself to the descriptions of the animal's reactions. (2) To state precisely, as far as possible, the conditions of the experiments, in taking account of variations of internal conditions as well as of external; of past influences (*causes passées*), as well as of present influences (*causes actuelles*). (3) To avoid idealization of the facts, anthropomorphism, psychology and philosophy. (4) To employ purely objective language. (5) Not to liken an animal to an inanimate machine. (6) Not to generalize for all animals. (7) To separate clearly the interpretation of the facts from the exposition of these facts, and in this domain, to admit only hypotheses easy of verification."

Of the papers in the first group, No. 12 is worthy of special attention. In it the author describes his studies of the social relations, receptive capacity and modifiability of reaction in the hermit crab. There is an important list of papers which deal with the relations of the crabs among themselves and with other animals, and in addition, valuable historical and critical notes. BOHN's original observations concern: (1) The nature of the locomotor and prehensile movements of the animals; (2) their perception of the nature of surfaces of different forms (flat, convex, concave); (3) their perception of the dimensions of a body or cavity; (4) their perception of the weight of a body. The general results of the large number of observations, which were made under natural and experimental conditions, are indicated in the following (No. 12, p. 626): "Eupagurus bernhardus is capable of perceiving by various means (touch, position, trial), the state of the surface of a shell, certain elements of its external form (degree of curvature, line of greatest slope etc.) and of its interior form (degree and direction of curvature, etc.), its dimensions, especially the interior dimension, and its weight.''

Just such detailed studies of the behavior of an animal, as the author has given us for the hermit crab, are of inestimable value for the furtherance of the science of organic activities, for they furnish the facts which enable us to undertake classification and generalization.

The papers of the second group I shall review only by title, in order to devote all available space to those of the third and fourth groups.

BOHN has done good service to his science in showing (No. 5, p. 2, *et seq.*), by an analysis of conditions which influence the movements of Convoluta, that stimulating factors must be studied in their relations to one another, and that at the same time, account must be taken of the physiological state of the organism, and of the conditions which have previously influenced its activities. As the author puts it, there are *causes actuelles et causes passées*, neither of which can be understood in its relations to the behavior of the animal without knowledge of the other. In Convoluta, for example, reactions to gravity change with sun and tide. As the tide rises the worm becomes positively geotropic and burrows into the sand thus finding protection from the waves. As the tide falls the reaction to gravity changes to negative and the worm comes to the surface of the sand to feed. This regular change in the sense of the response to gravity (surely we should not call it a response to gravity) has become habitual and persists even when the animal is placed beyond the reach of sun and tide.

Since it is impossible to state even the general results of all the author's investigations, I choose for special attention the memoir (No. 28), in which he has brought together the chief results of many of his briefer papers. It deals especially with the reactions of the molluscs, Littorina rudis, L. littorea and L. obtusata, and the annelid, Hedista diversicolor, to light and with the influence of other environmental factors on these reactions. To indicate the general nature of the author's studies with these animals, I quote the following translation of a portion of paper No. 25, which is in a sense a summary of the contents of the memoir.

"Upon the Boulogne coast, at the foot of dismantled rocks or dunes, there are found some large calcareous blocks which are reached by the sea only every five hours, during high tide; in the fissures and crevices which they present are lodged a multitude of small Littorinas (L. rudis). When the blocks are dry, during the periods of low water, these molluscs are retracted into their shells; during high tide under the influence of the beating of the waves, they emerge from their torpor and begin to wander over the wet rocks.

"If they are placed upon the sand, several meters from the rocks, the following curious facts may be observed: instead of moving in the direction of the sun's rays, in accordance with the classical theory of phototropism, the Littorinas move toward the rocks which are situated at a relatively considerable distance, and it is to the highest rock that all the paths lead. Leaving out of account irregularities in the surface of the ground, these paths are from the beginning parallel with one another, and perpendicular to the sombre vertical wall of rocks. In the vicinity of the lower rocks, however, the paths may undergo slight deviations toward the latter.

"This looks as if the Littorinas were attracted at the same time by the two rocks, and as if they followed the direction of the resultant of the two attractive forces.

"Replacing the rocks by screens of wood, cloth or paper, one obtains the same results. It is then the shapes of the shadows which are important here, not odors. In the presence of these facts one is almost infallibly led to attribute to the Littorinas all the elements of higher consciousness, and to recognize perception, will and feeling. Littorinas seem in fact to have visual perception of objects which surround them and to recognize rocks at some distance; they would thus be capable of directing their movements toward the rocks, knowing that they would find there a feeling of well-being. They would conduct themselves as do human beings."

For his experimental study of the influence of light on Littorina, BOHN used what he calls, the *révélateur*, because it reveals latent tendencies. This device was a parallel sided glass dish 30 x 15 cm., with two movable screens, one black, the other white, which could be placed in the dish as the experimenter desired.

The number of facts brought to light by the *révélateur*, facts which BOHN has seen fit to set forth in italics, each with a number of its own—is too great for the restatement of all of them in this review. Among the most important are the following: A black screen when placed parallel to the direction of the luminous field (the direction of increasing or decreasing intensity) attracts the animals slightly, *i. e.*, their path toward the light swerves toward the screen; a white screen slightly repels them. This attraction or repulsion depends upon the size, brightness and nearness of the screen. At any given point of a luminous field the direction of the field is only that of the resultant of all the attracting and repelling influences of the illuminated surfaces, especially of the largest and highest surfaces (No. 28, p. 28). From this it follows that objects about the animals, pebbles, rocks, etc., according as they are black or white, exercise an attracting or repelling influence, the strength of which depends upon their size and illumination.

The importance of these facts for theories of phototropism and for our conception of what has long been spoken of as response to the direction of light is obvious. The fact that the reactions to light in these animals are influenced by the size of the illuminated surfaces about them, as well as by the intensity of their illumination, suggests a promising direction for inquiry, and indicates that possibly the situation may not be completely describable in terms of the intensity of the light at a given point, or of the relative intensities of illumination of different portions of the organism. BOHN beautifully illustrates the equilibrium of forces by showing that when gravity and light act on the animals simultaneously and in partial opposition to one another the movements which occur are resultants of the influences of the two forces. Curiously enough, if the incination of the surface on which a littorina is moving be increased and the illumination diminished, the influence of the light becomes zero when the surface is vertical, and changes to a reaction of the opposite sign as the surface is moved on beyond the vertical (No. 28, p. 33).

In a glass tube covered at intervals with black rings, the molluscs move in ellipses within the illuminated regions, for the black regions alternately attract and repel them, as is obvious from the previous statement. As the author points out, the devious courses of the molluscs, often interpreted as food-seeking or other forms of voluntary movements, are describable in terms of just such relations of forces as those studied in this memoir. It is easy enough so to alter the relations of light and gravity, from moment to moment, that an animal under their influence moves in an irregular course, as if seeking something.

Of the variations in response to light in Littorina, there are irregular changes due to variations in the illumination or other factors which condition the influence of light, and regular, rhythmic changes due to the tidal conditions of the sea (hydration). Bohn has discovered that certain fluctuations in the light reactions of the three species of Littorina studied, are synchronous with the movements of the sea, while the amplitude of the fluctuations is proportional to the amount of hydration. Furthermore, there are two kinds of fluctuations in the response to light; one of great magnitude corresponding to the period of the great tides (about 14 days), the other of slight magnitude, corresponding to the daily tides (about 13 hours). The animals continue to exhibit rhythmic fluctuations in their reactions to light for months after being subjected to conditions of life in an aquarium, but the amount of the change progressively decreases.

As is stated early in the memoir, the three species of Littorina used, live at different levels on the shore. Those which live at a high level (L. rudis), and which therefore undergo prolonged and intense desiccation, habitually move, according to the direction of the luminous field, in the negative sense (negative phototaxis). Those of the low levels (L. obtusata,) which undergo only very brief and slight desiccation, habitually move in the positive sense. The change in the sense of the phototactic reaction corresponds, in the first case, to the period when the tide is highest, in the second case to the period of low water. The species of the middle level (L. littorea) show changes in reaction the more pronounced the greater the amount of desiccation. In all cases, when the animals are in an aquarium, toward the time of low water, the time at which desiccation occurs in nature, the direction of the luminous field undergoes a negative change that is to say, it inclines toward the black screen (No. 28 p. 54).

Aside from the importance of the many new facts which Bohn has discovered, it is evident that his work is of great value, in that it emphasizes strongly the necessity, in the study of the tropisms, of considering many factors rather than one alone, and of past influences as well as present influences. The behavior of Littorina in response to light can be understood only after a study of the habits and habitat of the various species, and of the influence of tides, moisture, temperature, gravity, etc.

The investigation of the reactions of Hedista has demonstrated that they exhibit oscillations in their responses to light much as do the Littorina. The direction of movement is determined in part by the relative intensities of the illumination of the two eyes. "When the Hedista have undergone desiccation, light brings about, through the eye and the nerves, muscular movements, and it results: (1) That the worms come to rest in the shadow (negative phototropism, or in Bohn's terminology, phototactisme négatif); (2) that they direct themselves toward the dark surfaces, the path therefore curving toward the side of lowest stimulation (negative phototaxis, phototaxie négatif). When the Hedista have undergone hydration, light inhibits muscular movements and the reactions are of the opposite sign (No. 28, p.63).

In Hedista "several systems of muscles may enter into an action and determine sinuous undulatory movements of different kinds. Sometimes lateral undulations of slight length and amplitude determine in the anterior region of the body, the balancing of the parapodia and consequently progress; sometimes other lateral undulations, in number from eight to two and of greater and greater amplitude, run from behind forward over the length of the body, and determine the swimming movement, if the amplitude be sufficiently great. Sometimes sagittal waves of medium length and amplitude, determine, if the annelid is in the sand, the circulation of the water.

"The light received by the eyes has a manifest influence upon these diverse undulatory movements. The suppression of the illumination of the whole of the eyes (obscurity, section of the head) brings about the supression of the lateral waves and the exaggeration of the sagittal ones, etc." (No. 25, p. 173).

Paper No. 31 is the author's second memoir relative to "phototactisme" and "phototropisme." It describes the results of experiments with crustacea. The trend of results may be gathered from the following summary statements. The phenomena of the tropisms are considerably more complex in the crustacea than in the worms and molluscs. The tropic (*tropiques*) actions of light are the results of a series of rotatory movements of several different kinds. All of these rotations are due to the influence of illuminated surfaces, and they can be easily determined by the use of black and white screens. The phenomena observed, in reality, depend upon the illumination of the surfaces of the eyes.

I wish now to call attention to BOHN's discussion of tropism theories and the bearing of his results on the same. After pointing out several inconsistencies in the orthodox theory, he gives a *critique* of JENNINGS' recent theory, mentions the sad confusion of terms and finally concludes that it is better worth our while to study the form and mechanism of reactions, than to discuss a terminology for what is very superficially known (No. 28, p.79, *et seq.*).

In their relation to our conception of the nature of phototropism, the following facts discovered by BOHN are of unquestionable importance: (1) In certain annelids and molluscs the light received by the eye exercises an excitory or inhibitory influence, according to the state of hydration of the animal, on the muscles of the same side of the body. (2) When an animal is subjected for a sufficiently long time to the influence of light, that influence gradually changes from excitation to inhibition; fatigue for light manifests itself. (3) While the light is still an excitant, a slight diminution in its intensity produces an arrest of locomotor activity. (4) Similarly, while the light is an excitant, a slight decrease in the illumination of one eye in relation to the other induces asymmetrical action of the muscles of the two sides of the body, and therefore a turning movement which results in bringing the eyes into regions of equal illumination (No. 28, p. 87).

These and similar facts indicate that JENNINGS' theory does not cover all phototropic reactions. JENNINGS argues, from the results of his studies of unicellular organisms, that in the tropisms, orientation is a secondary phenomenon, the result of movements which are determined by the structure and internal states of the organism, rather than by external conditions. The facts presented by Bohn make it apparent that there is more than one mode of orientation, and that no single theory at present accounts for all the observed facts. It is interesting to note that Bohn distinguishes two forms of reaction to light, and makes use of the terms *phototaxie* and *phototactisme* in the senses in which certain papers have used phototaxis and photopathy.

The chief value of the papers, which we have been discussing, is their stimulating influence. They are not thoroughly satisfactory scientifically; for they constantly suggest questions, doubts and new problems; yet just because of this, the reader leaves them with new interest in the problems of animal behavior and increased enthusiasm for investigation.

ROBERT M. YERKES.

LITERARY NOTICES.

Van Gehuchten, A. Le corps restiforme et les connexions bulbo-céréb.elleuses. *Le Névraxe*, Vol. 6, pp. 123-154. 1904.

VAN GEHUCHTEN concludes from a series of observations upon the corpus restiforme that it is composed exclusively of ascending fibers. The spinal component arises from the column of CLARKE. The bulbar portion consists of four groups of fibers: "(1) Des fibres olivo-cérébelleuses croisées. (2) Des fibres réticulo-cérébelleuses ventrales directes et croisées. (3) Des fibres réticulo-cérébelleuses dorsales directes et croisées. (4) Des fibres nucléo-cérébelleuses égelement directes et croisées." G. E. C.

Van Gehuchten, A. Contribution à l'étude des voies olfactives. *Le Névraxe*, Vol. 6, pp. 191-200. 1904.

All of the olfactory neurones of the second order send their axones into the t. olfactorius lateralis. Only neurones of the third order are associated with the anterior commissure. These connect the olfactory lobe of one side with the olfactory bulb of the other side, and, therefore, do not form a true commissure. The paper includes a review of literature and a report of degeneration experiments by the author upon the olfactory bulb of the rabbit. G. E. C.

Van Gehuchten, A. Boutons terminaux et réseau péricellulaire. *Le Névraxe*, Vol. 6, pp. 217-234. 1904.

This paper is chiefly a critical review of recent observations by HELD, AUERBACH, DONAGGIO, BETHE and CAJAL. From his own observations VAN GEHUCHTEN agrees with CAJAL that the nerve terminals end upon the cell by irregularly shaped expansions. The pericellular net is formed of axone terminals

G. E. C.

Soukhanoff, Serge. Contribution a l'étude de l'aspect externe des prolongements protoplasmatiques des cellules nerveuses colorés par le bleu de méthylène. *Le Névraxe*, Vol. 6, pp.117-122. 1904.

By the application of this method numerous gemmules are found upon the nerve cells of the cerebellum, nucleus caudatus and spinal cord. G. E. C.

Michotte, Albert. La fibre nerveuse et sa bifurcation dans les ganglions (méthode de CAJAL). *Le Névraxe*, Vol. 6, pp. 201-216. 1904.

With the exceptionally clear preparations which the method of CAJAL gives the author fails to find any fibrillæ passing from one branch of the bifurcating fiber directly to the other branch. Nor does he find any anastomoses of fibrillæ at this point. The fibrillæ all pass into the cell body. MICHOTE believes, therefore, that the spinal ganglion cell is functionally concerned in conduction, and that the neurofibrillæ are the conducting elements of the nerve. G. E. C.

Unger, Ludwig. Untersuchungen über die Morphologie und Faserung des Reptiliengehirns. I. Bericht. Das Vorderhirn des Gecko. *Aus den Sitzungsberichten der kaiserl. Akademie der Wissenschaften in Wien*, Vol. 113, pp. 141-159. 1904.

The observation of the following structures is considered by the author of especial importance: a non-medullated commissura septæ, a fasciculus corticoolfactorius, a fasciculus septo-parolfactorius, and the distribution of fibers from the psalterium to the cortical region over the ammons horn. G. E. C.

Panegrossi, Giuseppe. Weiterer Beitrag zum Studium der Augenmuskelnervenkerne. *Monatsschrift für Psychiatrie u. Neurologie,* Vol. 16, pp. 268-281, 344-376.

Detailed separate studies of Cyanocephalus, Macacus (three specimens), dog, cat and sheep, followed by a comparative review of these types.

G. E. C.

Dräseke, F. Zur Kenntnis des Ruckenmarks und der Pyramidenbahnen von Talpa europaea. *Monatsschrift für Psychiatrie u. Neurologie,* Vol. 15, pp. 401-409. 1904.

The very small pyramidal tract becomes nonmedullated for a long distance into the spinal cord and appears in cross section as an oval area of gray. On this account it is not possible to demonstrate positively the decussation of the pyramidal tracts. G. E. C.

Child, C. M. Studies in Regulation. VI. The Relation Between the Central Nervous System and Regulation in Leptoplana: Anterior and Lateral Regeneration. *Jour. Experimental Zoölogy,* Vol. 1, pp. 513-557. 1904.

"The influence of the ganglia on anterior or lateral regeneration in the head region is qualitative as well as quantitative." G. E. C.

Bovard, John F. The Distribution of the Sense Organs in Microscolex elegans. *University of California Publications,* Vol. 1, pp. 269-282. 1904.

The distribution of the organs is adaptive, and the sensitiveness of a given region as expressed by the time reaction is correlated with the number of sense organs in the region. Some of the organs seem to be in a degree gustatory.

G. E. C.

Michotte, Albert. Contribution à l'étude de l'histologie fine de la cellule nerveuse. *Le Névraxe,* Vol. 6, pp. 235-278. 1904.

A study by the silver nitrate method of CAJAL and SIMARRO. Cells of the spinal cord and ganglia, cerebral cortex, olfactory centers and retina are described and figured in considerable detail. In all types of these cells a net is found, and in some is added a system of fibrils which enter the perikaryon from the processes. These fibrils, however, are considered continuous with the net and not continuous from one cell to another. G. E. C.

Rossi, E. L'intima stuttura delle cellule nervose umane *Le Névraxe,* Vol. 6, pp. 329-349. 1904.

A study of the cells of the spinal cord and ganglia, cerebellum and cerebral cortex by a gold chlorid method which brings into view a very dense reticulum throughout the cytoplasm and a pericellular net. G. E. C.

Tricomi-Allegra, Giuseppe. I calici di Held nei centri acustici. *Le Névraxe,* Vol. 6, pp. 157-188. 1904.

A study of the special nervous arborizations which are found to occur alike in the nucleus corpus trapezoideus and in the nucleus acusticus anterior. Illustrated with 49 figures by the GOLGI method. G. E. C.

Cabibbe, G. Histologische Untersuchungen über die Nervenedigungen in den Sehnen und im Perimysium der Ratte und des Meerschweinchens. *Monatss. für Psychiatrie u. Neuorologie*, Vol. 15, pp. 81-89. 1904.

Pacinian corpuscles are found in very intimate relation with the Golgi corpuscles. G. E. C.

Bernheimer. Ueber Ursprung und Verlauf des Nervus oculomotorius im Mittelhirn. *Monatss. für Psychatrie u. Neurologie*, Vol. 15, pp. 151-153. 1904.

A reply to criticism by MAJANO upon certain of the author's experiments. G. E. C.

Braus, Hermann. Experimentelle Beiträge zur Frage nach der Entwickelung peripherer Nerven. *Anat. Anz.*, Vol. 26, pp. 433-479. 1905.

Transplanted fundaments of limbs have the power of developing nerves *in situ*. This power is ascribed to the presence of "Etwas" which must antedate the axone process of HIS and the cells of SCHWANN, and which probably correspond to the embryonic intercellular bridges of KERR in Lepidosiren. The neuromuscular connection may be secondary but is more probably primary, subject to peculiar regulating influences. The conclusions are of special interest since they are essentially opposed to HARRISON's recent and convincing presentation of the same subject. G. E. C.

Kolmer, Walther. Ueber das Verhalten der Neurofibrillen an der Peripherie. *Anat. Anz.*, Vol. 26, pp. 560-570. 1905.

Perinuclear nets of neurofibrils are found in the sense-cells of certain worms, fishes and amphibians. G. E. C.

Dogiel, A. S. Der fibrillare Bau der Nervenendapparate in der Haut des Menschen und der Saugetiere und die Neuronentheorie. *Anat. Anz.*, Vol. 27, pp. 97-118. 1905.

The various types of cutaneous sensory endings are found to consist of a perifibrillar net embedded in a perifibrillar substance. There are two categories of nerve cells: (1) Typical neurones, which are anatomically distinct from all others; (2) neurones in colonies, the members of which anastomose by their dendrites and are identical in their development, structure and function. Neurofibrillæ are differentiated elements of the protoplasm and are not found outside the nerve cell. The fibrillæ of the first category of cells do not pass beyond the boundaries of a single cell, but among the cells of the second type they pass from one cell to another through the anastomosing dendrites. But this occurs only within the neurone colony, the members of which are a unit in function. Hence, the author claims, the findings are not contrary to the fundamental principles of the neurone theory. G. E. C.

Wallenberg, Adolf. Sekundäre Bahnen aus dem frontalen sensibeln Trigeminuskerne des Kaninchens. *Anat. Anz.*, Vol. 26, pp. 145-155. 1905.

There is a dorsal tract of large fibers which connects with both motor nuclei of the trigeminus, both midbrain trigeminal nuclei, both nuclei of the oculomotorius and the nuclei of the formatio reticularis. There is also found a ventral tract of very small fibers which enters the opposite medial lemniscus and ends in the ventral nuclei of the thalamus. G. E. C.

Takasu, K. Zur Entwickelung der Ganglienzellen der Kleinhirnrinde des Schweines. *Anat. Anz.* Vol. 26, pp. 225-232. 1905.

The author establishes the time of appearance and the relative development at different ages, of the various types of cells and of the medullated fibers.

G. E. C.

Borchert, Max. Ueber eine bisher unbekannte Gesetzmässigkeit im Zentralnervensystem von Torpedo. *Anat. Anz.*, Vol. 26 pp. 289-292. 1905.

In those cranial nerves which have a more cephalic and a more caudal root the former passes out to its destination ventrally of the latter. In this respect the roots of the electric nerves and vagus roots would appear to be parts of one and the same nerve. G. E. C.

Fischer, Johannes. Ueber den Bau der Nerven des sympathischen Nervensystems. *Anat. Anz.*, Vol. 26, pp. 388-399. 1905.

From a study of the sympathetic nervous system of the cat, particularly, an attempt is made to classify the sympathetic fibers according to the size of the fibers and the thickness of the sheath. Four types are distinguished, and a tabulated record is given of the occurrence and frequency of the various types in different parts of the system. G. E. C.

Zuckerkandl, E. Die Riechstrahlung. *Arbeiten aus dem Neurologischen Institute an der Wiener Universität*, Vol. 11, pp. 1-28. 1904.

A comparative study of the medial olfactory tract with special reference to the fornix longus in its relation to the fibræ perforantes corpus callosi et psalterii. The fornix longus of authors is only a part of a system which includes the fibræ perforantes corpus callosi and the whole psalterium. The integrity of this system may best be seen in those brains which have a wide splenial angle.

G. E. C.

Hatschek, Rud. Bemerkungen über das ventrale Haubenfeld, die mediale Schleife und den Aufbau der Brucke. *Arbeiten aus dem Neurologischen Institute an der Wiener Universität*, Vol. 11, pp. 128-156. 1904.

A thorough comparative discussion of this part of the mammalian brain. Some attempt is made, also, to correlate the structural peculiarities of the region with certain characteristic activities in various types. G. E. C.

Karplus, J. P. Bemerkungen über die grauen Massen im Funiculus cuneatus der menschlichen Medulla oblongata. *Arbeiten aus dem Neurologischen Institute an der Wiener Universität*, Vol. 11, pp. 171-183. 1904.

Eighteen original figures in the text, with descriptions, are presented to demonstrate the author's main thesis, that areas of substantia gelatinosa Rolandi, frequently mistaken for the nucleus lateralis funiculi cuneati, are distributed through the funiculus cuneatus: a condition which has been overlooked by numerous leading authors. G. E. C.

Yale Psychological Studies, edited by Charles H. Judd: Monograph Supplement of *The Psychological Review*, Vol. VII, No. 1, March, 1905, 226 pp.

The first of these eight studies describes a new and ingenious means of photographing movements of the eye. A thin layer of Chinese white is treated on both sides with paraffin, and then cut into small squares about 1 mm. across. Such a square laid on the sclera just below and nasally from the cornea, keeps its place on the eye-ball and is readily photographed. The merits of this method are that the white fleck is so insignificant that it occasions no abnormalities in the movements of the eye, and it gives a more easily interpretable record than a reflected image from the cornea can give. The movements of such a reflected image are unlike and very much less than the movements of the eye. So harmless is the square of Chinese white that, a few seconds after application, the subject forgets its presence. The eye-movements were photographed by a cinematographic camera that could be operated at various speeds, the periods of closure and exposure being equal. Each exposure, along with a time-curve, could be recorded on a drum. An exposure of 60 σ was usually found convenient.

The following four papers by Prof. Judd, Dr. Cloyd N. McAllister, Mr. E. H. Cameron, Mr. W. M. Steele, and Mr. Henry C. Courten, respectively, give the results of a photographic study of eye-movements made during the contemplation of simple figures and of three "geometrical-optical" illusions. There seems to be no rigid fixation by the eye. "The image of a point fixated . . . may fall upon any point of a considerable area of the retina, around about, and including the *fovea centralis*." In short the eye perpetually wobbles; and it is only by chance that in successive instants of rest retinal elements once stimulated are stimulated a second time. When the eye changes its fixation from one part of the field of vision to another, the movement is seldom twice alike either in its exact direction or in the number of intermediate pauses made. The movements of the two eyes are only roughly coördinated; one eye, for instance, may pause while the other moves on. The movements during attempted fixation reveal no coördination.

The movements made by the eye in surveying the illusions, are of less interest in this place, particularly since their relation to the illusion as perceived is not yet certain. The surprising incompleteness of the binocular coördination was shown in all the experiments.

The fifth paper studies unintentional movements made by the hand in reacting. If a subject presses on a key and awaits a signal to release the same, he will often, when the signal comes, press down still harder for a moment before he releases. Mr. W. G. Smith has called this an "antagonistic reaction." By means of a special reaction-key too complicated to be here described, the authors studied both the up and down tensions of a finger while pressing on the key and reacting to a signal. A preparatory warning signal was given, and both before and after this a wavy line was usually traced by the finger. "In the wavy form we see a rhythmical balance maintained between the tendency to react and its antagonistic." In the "antagonistic reaction" nervous energy seems to be contributed to this latter tendency that should be expended in the opposite direction—the release-movement. This antagonistic reaction seems due entirely to the steady, downward pressure excited previous to the reaction, for it largely disappears when a gentle upward pressure preceded the final upward reaction. The antagonistic reaction is always a disturbance, especially because it produces a large variability, and can be avoided by the use of a key in which the reaction is a pressure downward, preceded by no tension or by a slight downward one. In the paper other interesting features of the tensions preceding reaction are discussed.

In the seventh paper Professor JUDD reports some experiments on practise without knowledge, by the subject, of the results. Practice does not tend to eliminate errors unless the subject knows what mistakes he is making.

The last paper, by Professor JUDD is an interpretation of the experiments on eye-movement and illusion, and a theoretical discussion of the relation of movement to consciousness. He discards the sensation of movement explanation of geometrical illusions, and advocates a theory of sensory-motor equilibria and disturbances thereof, very similar to the "vital series" of AVENARIUS. Sensation and perception do not, according to this, depend on sensory currents alone, but on the sensory and motor processes together. Professor JUDD has renounced the sensation school and joined what is admittedly a new and growing movement.

E. B. H.

Beebe, C. William. Some Notes on the Psychology of Birds.[1] Abstr. *Proc Linn. Soc. N. Y.*, Nos. 15, 16, pp. 40-47. 1904.

Objection is made to attempts to ascribe too much in the behavior of birds to *instinct*, the author maintaining that "Even a superficial study of the psychology of birds compels us to attribute to them a highly developed intellectual and emotional life." Special point is made of birds' "memories," of the "sympathy" they exhibit, their "language," or means of conveying emotions by voice and manner, and of their "individuality." It is stated that "birds show us examples of revenge being taken after long and patient waiting for a favorable opportunity," and that "crows have been known again and again to sit in judgment upon one of their number, and to sentence and punish it with death"; but the facts upon which these conclusions are based are not stated. As evidence against current views of sexual selection two instances are cited where it was not the most showy and pugnacious males that succeeded in winning and mating with the female bird. Interesting notes are added upon the behavior of wild birds that visit the New York Zoölogical Park, for which a high order of intelligence is attributed to them. Mr. BEEBE has apparently improved his excellent opportunities as curator of the birds at the Park to make many valuable observations on their habits, and it is to be hoped that he will sometime set them forth in a fuller and more complete form which will enable his readers to make impartial judgments of their own upon the amount of "intelligence" implicated in them. L. J. C.

Lydell, Dwight. The Habits and Culture of the Black Bass. *U. S. Fish Com. Bull. for* 1902, pp. 39-44, pl. 8. 1904. (This paper was also published, with minor differences and more illustrations, in *Trans. 31st Ann. Meeting Am. Fisheries Soc.*, 1902, pp. 45-57.

Mr. LYDELL, who has had an extensive experience in their practical manipulation, gives in this paper a concise account of the habits—especially the breeding habits—and the culture of the black bass. The former will be of most interest to readers of this *Journal*. It is found that the nest is built by the male fish alone—

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[1] Revised and rewritten since first published in the Seventh Annual Report of the N. Y. Zoölogical Society, for the year 1902.

taking four to forty-eight hours—and as soon as it is completed he goes into deep water and returns with a female. He appears to coax and drive her to the nest, and then drives her away after she has spawned. The actions during spawning are described in considerable detail. The male guards the eggs until they hatch—requiring five days at ordinary temperature—and stays by the young until they disperse. The breeding habits of the large-mouthed and small-mouthed black bass are compared

In the part dealing with their culture notes are given on the method of feeding, handling and caring for the fish that have been successfully employed at the Mill Creek, Mich., station. L. J. C.

Smith, Hugh M., and Harron, L. G. Breeding Habits of the Yellow Cat-fish. *U. S. Fish Com. Bull. for 1902*, pp. 149-154. 1904.

This paper, though short, gives some very interesting and important notes on the breeding of some yellow cat-fish (Ameiurus nebulosus) in the Bureau of Fisheries aquaria at Washington. The method of nest-building and caring for the eggs and young corresponds in a general way to that of the bass and the fresh water dogfish (Amia calva), but also differs in several important details. Thus both parents participate in the construction and care of the nest, and the eggs and young fry are often cleaned by being drawn into the mouth and then expelled. It was found that as the young grew older they were not always liberated again, "the feeding instinct becoming paramount to the parental instinct."

L. J. C.

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THE CRANIAL NERVES OF TRITON TÆNIATUS.

BY

G. E. COGHILL.

(*Contribution from the Laboratory of Pacific University.*)

The studies which have led up to the results which are presented in this paper were undertaken for the purpose of comparing the cranial nerves of Triton with those of Amblystoma, which I have already described ('02), and with a view to examining the position which DRÜNER ('01) has taken with reference to certain nerves of the Urodela. Rather than make the comparison with Amblystoma point by point throughout the cranial nervous system, I have introduced only those features which seem to me of morphological significance. In the case of the eye-muscle nerves I have gone into greater detail because DRÜNER has not included these nerves in his descriptions, which, with the possible exception of his "N. cutaneus retrocurrens IX," must be accepted as accurate so far as general topography is concerned. It is only with reference to the components of certain of the nerves that my observations conflict with his.

The heads of Triton tæniatus upon which my observations have been made were given to me by Professor TH. BOVERI, during a brief period in which I enjoyed the hospitality of his laboratory in Würzburg, and I would here express my keen appreciation of the courtesy which he extended to me at that time.

The heads studied were of adults. They were treated with FLEMMING's stronger chromic-acetic-osmic solution till decalcified. They were cut into serial sections in the three conventional planes. Those of the transverse and sagittal planes were most useful. Although the transverse series are better for the study of the peripheral distribution of the nerves, the sagittal series are indispensable for the study of the roots and ganglia, especially of the ninth and tenth nerves. The sections were stained in Weigert's hæmatoxylin after mordanting with one-half saturate solution copper acetate.

THE OLFACTORY NERVE.

My studies of the description of the olfactory nerve of Triton by Burckhardt ('91) led me to expect a sharp division of the root of this nerve into two fascicles. My serial sections have disappointed me, however, in this, for I find the two divisions of the nerve quite as obscure in their relations in Triton as they are in Amblystoma.

In several of my series of sections of Triton tæniatus it is impossible for me to follow that division of the olfactory nerve which innervates Jacobson's organ to its destination in the olfactory glomeruli and distinguish it sharply from the remainder of the olfactory nerve; but in two of my series it is clear that the branch of the nerve which arises in Jacobson's organ forms the most ventral portion of the olfactory nerve and enters the brain further caudad than the rest of the nerve, and in one case it forms a distinct fasciculus of fibers which is more separated from the rest of the nerve in its proximal part than it is farther out.

It would seem, therefore, that Triton and Amblystoma are essentially alike in respect to the arrangement and distribution of the olfactory nerve.

THE EYE-MUSCLE NERVES.

1. *N. Oculomotorius.*—In its ultimate distribution the oculomotorius of Triton is exactly as in Amblystoma: a r. superior innervates m. rectus superior and a r. inferior innervates m. rectus internus, m. rectus inferior, and m. obliquus inferior. In its position relative to other parts, however, the nerve of Triton is peculiar in this respect, that the r. superior passes ventrally of the r. ophthalmicus profundus V, while in Amblystoma it passes on the dorsal side of this nerve. This is true in every case excepting one. In this exception the r. superior divides upon leaving its foramen. The more ventral division holds the position which the entire nerve regularly takes, while the more dorsal division passes dorsad on the mesial side of the r. ophthalmicus profundus

and enters the m. rectus superior. But in this case, which occurs only on the one side of this specimen, the r. ophthalmicus profundus penetrates the m. rectus superior, whereas it usually passes dorsal of this muscle. This peculiarity of the ophthalmicus in this case no doubt explains the exceptional behavior of the r. superior III.

The r. inferior is less constant than the r. superior in its position relative to the muscles. It is quite as variable in this respect in Triton as in Amblystoma. In Triton the nerve usually passes caudal or ventral of muscle rectus inferior to arrive at the other two muscles. Frequently, however, the r. inferior is penetrated by the proximal portion of the m. rectus inferior and rectus internus.

As compared with the third nerve of Amblystoma, that of Triton requires special notice, also, with reference to the distribution of nerve cells upon it. The occurrence of these ganglion cells can not be adequately treated, however, without first considering two other important relations of the oculomotor nerve of Triton, viz: the branch of the oculomotor to the interior of the eye, and the anastomosis of the r. inferior III with a branch of the r. ophthalmicus profundus V.

The oculomotor branch to the interior of the eye comes off the main nerve in or near its foramen. It follows the general direction of the optic nerve and is partially enveloped in the posterior border of the connective tissue sheath of the optic nerve. It is a very small nerve and its fibers are only faintly medullated till they reach the eye, where they lose their medullary sheaths entirely. After penetrating the sclera the nerve can be traced a long distance around the posterior border of the choroid. In a close study of three specimens I have found no important variation in these relations.

The anastomosing branch from the profundus usually arises from the main nerve as the latter crosses the oculomotorius. It then turns directly ventrad and joins the r. inferior III. In case the r. superior III arises farther centrally than usual, the communicating nerve has been seen to turn a very short distance centrad on the r. superior and enter the r. inferior. In other cases the communicating nerve arises near the Gasserian ganglion. It then becomes a nerve of considerable length, and resembles the corresponding nerve of Amblystoma.

While this communicating filament between the oculomotorius and the trigeminus appears superficially to be wholly different from anything found in Amblystoma, it actually corresponds to the twig of the profundus which, in Amblystoma, comes in contact with the oculomotorius only after the latter has reached the m. rectus inferior, or which, in some instances, passes independently into the eye under the insertion of the muscle r. inferior without coming in touch with the oculomotorius. At a similar point in Triton a division of the r. inferior passes into the eye. The real difference, then, between Triton and Amblystoma in this respect is that the inferior ciliary branch of the profundus is more closely fused with the oculomotorius in Triton.

Now the ganglion cells in question occur on both the communicating branch from the profundus and the branch of the oculomotorius to the interior of the eye, and at various points along the main branches of the oculomotorius. They are found upon the r. ophthalmicus profundus at the origin of the communicating branch, upon the latter between the two main nerves, or on the r. inferior III just after it has received the communicating branch. Of these three positions the last has cells most commonly and in greatest numbers. Only in one case have I found cells on the r. superior III. Commonly there is a cluster of cells in comparatively large numbers at or near the point of branching of the r. inferior III to form its three terminal rami to the muscles. In one specimen, however, no cells occur in this position on one side, while on the other side they are found here in considerable numbers. Cells are found, also, in varying numbers on the distinct rami to the m. rectus inferior, rectus internus, and obliquus inferior. Frequently nerve cells are found embedded in these muscles and in close relation with medullated fibers of the oculomotorius. In these cases, however, I have not been able to demonstrate that these cells give rise to the medullated fibers near them. Occasionally nerve cells are found even in isolated positions between the eye-muscles, but apparently connected more or less distinctly with one of the rami of the oculomotorius.

The occurrence of ganglion cells upon the distinct branch of the oculomotor to the eye is subject to wide variation. In one specimen examined there is a distinct cluster of ganglion cells upon this nerve and a very small connective between it and the main ramus inferior of the oculomotorius. In another instance nerve cells occur on a connecting filament between the two nerves. Ordinarily, however, there are no ganglion cells found on this nerve. In all probability the cells which occur here belong to the few fibers which in those instances connect the two divisions of the third nerve, and do not contribute to the essential composition of the nerve to the eye.

The most natural interpretation of these nerve cells is that they belong to the sympathetic system, and that they represent the ciliary ganglion. But it is very improbable that many of them have any connection with the ciliary nerves, for, as noted above, they are frequently found isolated from the main nerves, or embedded singly or in small groups in the muscles, or even on the nerve to the rectus internus, from which nerve there is no visible connection with the eye. If, then, they belong to the sympathetic system they must be vasomotor cells. But that there should be such an abundance of vasomotor cells in this region in Triton is exceedingly improbable.

If these cells are not sympathetic cells, it remains only to interpret them as muscle-sensory cells. This is, perhaps, a hazardous suggestion, for it would necessitate the presence of afferent fibers in the oculomotor root, which ranks with the ventral spinal roots as purely motor. But in my paper on Amblystoma I have described a ganglion on the root of the first spinal nerve which has no dorsal root, and, so far as I have been able to determine, it has no fibers which reach the skin. I have considered this latter as a vestigial spinal ganglion, since it does not occur in all specimens. Yet there is no proof that it is functionless. In T. tæniatus, on the other hand, nerve cells occur on the oculomotorius of every specimen which has come under my observation. They are much more numerous, also, than similar cells are on the oculomotorius of larval Amblystoma, and since they are constant in occurrence they must be of physiological significance.

But whatever the significance of these cells may be, it is noteworthy that, provided the muscle-sensory fibers of these amphibians are medullated, the mm. rectus internus and obliquus inferior of Amblystoma, and in some instances the mm. recti superior and inferior also, are completely cut off from sensory innervation unless there are afferent fibers in the oculomotor root. The same is true of the mm. rectus internus and obliquus inferior in some specimens of Triton.

However, that the nerve cells upon the oculomotorius of Triton and Amblystoma may be the source of sensory innervation of the eye-muscles is merely a suggestion. Further work which I have in progress may contribute something more positive upon the question.

2. *N. Trochlearis.*—The proximal, intracranial part of the trochlearis is pressed down very closely upon the surface of the brain, underneath or in the meninges, and is, for this reason, so obscure that it might easily be overlooked in good dissections. It passes out of the cranium either as a single nerve or in two divisions. The latter condition, however, is probably rare, and when it does occur the two divisions of the nerve fuse again before they reach the m. obliquus superior, which the trochlearis innervates.

As in Amblystoma, the trochlearis always comes in close relation with a branch of the ophthalmicus profundus. While it is impossible to demonstrate any profundus fibers passing into the trochlearis at this point, it is impossible also to assert that there is not such an interchange of fibers. If the m. obliquus superior has any sensory innervation this connection of the trochlearis would seem to be the only possible course for the afferent fibers to enter the profundus. In comparing this trochlearis-profundus connection with the oculomotorius-profundus connections, it is interesting to note that there have been no nerve cells found upon the trochlearis.

3. *N. Abducens.*—This nerve innervates the usual muscles, rectus externus and retractor bulbi. That either of these muscles ever receives any motor innervation from the fifth nerve is made extremely improbable by the fact that in some instances the sixth nerve does not touch the fifth at any point. In other cases, however, the sixth mingles with the ganglion cells of the profundus ganglion so that the relation between the two nerves is very obscure. In still other instances, a ganglionated branch of the profundus, just beyond the ganglion, is observed to join the sixth nerve. In one case of this kind, however, there seems to be a passage of fibers from the sixth into the third nerve, and in this particular instance the usual connective between the profundus and the oculomotorius is wanting. This connective between the sixth and fifth may, therefore, be only the commissure to the third nerve. Yet in other cases, when no such connection with the third nerve can be made out, there are ganglion cells on the sixth

nerve. I see no reason why these may not be muscle-sensory cells which have passed out from the profundus ganglion to the motor nerve. Yet such cells are found upon the sixth nerve when it has no connection with the ganglion or any branch of the fifth.

THE FIFTH AND SEVENTH NERVES.

There is no noteworthy difference, so far as my observations go, between Amblystoma and Triton with respect to the roots and ganglia of the fifth and seventh nerves. With respect to certain of the rami, however, there are some peculiarities which demand notice.

1. The Ramus Ophthalmicus Profundus V.—The most conspicuous peculiarity of this nerve is that it passes on the dorsal side of the m. rectus superior and the r. superior III. It passes ventrally of these structures in Amblystoma.

In the arrangement of the smaller branches of this nerve there are peculiarities which are apparently due to the general topography of the head, but they do not affect the ultimate distribution, which can not be distinguished from that of Amblystoma. The peculiarity of the inferior ciliary nerve has been noticed in connection with the r. inferior III. The superior ciliary, as in Amblystoma, in some cases comes in close relation with the r. superior III, and penetrates the muscle rectus superior, while in other cases it comes in touch with neither this nerve nor the muscle, excepting under the insertion of the latter, where it penetrates the sclera to the interior of the eye.

The terminal branches of the profundus differ from those of Amblystoma only in unimportant details which are probably incident to skeletal peculiarities. The relation between the ventral terminal branch and the palatinus VII is obscure unless the sections are cut in exactly the right plane, and even then it requires close study to determine the exact conditions. It is clear enough that a large bundle of profundus fibers passes through the palatine ganglion and unites with fibers from r. palatinus VII. The resulting nerve continues cephalad on the mesial side of the internal nares. Some of its fibers seem to terminate in the ventral portion of the nasal epithelium and the nerve lies for the most part within the nasal chamber and is intimately associated with branches of the olfactory nerve at different points. Several small branches pass ventrad through foramina in the floor of the nasal chamber, and branch out to the oral epithelium. Some of these twigs reach the vicinity of the gums. Whether they connect with the teeth or with taste buds that occur very near them is not clear. The lateral division of the ventral ophthalmic branch is much more difficult to trace. Nevertheless my preparations have enabled me to determine conclusively that the branch of the palatine which passes laterad around the caudal border of the internal nares is accompanied by profundus fibers. This relation is not clear in all cases, but enough cases are clear to convince me that the apparent exceptions are due to the complexity of the anastomosis and the direction of the plane of section. In at least two of my specimens the lateral branch of the palatine connects, also, with a division of the lateral terminal branch of the profundus. In these particular cases, however, it is impossible to trace any fibers from the ventral terminal branch of the profundus into the lateral palatine branch.

With these exceptions Triton and Amblystoma seem to agree exactly with respect to the relations of the r. palatinus VII and r. ophthalmicus profundus V. A peculiar relation of the r. buccalis VII to these nerves in Triton will be described in connection with the buccal nerve.

2. *The Truncus Infraorbitalis.*—The only feature of this division of the trigeminus which demands special notice is the relation of the so-called r. maxillaris V and the r. buccalis VII to one another and to the r. palatinus VII.

The term *maxillaris*, as applied to the general cutaneous branch of the trigeminus which passes beneath the eye in the upper jaw of Urodeles, is used here with the qualification that it is not to be considered the homologue of the r. maxillaris superior of Anura. My reasons for this interpretation have been given in my earlier papers ('01, '02), and some further consideration of it will be offered in the general discussion which follows the descriptive part of this communication.

These nerves, in their proximal region, are best studied in sections cut parallel to the sagittal plane. In some instances the buccalis is purely lateralis, and the maxillaris is purely general cutaneous as far as their point of flexure cephalad. Here the nerves cross each other in such an intricate manner that it has been impossible for me to assure myself that beyond this point either nerve is made up of one component exclusively. But it is certain that if the r. buccalis receives general cutaneous fibers at any point, the number of such fibers is exceedingly small. The r. buccalis is always composed of uniformly large fibers, which are characteristic of the acustico-lateralis system. Also, if lateralis fibers occur in the r. maxillaris, they are very few and of irregular occurrence.

These two nerves do not differ in any important feature from the corresponding nerves of Amblystoma till they reach the level of the cephalic border of the eye. Here, or in some cases considerably farther cephalad, the r. maxillaris passes through the maxillary bone and passes outward and downward into the upper lip; while the r. buccalis, ordinarily lying farther mesad, sends a slender filament mesad, which penetrates the cartilaginous wall of the nasal capsule and, passing around the caudal border of the nasal epithelium and the internal nares, joins the mesial branch of the ophthalmico-palatine nerve. This communicating nerve is sometimes fused with the lateral terminal branch of the palatine, but in some instances it is wholly separated from this nerve and from the palatine ganglion also, and joins the nerve from this ganglion only after passing a considerable distance cephalad mesially of the internal nares.

On one side of one of my specimens the nerve in question arises from the r. maxillaris. Yet, since in this one exception, because of the intimate relation of the r. maxillaris with the r. buccalis, it is possible that lateralis fibers are carried out with the r. maxillaris, the natural inference is that this communicating nerve belongs to the acustico-lateralis system. This interpretation is further borne out by the fact that the terminal twig of the palatine nerve, with which this nerve unites, after traversing the whole length of the nasal chamber ventrally of the nasal epithelium, passes through the cephalic wall of the capsule and through the premaxillary bone and terminates in the lateral line organs at the very tip of the snout.

Just outside the foramen in the premaxillary bone this terminal filament of the palatine crosses a branch of the mesial terminal ramus of the ophthalmicus profundus which carries general cutaneous fibers from the adjacent region. Since the latter nerve does not at any point come into close relation with the acustico-lateralis system of fibers, and since no lateralis fibers from any other source can be traced into the vicinity of the lateral line organs in question, the communicating nerve from the r. buccalis to the palatine must be the only path by which lateralis fibers can reach these organs. This is strong indirect evidence to show that the communicating nerve carries lateralis fibers, but it does not prove that it is exclusively lateralis in composition. The possibility remains that it is composed partly of general cutaneous fibers. However, it would not seem reasonable for general cutaneous fibers to travel this round-about road to a region which is already, by most direct route, profusely supplied with general cutaneous innervation by the mesial terminal ramus of the ophthalmicus profundus. Both indirect and direct evidence, therefore, is very strong to prove that the communicating nerve between the r. buccalis and the palatine nerve belongs to the acustico-lateralis system.

3. The Communis Component of the Facial.—Beyond the descriptions of the terminal branches of the r. palatinus, already given, there is nothing particularly noteworthy regarding this nerve in Triton as compared with Amblystoma. It arises from the cephalic portion of the geniculate ganglion, from which the fibers of the r. alveolaris pass directly laterad with the hyomandibular trunk. The nerve called palatinus caudalis in Amblystoma occurs also in Triton. It varies considerably in its point of origin, sometimes coming out of the ganglion almost at the base of the r. palatinus, sometimes about half way through the facial canal leaving the hyomandibular trunk through a special foramen. In one case it seemed to be represented by fibers which leave the communis component of the hyomandibular just outside of the facial canal. My preparations show conclusively that this is a communis nerve from the geniculate ganglion, and that it anastomoses with a nerve of about the same dimensions from the glossopharyngeus. The fibers of the two nerves pass cephalad together from the point of anastomosis. They can be traced cephalad in the roof of the mouth as far as the central level of the eye. This is the true JACOBSON's anastomosis, and should not be confused with the other connective between the vagus and facial.

There is one peculiarity of the r. alveolaris: It receives no fibers from the glossopharyngeus, such as were described in Amblystoma. There is a large branch of constant occurrence which arises near the angle of the jaw and turns mesad to the epithelium between the hyoid and mandibular arch.

THE NINTH AND TENTH NERVES.

1. The Roots and Ganglia.—As to general morphology DRÜNER has correctly described the ganglia of the glossopharyngeus and vagus and the nerve trunks which arise from them. The composition of the roots and trunks of these nerves, however, demands some further definition.

The roots which correspond to my second, third and fourth vagus roots of Amblystoma are variable in their arrangement relative to each other, but always exhibit more compactness than in larval Amblystoma—a peculiarity due, no doubt, to the adult condition and of no morphological significance. But in my specimens which show the origin of the roots most clearly one fact of importance is clear: There are no motor axones in the general cutaneous root of the vagus. This can not be stated as a universal condition, but it is certainly true in some indviduals, while no positive exceptions have come under my observation. This would appear at first thought to be essentially different from the condition described for Amblystoma ('02, Plate I, X 3), but in all probability the motor axones figured in my third vagus root of Amblystoma belong to the fourth root, as was stated in my original description ('02, p. 234). This being true, the general cutaneous root of Triton and Amblystoma alike would be unaccompanied by motor axones.

In composition, the nerves which arise from the IX-X ganglionic complex of Triton correspond exactly with those of Amblystoma. This can be positively stated for all but the motor components, which can be differentiated from the sensory neurones within the ganglia only in very young specimens. As these were not accessible to me I have been unable to follow the motor axones through the ganglia of Triton successfully, as I have done in Amblystoma. But the exact resemblance of the two types in respect to the other features of these nerves would seem to justify one in assuming that the motor components of the two forms, also, would follow the same laws of distribution.

2. The Truncus Glossopharyngeus.—There are no general cutaneous fibers in the root of the glossopharyngeus, but this component enters the trunk of the nerve from the ganglion of the vagus. These fibers usually enter the nerve within the ganglion and are hard to identify with certainty. In one case, however, I find this component leaving the vagus ganglion as a distinct nerve and passing out a considerable distance before it unites with the glossopharyngeus just before the latter gives off the r. communicans X ad VII. The fibers of this nerve, within the ganglion, have all the appearance of sensory fibers; and since, as stated above, there appear to be no motor fibers in the general cutaneous root of the vagus, one seems to be justified in interpreting this component of the glossopharyngeus as sensory. Furthermore this is the only interpretation which will account for the fibers of this nerve which have a general cutaneous distribution. On any other supposition one would have to assume that communis fibers have a general distribution to the skin without relation to sense buds—a supposition which would scarcely be warranted by our present knowledge of nerve components.

The general cutaneous component of the glossopharyngeus in Amblystoma is distributed to the skin of the first external gill and over the base of this structure, and through the r. communicans to the r. jugularis VII. In the absence of the external gill in the adult Triton, a general cutaneous branch of this nerve is distributed to a corresponding region and, as explained below, there is good proof that the remainder of the general cutaneous component of the glossopharyngeus enters the r. communicans X ad VII.

3. The Ramus Communicans X ad VII.—It is impossible for me to trace the axones of this nerve with perfect certainty to their origin in the nerve roots and thus to determine its composition beyond dispute as I have done in the case of Amblystoma; but in the case cited above, in which the vagus component of the glossopharyngeal trunk joins the latter just before the r. communicans is given off, there is a space of only ten sections ten micra thick in which it is impossible to distinguish the vagus component or the r. communicans clearly from the rest of the nerve. This indistinctness is due to the tortuous course of the nerve at and near this point of flexure ventrad where the r. communicans arises. However, a study of the position which the vagus component takes in the trunk and of the point of origin of the r. communicans makes it almost certain that the r. communicans is derived, at least in part, from the vagus component.

As the r. communicans passes cephalad to join the r. jugularis VII, it gives off no fibers to any muscle, but it meets fibers from the motor VII component which enter the m. depressor mandibulæ.

After the r. jugularis VII receives the r. communicans it passes around the cephalic to the lateral border of the m. depressor mandibulæ, and gives fibers to this muscle and to the skin. The only possible source for these general cutaneous fibers is the vagus ganglion via r. communicans, since there are no general cutaneous fibers in the roots of the facial nerve.

4. Other Branches of the Glossopharyngeus and Vagus.—Drüner's descriptions of the other branches of the ninth and tenth nerves are accurate, with the possible exception of his r. "N. cutaneous retrocurrens IX." This nerve, he believes, innervates sense organs on the ventral surface of the head. Such a nerve can not be made out with certainty in my preparations, but since the corresponding nerve of Salamandra, according to Drüner, disappears during the metamorphosis, it may tend to disappear in the adult of Triton. However, wherever such a nerve may appear the fact should be emphasized that there are no fibers of the lateral line system in the glossopharyngeus of Triton. My preparations are perfectly clear on this point. The "N. cutaneus retrocurrens IX," then, can not be a lateral line nerve, for in my specimens the lateral line organs and nerves are well preserved and stained.

This nerve is deserving of further study, for if it really innervates sense organs it must be a communis nerve, and the presence of taste buds of this system in the skin of Amphibia would be an interesting discovery. Observations which I have begun on larvæ of Triton torosus may contribute something to this subject.

GENERAL DISCUSSION.

1. The Relation of the R. Maxillaris Superior to the R. Palatinus.—The connective between the r. buccalis and the palatine nerve as I have described it above is of interest when compared with the anastomoses between the corresponding nerves of Amphiuma, as described by Kingsley ('02). But unfortunately this author has not, in his treatment of this nerve, differentiated the lateral line and cutaneous components, that is to say, the r. buccalis and r. maxillaris; although he says the maxillaris superior "equals not only the maxillaris superior but the buccalis as well," and that "this nerve is clearly a double one." He identifies various branches of the nerve as "buccalis" divisions, but by their distribution only, and not by their certain origin from the lateralis ganglion. Two of the divisions of the nerve which may be so identified from KINGSLEY'S descriptions are the middle and inner terminal branches, which arise from the main nerve near the level of the cephalic border of the eye and almost immediately anastomose with the rami of the ophthalmicus profundus. The two nerves thus formed pass through foramina in the maxillary bone and innervate organs of the infraorbital line.

Now, in Triton there is a single small nerve which arises in the same locality from the r. buccalis and passes mesad into the nasal capsule. Here it anastomoses with the mesial nerve which arises from the palatine ganglion and which is composed of both profundus V and communis VII fibers. In these relations the nerve differs conspicuously from the anastomoses which KINGSLEY describes for the maxillaris superior of Amphiuma. Nevertheless, in both instances the tendency is shown for the buccalis fibers which are destined for the more cephalic organs of the lateral line to fuse with rami of the profundus. This tendency seems to be more pronounced in those forms which have greater ossification in the maxillary region. Indeed, it may be only incident to this skeletal condition, since in larval Amblystoma, in which ossification is very slight in the maxillary region, the buccalis does not anastomose with the ophthalmicus at any point.

But the most important feature of these anastomoses is the fact that, so far as they have been analyzed, they are between the profundus (plus r. palatinus in Triton) and *lateralis fibers and not between the profundus and other general cutaneous fibers.* Consequently KINGSLEY'S statement ('02, p. 302) that "In higher vertebrates this union, or a similar one between maxillaris and lachrymal, is common," can scarcely be correct; for such an interpretation would require that we make a general cutaneous nerve of the sauropsida or mammalia homologous with a lateral line nerve of the ichthyopsida.

It is not clear from his paper that Professor KINGSLEY would himself adopt such an hypothesis as a sound morphological principle, although he states clearly that these maxillaris divisions in question carry lateral line fibers and offers no evidence to show that they contain trigeminal fibers.

Another point of interest, also, attaches to this communicating nerve between the buccalis and the palatine nerve in Triton, for KINGSLEY ('02 a, p. 378) describes a very similar connective between the maxillaris superior and the r. palatinus in Ichthyophis. Although in this account, which is brief and only preliminary, Professor KINGSLEY has given nothing to establish the composition of this anastomosis, he considers it homologous with the anastomosis between the r. maxillaris superior and the r. palatinus of the frog. Yet I can see no reason why this connective in Ichthyophis may not be simply a lateral line nerve like that of Triton.

In his discussion of the taxonomic position of the cæcilians Professor KINGSLEY attaches "a considerable weight . . . to the relation existing between the palatine branch of the seventh and the various branches of the fifth nerves." But the bearing of the evidence to be drawn from this relation, it seems to me, hangs largely upon the morphology of the trigeminal branches themselves. It is my conviction that the nerves which are called maxillaris superior in Anura and in Urodela are not equivalent nerves in the two groups; but that the maxillaris of Urodela is the equivalent of STRONG'S "r. accessorius" of the tadpole, while the r. maxillaris superior of Anura is represented in the Urodela by lateral divisions of the ophthalmicus profundus. My reasons for this interpretation have been stated in my earlier papers ('01; '02, p. 260–262), and my study of Triton, with the discovery of the lateral line connective between the r. buccalis and the palatine nerve, has confirmed my position on this point. The essential facts concerning the relation of these nerves among themselves may be summarized as follows: The r. accessorius and r. maxillaris of Urodela are alike both in their distribution and in their relation to the r. buccalis VII, and do not anastomose with the r. palatinus VII; while the r. maxillaris of Anura and certain lateral divisions of the r. ophthalmicus profundus of the Urodela are alike in their distribution to the skin and in the anastomoses with the r. palatinus VII. And, here, it should be emphasized that the connective between the r. buccalis and palatine nerve in Triton is not comparable to the maxillo-palatine anastomosis of Anura for two reasons. In the first place, all the evidence goes to prove that it is a lateral line nerve. In the second place, it passes to the mesial side of the internal nares, so that, even if it were a general cutaneous nerve, its distribution would exclude it from being homologized with the maxillopalatine anastomosis of Anura for the latter is distributed to the lateral side of the internal nares. In this connection, also, KINGSLEY's description of the anastomosis between the r. palatinus and profundus of Amphiuma is of special interest; the conspicuous part of the anastomosis passes to the lateral side of the internal nares. In Amblystoma and Triton this lateral nerve from the anastomosis is obscure in its composition, which can be determined only under favorable conditions, while the mesial division is the larger and is clearly composed of trigeminal and facialis fibers. It is my belief that this nerve "e" of KINGSLEY in Amphiuma, which is composed of fibers from the r. palatinus and r. ophthalmicus profundus, represents the nerve which is formed from the r. palatinus and r. maxillaris superior in Anura.

In the light of the more recent work on the cranial nerves of Amphibia I can not understand why the r. maxillaris superior of Anura should be homologized with the nerve which the earlier authors called r. maxillaris in Urodela. These authors apparently knew nothing of the nerve which STRONG named r. accessorius in anuran larvæ. They found in the adult Anura only the one nerve which could be compared with the r. maxillaris of Urodela and to which they gave the same name. It seems to me unfortunate that this error should be perpetuated in opposition to facts which have become established by more exact methods than were at the command of earlier investigators.

With reference to the comparison of Amphibia with fishes as to the relation existing between the r. palatinus VII and the trigeminus, KINGSLEY ('02 a, p. 339) cites POLLARD's description of a connective between the r. palatinus and maxillaris superior in Polypterus. Now the significance of this connective hangs upon its composition. So far as we know it may be a communis nerve. If it is such, it then has no relation whatever to a general cutaneous connective between the trigeminus and the r. palatinus, for the communis fibers which associate with the r. maxillaris in fishes belong to the facialis.

2. *Jacobson's Anastomosis and R. Communicans IX–X ad VII.*—In his paper on Amphiuma KINGSLEY uses these two terms as synonymous. NORRIS ('05), also, in his description of certain cranial nerves of Amphiuma applies the term JACOBSON's anas-

tomosis to the r. communicans IX–X ad VII. It seems necessary, therefore, to emphasize the distinctness of these two structures. COLE ('98) has stated clearly the ground for distinguishing between them. The true JACOBSON's anastomosis belongs to the communis system and is distributed to the oral epithelium; while the r. communicans sends fibers to the skin and must be considered as a general cutaneous nerve, at least in the larger part. On the last point DRÜNER differs with me, since he considers this nerve as motor. But whether it be general cutaneous or motor it should not be confused with JACOBSON's anastomosis.

In Amblystoma, it is true, I found communis fibers in the r. communicans. But in this case the communis fibers joined the r. alveolaris and passed ventrad toward the floor of the mouth, so that their distribution is clearly different from that of the fibers in JACOBSON's anastomosis. The two anastomoses between the facialis on one hand and the glossopharyngeus and vagus on the other exist side by side in both Amblystoma and Triton, and a close study of these two structures here convinces me that the r. communicans IX–X ad VII is in no way comparable to JACOBSON's anastomosis.

As already mentioned, DRÜNER holds that the r. communicans is a motor nerve. I have been unable, however, to find any motor fibers in it, either in Amblystoma or in Triton. The fibers which may appear to go from it to the muscle depressor mandibulæ before the r. communicans reaches the r. jugularis are, in Triton as well as in Amblystoma, clearly derived from the r. jugularis. They pass caudad a variable distance in more or less close relation with the r. communicans. On the other hand, as presented in my description of this nerve, there is convincing evidence that the nerve is general cutaneous. And, being general cutaneous, it belongs to the vagus, for the glossopharyngeus gets its general cutaneous fibers from the vagus root. The term r. communicans IX–X ad VII, or X ad VII is, then, a better expression of the actual relations of the nerve. In Amblystoma I found that it belongs to both the glossopharyngeus and vagus. In Triton, I believe it belongs exclusively to the vagus.

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RETROGRADE DEGENERATION IN THE SPINAL NERVES.

BY

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1. *Summary of the Literature.*

Retrograde degeneration, sometimes also spoken of as "ascending degeneration" (FLEMING '97) and "indirect Wallerian degeneration" (VAN GEHUCHTEN '03), is a process resulting in the destruction of that portion of a divided fiber which is still connected with its cell of origin. Such cellulipetal changes are not in accord with the law of WALLER, which requires that of a divided nerve fiber only the portion severed from its trophic center should disintegrate, while all the rest of the neurone remains intact; nevertheless, this retrograde degeneration has been observed by a large number of investigators; it has been found in the cerebral as well as in the spinal nerves and occurs under certain conditions in various fiber tracts of the central system.

The investigations, which lead to the discovery of this form of degeneration, were carried out in the first instance upon the nerves in the central stumps of amputated limbs and upon the associated segments of the spinal cord. Experimental amputation and nerve resection in animals have served to confirm the observations made on human material and to eliminate complications introduced by the cause of the amputation or by the terminal disease. Since the cellulipetal changes resulting from the section of the spinal nerves are typical of retrograde degeneration, it has not seemed desirable to complicate matters by a review of the literature on similar changes in the cerebral nerves, nor in the fiber tracts of the central system. The observations along these lines have been

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[1] While at the St. Louis University the writer received very valuable assistance, both in the operations and the enumerations, from Dr. FRED. B. WHITTIKER, to whom he is especially indebted.

very well analyzed by VAN GEHUCHTEN ('03) and briefly summarized by the present writer ('04). It is also believed that we may omit without loss any mention of the theories of the different investigators concerning the nature and cause of the cellulipetal alterations resulting from the section of nerves.

In studying the literature on retrograde degeneration in the spinal nerves, it was found convenient to arrange the results of the different investigators in tabular form, placing the changes found in the various parts of the nervous system in separate columns under the following headings: central stumps of the severed nerves, ventral roots, dorsal roots, spinal ganglia, the spinal cord in general, the ventral horns and motor cells, the dorsal horns and the dorsal funiculi. In this way were tabulated the changes found in sixty-nine autopsies upon cases of more or less long standing amputation. In a separate table of the same kind were summarized the changes observed by eighteen different investigators who had carried out experimental amputation and nerve resection in animals. When these tables were completed, it was possible to compare the results of the different investigators and see what changes were constant in any part of the nervous system. It is with reference to these tables that the following has been written, and for this reason it has been possible to make accurate, but at the same time very general, statements.

The first observation of an alteration propagated centrally along the course of an injured nerve was made in 1829 by BERARD, who noticed that the ventral roots, associated with the nerves of an amputated limb, were smaller than their fellows on the opposite side. But it was not until 1868-69 that VULPIAN and DICKINSON aroused general interest in the subject, an interest which has led to an almost uninterrupted series of investigations and even at the present time has not abated. The results of this series of investigations may be stated rather briefly.

In a considerable proportion of the cases, no notice was taken of the central stumps of the severed nerves. Of those who did include these structures in their investigations only two found them normal (FRIEDREICH '73, and DRESCHFELD '79). The complete degeneration, seen in one of DICKINSON'S ('68) cases, was undoubtedly due to extraneous causes, probably septic infection. In all the other cases of amputation a simple atrophy, associated with a marked decrease in the average diameter of the nerve fibers, presents itself with striking uniformity (VULPIAN '68-'69, ERLENMEYER '72, HAYEM '76, DÉJERINE and MAYOR '78, HAYEM and GILBERT '84, FRIEDLÄNDER and KRAUSE '86, DUDLEY '86, REYNOLDS '87, MARINESCO '92, ELZHOLZ '00, on human material; and HOMÉN '90, VANLAIR '91, PILCZ '99, on animals). The microscopical changes are of some importance. The individual fibers are much decreased in size, the change affecting chiefly the myelin sheaths. Many of the fibers are entirely devoid of myelin and there is a tendency for them to be grouped in bundles. These altered fibers have been interpreted, sometimes as atrophied, sometimes as regenerated fibers; but the former interpretation seems to be the better supported. Of the authors who have placed themselves on record with regard to this point, six regard the change as an atrophy, while four believe that the altered fibers represent an attempt at regeneration; and on the side of the majority are included the two most thorough investigations: that of FRIEDLÄNDER and KRAUSE ('86) recording eight cases of amputation, and that of HOMÉN ('90) recording experiments on more than forty dogs.

As a typical account of these alterations we may summarize the description given by FRIEDLÄNDER and KRAUSE ('86). In their eight cases the nerve stumps presented patches of normal appearance separated by areas entirely devoid of medullated fibers; still other areas, constituting the larger portion of the cross-section contained about half the proper number. In the atrophied bundles the individual fibers are about one-third their normal size, and may be recognized as faint refractile rings, which do not take the WEIGERT stain. At the center of these rings a barely recognizable point represents the remains of the axis cylinder.

In addition to this simple atrophy there occurs in the proximal portion of some of the severed nerve fibers a true degeneration, not distinguishable histologically from Wallerian degeneration. This may be seen in MARCHI preparations from the central stumps of experimentally resected nerves, removed twenty to forty days after the operation (REDLICK '93, MOSCHAEW '93, BIEDL '97). Some observers have reported negative results with this stain; but it must be remembered in this connection that the degeneration in the central stump occurs about fifteen days later than true Wallerian degeneration (BIEDL '97, VAN GEHUCHTEN '03), and that the peripheral degeneration is at its height at a time when the alterations in the central stump are just beginning. Too early an examination of the material may thus lead to erroneous conclusions.

The changes in the ventral root are less marked than in the mixed nerve, and until the last twenty years these structures were often reported normal (VULPIAN '68-'69, DICKINSON '68, DÉJERINE and MAYOR '78, DRESCHFELD '79, FRIEDLÄNDER and KRAUSE '86). Atrophy of the ventral roots was reported by BÉRARD ('29), TÜRCK ('53), GENZMER ('76), HAYEM and GILBERT ('84), and EDINGER ('88); and during the last two decades has been quite uniformly observed (KAHLER and PICK '80, REYNOLDS '87, MARINESCO '92 and WILLE '95). According to REYNOLDS the atrophy is due to an increase in the proportion of the small fibers, while in two of WILLE's cases it was due to a decrease in the total number. On his forty dogs HOMÉN found a decrease in the ventral root fibers within the spinal cord. There was also a slightly larger proportion of small fibers on the operated than on the normal side. That some fibers degenerate and disappear from the ventral roots after the section of the mixed nerves has also been demonstrated by the MARCHI reaction in animal experiments (DARKSCHEWITSCH '96, REDLICK '93, MOSCHAEW '93, CASSIRER '98, CENI '99, VAN GEHUCHTEN '03).

The dorsal roots have undergone changes very similar to those in the ventral roots; the authors usually describe them together and in identical terms, so that the account just given of the latter would, with the following exceptions, serve equally well for the former. DICKINSON ('68), and FRIEDLÄNDER and KRAUSE ('86) found a considerable diminution in the number of dorsal root fibers although in both cases the ventral roots were reported practically normal. MARINESCO ('92) also found more advanced atrophy, and DARKSCHEWITSCH ('96) more degenerating fibers in the dorsal than in the ventral root. The roots of the spinal nerves are subject to considerable normal variation in size, so that a large root might suffer considerable atrophy and still appear normal; and this is, no doubt, in large part responsible for the conflicting statements to be found in the literature.

It is obvious from the foregoing account that the roots show less pronounced alterations than the central portions of the severed nerve trunks. FRIEDLÄNDER and KRAUSE's ('86) statement of this relation is worth some attention. We have already described the atrophic nerve fibers which these authors saw in the central stumps and noted that they considered the ventral roots normal, and the dorsal roots altered only to the extent of the loss of a small portion of the fibers. The altered elements seen in the nerve were to be found neither in the ventral nor dorsal roots. But within the ganglia and especially at their distal extremities before the afferent fibers have mixed with those of the ventral roots the changes are seen at their maximum; hence the atrophy seen in the nerve stumps affects chiefly the peripheral branches of the T-processes. This has recently been confirmed by KLEIST ('04).

Asymmetry of the spinal cord due to atrophy of the corresponding halves of the segments associated with the injured nerves is an almost constant finding (not present in the cases reported by TÜRCK '53 and FRIEDREICH '73), and is due to changes in both the gray and the white substance. The only change in the white substance which occurs with sufficient regularity to be of significance is found in the dorsal funiculus; atrophy of the ventral and lateral funiculi have been occasionally reported. (Atrophy of the ventral funiculus, VULPIAN '69 and KAHLER and PICK '80; of the lateral funiculus, SWITALSKI '01; atrophy uniform over the entire half of the area of the white substance, LEYDEN '76, DÉJERINE and MAYOR '78.) That some loss of substance should occur in these fiber tracts is a necessary corollary of the cell destruction which, as we shall see, occurs in the ventral and dorsal cornua and in CLARKE's column; but this could lead to only a very slight atrophy. It is more probable that these few observations depend upon a natural asymmetry of the cord or a too superficial examination of the material. FRIEDLÄNDER and KRAUSE ('86) state that in many of their preparations it seemed as if the entire half of the cross-section were atrophied, but closer study showed that the loss was confined to the gray matter and the dorsal funiculus.

As is to be expected from its anatomical relations with the atrophied dorsal roots, the dorsal funiculus shows a decrease in the area of its cross-section which can be followed cephalad far beyond the segments primarily affected. In only four of the autopsy cases was it reported normal (VULPIAN '69, three cases; FRIEDREICH '73, one case). In some instances it was found reduced to two-thirds its original dimensions. To explain this, HOMÉN ('90) asserts that the individual fibers are smaller on the operated side;

but on the other hand FRIEDLÄNDER and KRAUSE ('86) state that they are normal and that the atrophy must be due to a decrease in their number. There can be no doubt that some disappear since the MARCHI stain reveals a certain number in the stages of disintegration (human material, FLATAU, '97; animal material, MOSCHAEW '93, CASSIRER '98, CENI '99). The degeneration does not appear to affect more than a small part of the fibers of the funiculus.

In all the cases of amputation reported since 1875 there is essential uniformity as regards the changes in the ventral cornu on the side of the amputation in the segments associated with the injured nerves. The area of the cross-section of the cornu as a whole is considerably decreased, sometimes by as much as one-third its normal dimensions. The number of motor cells has been determined in a number of cases and found below that of the normal side. It is especially the dorsolateral group of cells that is most affected; here there may be no more than two-thirds the original number (MARINESCO '92). The remaining cells are often shrunken, and devoid of processes.

In none of the amputation cases of the last thirty years has the dorsal cornu of the operated side been reported normal. The decrease in the area of the cross-section, which may amount to one-half the original area (SWITALSKI '01, case 4), is due in large part to the loss of medullated fibers (KNOPE '01). The substantia gelatinosa and the column of CLARKE are also markedly atrophied. The decrease in the size of the column of CLARKE is due to a loss of both fibers and cells, and is found in the segments some distance removed from those primarily affected (FRIEDLÄNDER and KRAUSE '86, HOMÉN '90, and others).

By far the most interesting point for us is the lack of data on the spinal ganglia; most observers have failed to take any note of them at all, or have overlooked the essential changes. REYNOLDS ('87) found an increased amount of connective tissue. MARINESCO ('92) states that although many nerve fibers had disappeared the spinal ganglion cells were intact. That these are the only instances where the spinal ganglia were studied in the autopsy cases is due, no doubt, to the difficulty of securing these structures in the hurry of the autopsy room.

HOMÉN ('90), in his extensive series of animal experiments, gave special attention to this subject, but failed to find any change except an atrophy of the ganglion as a whole and of the nerve fibers contained in it. There seemed to be some atrophy of the ganglion cells but of this HOMÉN could not be sure. He did not consider the possibility of a decrease in the number of cells. CASSIRER ('98) states that a few cells in all probability undergo complete destruction. He says that the question of the loss of spinal ganglion cells can only be settled by resorting to an enumeration. Thus we see that in only four of the investigations were the spinal ganglia studied and even in these cases no important observations were made.

Some additional data have been furnished by various investigations based on NISSL's axonal reaction. After cutting the sciatic nerve near its exit from the pelvis in a number of dogs, LUGARO ('96), found that not all the cells of the spinal ganglion showed an equal degree of chromatolysis, a fact which he attributed to variations in the resistance of the individual cells. Thirty-nine days after the operation, there was a manifest diminution in the number of cells and an abundant proliferation of connective tissue. FLEMING ('97), who performed a similar operation on dogs and rabbits, found a decrease in size of the spinal ganglion cells soon after the operation. Cell destruction is, however, slow in making its appearance; in only one case is "disintegration of the protoplasm" noted at six weeks; after 18 weeks, however, many cells have disappeared. VAN GEHUCHTEN ('97), after cutting the vagus in rabbits, observed that the majority of the nerve cells in the ganglion nodosum underwent complete degeneration and disappeared. He believes that these results may be considered typical for the spinal as well as for the cerebral ganglia. On the other hand, MARINESCO ('98), after a similar operation on the vagus of dogs, found that the cells in the ganglion nodosum passed through the phase of reaction to a phase of restoration, and, therefore, did not undergo complete degeneration. In a rabbit six months after the operation he could not find the cell destruction of which VAN GEHUCHTEN speaks. MARINESCO also regards the reaction of the vagus as typical for all the cerebro-spinal ganglia. VAN GEHUCHTEN'S observation has recently received support from the observations of KOSAKA and YOGITA ('05), who found, fourteen days after the section of the vagus in a young dog, an almost complete disappearance of the cells of the ganglion nodosum; of the thousands of cells only sixty-five remained.

Köster ('03), having cut the sciatic immediately after its exit from the vertebral canal in cats, dogs and rabbits, found that all the spinal ganglion cells presented alterations of their tigroid bodies. Only a part of these cells suffered complete degeneration and this occurred for the most part after the 284th day. The phase of repair followed the chromatolysis in a large part of the cells and it was particularly in the large cells that the restoration of the tigroid substance was most evident. The cells that survived had undergone considerable atrophy. Kleist ('04) made his experiments on half-grown cats and rabbits, cutting some of the upper cervical or lower thoracic nerves. After from three to six months a large proportion of the spinal ganglion cells (estimated at 33 per cent.) had disintegrated and the remaining cells had undergone a marked atrophy.

The practical bearing of this problem has been indicated by Schäffer in his Text-book of Physiology: "If the observation of van Gehuchten upon the nerve cells of the vagal ganglion after section of their peripheral fibers is correct, and is a phenomenon of general occurrence, it is difficult to see how the sensory fibers regenerate. Restoration of function in such cases may, perhaps, often be explained by the ingrowth of sensory nerve fibers from adjacent areas of distribution."

2. *Observations on the Second Cervical Nerve of the White Rat.*

The unsatisfactory character of the data on the changes in the spinal ganglia, resulting from the section of the associated nerves, emphasizes the necessity of some further investigation along this line, and in the experiments now to be described special attention was given to determining the extent of cell destruction in the ganglion. It is necessary, by way of preface, to state a few of the essential points concerning the relation of the spinal ganglion to the afferent fibers of the nerve and dorsal root. We may safely accept as the essential element, the unipolar cell with its T-shaped fiber, despite the fact that Nissl ('03) has called attention to some facts that point to another view. Nevertheless there are many cells in the ganglion which are not connected with medullated fibers in either the nerve or dorsal root, since enumerations show that the number of nerve cells in the ganglion far exceeds that of the medullated fibers in the root (Hatai '02), and by nearly as large an amount the number of medullated afferent fibers in the peripheral nerve (HARDESTY '05). HATAI, working on the white rat, obtained the following results for the adult specimen of 167 gms. body weight.

TABLE I.

Ratio of Spinal Ganglion Cells to Dorsal Root Fibers. (HATAI.)

NERVE.	NUMBER OF CELLS.	NUMBER OF FIBERS.	RATIO.
VI C.	12,200	4,227	1: 2.8*
IV T	7,406	1,522	1: 4.8*
II L	9,442	1,644	1: 5.7

* The figures 2. 7 and 4. 3 given in the original are obviously misprints.

The writer in studying the normal relations in the second cervical nerve of the white rat has obtained results confirmatory of those of the authors already mentioned. In the three cases in which the dorsal root fibers and spinal ganglion cells were enumerated in the same individual nerve, a rather constant ratio of approximately 1 fiber to 3.2 cells was obtained. The first two specimens were seventy-two days old and weighed about 110 gms., the third was six months old and weighed 188 gms.

TABLE II.

Ratio of Spinal Ganglion Cells to Dorsal Root Fibers in the Second Cervical Nerve of the White Rat.

SPECIMEN.	NUMBER OF CELLS.	NUMBER OF FIBERS.	CELLS PER FIBER.
72 days old	7,721	2,472	3.1
72 days old	8,116	2,394	3.3
6 months old . . .	8,624	2,689	3.2

These results are corroborative of those obtained by earlier observers. The number of cells in a given spinal ganglion is about three times greater than the number of medullated fibers in the corresponding root. Without going into a discussion of the significance of this relation, it may be said that it is the large cells of the ganglion which alone are associated with medullated fibers (DOGIEL '96, HATAI '02). According to this view, 70 per cent. of the cells in the second cervical spinal ganglion of the white rat are small cells not associated with any medullated fibers which would be cut in dividing the peripheral nerve. It is obvious that these facts must have an important bearing on the results of injury to the nerve.

It is also important to note that the number of medullated dorsal root fibers is constantly increasing in the growing animal (HATAI '02). In the second cervical root of the white rat at twelve days of age the number of medullated fibers is less than that given in Table II, which represents the number in rats seventy-two days old. In two rats twelve days old the number of medullated dorsal root fibers was found to be 1608 and 1521, respectively. Hence, when the nerve is cut in animals of this age, even fewer medullated fibers are injured than would be the case in the adult animal.

It should also be mentioned that the number of dorsal root fibers may be taken as a fair indication of the number of afferent fibers in the peripheral nerve, the "distal excess" (HARDESTY '05) not being very large in this nerve of the rat. Table III shows that the ventral and dorsal rami of the nerve contain only 8 per cent. or 10 per cent. more fibers than are found in the ventral and dorsal roots. It is, therefore, not misleading to use the number of dorsal root fibers as an index of the afferent fibers in the peripheral nerve.

TABLE III.

Showing the Distal Excess in the II C. Nerve of the Adult White Rat.

WEIGHT.	VENTRAL ROOT.	DORSAL ROOT.	SUM OF ROOTS.	DISTAL EXCESS.	PERCENTAGE OF D. E.	SUM OF RAMI.	VENTRAL RAMUS.	DORSAL RAMUS.
302 gms.	646	2,386	3,032	257	8	3,289	887	2,402
161 gms.	672	2,090	2,762	276	10	3,098	708	2,390

The present studies were carried out on white rats in which the second cervical nerve of the right side had been divided. Some animals, operated on when twelve days old, were allowed to live for two months, others for four months; the nerve was also cut in adult rats which were allowed to survive the operation four months. A numerical analysis was then made of the spinal ganglion and of the ventral and dorsal roots of the injured nerves, in order to determine to what extent degenerative changes had taken place and what amount of repair, if any, had occurred.

Technique.—In operating upon white rats twelve days of age it is necessary to work rapidly and to conserve, as far as possible, the body temperature. The little rat was held in position in the hands of an assistant with its neck slightly stretched and head bent forward. An incision was made in the midline on the back of the neck, with the atlas at its middle point, and carried downward through the ligamentum nuchæ until the tuberculum posterius of the atlas was uncovered. The integument and long muscles of the neck were held aside by a spring retractor inserted through the median incision. The caudal margin of the atlas then served as a guide to the point where the right second cervical nerve emerges from the vertebral canal. A short stretch of the nerve[1] was laid bare and cut with sharp scissors about 1 mm. from the ganglion. No part of the nerve was resected and its central and peripheral ends were held in close proximity by the mass of tissue in which they were imbedded.

All blunt dissection was avoided; sharp instruments were used throughout, so that the tissues suffered a minimum amount of injury. It was not practicable to close the wound with deep sutures in the rats twelve days old, but this was done when the operation was performed on adult rats. The skin incision was closed with a collodion dressing.

Were it not for the fact that a standard objection to results obtained in this way is that they are due to a septic infection, the reader might be spared the usual paragraph on asepsis. Under the circumstances, however, some details must be given. The skin of the animal's neck, after it had been freed from hair, was thoroughly cleaned with ether-alcohol to remove oily deposits

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[1] Only the dorsal division of the nerve was cut; the ventral division, which is much smaller, was not injured. This turns abruptly ventralward just distal to the spinal ganglion and was quite out of the field of the operation. In order to form some idea of what proportion of the afferent fibers were severed in cutting the dorsal ramus it is necessary to know the relative size of the two branches. In two cases studied, the proportion of fibers was as follows:

Specimen.	*Dorsal Ramus.*	*Ventral Ramus.*	*Ratio.*
9 months, 302 gms.	2,402	887	1:2.7
4 months, 161 gms.	2,390	708	1:3.3

The dorsal division is thus seen to be much the larger. It is mainly sensory since it forms the N. occipitalis major, which, after giving off a few muscular twigs, goes to the skin on the back of the head. The ventral division goes, in large part, to the muscles about its origin, only a small twig going to join the common trunk of the N. auricularis magnus and N. cutaneus colli which, in the rat, is formed chiefly by the ventral division of the third nerve.

From these data we may roughly estimate that about 13 per cent. of the afferent fibers of the second nerve go by way of the ventral branch and were not affected by the operation. This figure is obtained by regarding the ventral branch as a purely muscular nerve, which according to SHERRINGTON'S ('94) observations should be composed of afferent and efferent fibers in the ratio of 2 to 3. This would give about 350 afferent fibers in the ventral branch, which, allowing for a 10 per cent. distal excess, would leave 315 represented in the dorsal root. The average number of dorsal root fibers in these two nerves was 2238, of which the 315 going to the ventral branch would constitute about 13 per cent.

and was then washed with a solution of mercuric chloride and left covered with a pad moistened in that solution, while the operator cleansed his hands. From this point on, the operator's hands touched nothing but the sterile instruments laid out on a sterile tray; all other things were handled by an assistant. Nothing touched the wound but the sterile instruments and sponges; the wound was too small to permit of introducing the fingers for any purpose.

Thanks to the natural resistance of the animals, as well as to the care taken to preserve the vigor of the tissues by the use of sharp instruments and hot sponges, the aseptic precautions were efficient, and not in a single case was there any sign of infection. (In one animal the collodion dressing came off after four days, but this one was at once discarded.) As final evidence that sepsis has nothing whatever to do with the results of these experiments, it may be said that in a series of animals killed five, six, seven, eight, twelve, seventeen and twenty days after the operation, the wound was found in perfect condition; and a microscopical study of the ganglion and nerve stump stained with toluidin-blue failed to show any indications of infection.

At the autopsy, note was made of the size of the neuroma and of any regeneration that had occurred. The operated nerve was then carefully dissected out together with its neuroma, ganglion, and roots, straightened out on a piece of card-board, and fixed in 1 per cent. osmic acid. The left, or normal nerves, were treated in the same manner as the right; but they were not used in the determination of the norm, since it was theoretically possible that their condition might in some way be influenced by the injury inflicted on the nerve of the opposite side. And, as a matter of fact, such a crossed degeneration has been reported in the ventral root fibers (BRAEUNIG '03). For this reason it was considered safer to take the control material from entirely normal animals.

After fixation in 1 per cent. osmic acid, the tissue was imbedded in paraffin and cut into transverse sections. The sections of the roots were 3μ to 4μ thick; those of the ganglion were 12μ thick and arranged in serial order. When a perfect series through the ganglion was not obtained the specimen was discarded.

The osmic acid not only stains the myelin of the nerve fibers, but also brings out the nerve cells so well that no further treatment is necessary. The technique of counting nerve fibers and spinal ganglion cells has been described in a number of papers from this laboratory, and especially in the publications of HARDESTY. In counting fibers the net method was used. The entire ventral root and each of the fasciculi of the dorsal root and mixed nerve were, with few exceptions, small enough to come within one field of the microscope. The field was divided into small squares by a net micrometer placed in the ocular. The fibers in each square were counted in the order of the squares until the enumeration of the entire root or fasciculus was completed. The counting was done automatically by pressing the lever of a counting machine once for each fiber and reading off the final number from the face of instrument. In the few cases in which it was necessary to shift the preparation during the enumeration of a root or fasciculus, a straight line joining two prominent points was regarded as the limit between the two fields, and the position of this line was indicated by a line of the micrometer made to lie across the two points.

The enumeration of the nerve cells in the serial sections of the spinal ganglia was somewhat more difficult, since several successive sections may contain parts of the same cell. The difficulty was avoided by counting in a given section only those cells which showed nucleoli. These structures are small enough to escape division by the knife and so to lie, in the vast majority of the cases, within the plane of a single section. In most cases each cell has but one nucleolus, in rare instances there are two; but the presence of a pair would lead to error only in those extremely rare instances when the knife passed between them in such a way as to give a nucleolus to each of two sections of the same cell. HARDESTY estimates that this would not give an error of more than 0.2 per cent. The cells with nucleoli were enumerated with the aid of the counting machine in each section of the series; the sum of the numbers for the individual sections gave the total for the ganglion. Since a section of the ganglion could not all be brought into the field at once, it was necessary to use a mechanical stage which permitted a ready shifting of the preparation. In the spinal ganglion the different portions of the section are so characteristic that one does much better to dispense with the net micrometer and depend entirely upon the natural markings, which are adequate to prevent confusion as to what part of the section has been counted.

Results.—The results of the present investigation may all be summarized in the following table:

TABLE IV.

Showing the Numerical Relations of the II C. Nerve of the White Rat in the Normal Condition and after Section of the Ramus Posterior just Distal to the Ganglion.

Specimens.	Body Weight in gms.	Ganglion Cells.	Ventral Root Fibers.	Dorsal Root Fibers.	Neuroma	Regeneration.
Normal Rats.						
(1) 72 days old (normal)	110*	7,721	689	2,472	—	—
(2) 72 days old (normal)	110*	8,116	660	2,394	—	—
(3) 72 days old (normal)	155	9,343	—	—	—	—
(4) 72 days old (normal)	110*	—	590	1,959	—	—
(5) 72 days old (normal)	110*	—	591	2,217	—	—
(6) 240 days old, left (normal)	188	8,624	703	2,689	—	—
(7) 240 days old, right (normal)	188	—	773	2,891	—	—
Rats Operated on at 12 Days of Age and Killed after 60 Days.						
(8) 72 days old (operated)	110	3,845	523	2,641	large	partial
(9) 72 days old (operated)	110*	3,896	—	—	large	none
(10) 72 days old (operated)	110*	3,764	537	1,236	very small	none
(11) 72 days old (operated)	110*	4,193	506	1,983	medium	partial
(12) 72 days old (operated)	110*	4,497	431	1,607	large	partial
Rats Operated on at 12 Days of Age and Killed after 120 Days.						
(13) 132 days old (operated)	274	4,020	515	1,455	large	partial
(14) 132 day sold (operated)	146	4,516	646	2,357	very small	quite perfect
(15) 132 days old (operated)	161	—	562	1,987	small	partial
Rats Operated on at 140 Days of Age and Killed 120 Days Later.						
(16) 260 days old (operated)	225	4,215	610	1,983	large	none
(17) 260 days old (operated)	302	—	630	2,176	small	very slight
(18) 260 days old (operated)	264	4,176	506	2,219	large	none

The weights marked with a star (*) have been calculated from the age, no record having been taken of the body weight in these cases.

I. *Changes Produced by Section of the Nerve in Young Rats.*

The most interesting of the observations to be recorded in this place concerns the pronounced cell destruction that occurred in the spinal ganglion; the extent and constancy of the degeneration is expressed in Table V.

TABLE V.

Showing the Decrease in the Number of Cells in the Spinal Ganglion Sixty Days After the Division of the Ramus Posterior of the II C. Nerve in Rats Twelve Days Old.

	Normal.	*Operated.*
	7,721	3,845
	8,116	3,896
	9,343	3,764
	8,624	4,193
		4,497
	4)33,804	5)20,195
Average.......	8,451	4,039

Average loss 4,412

Per cent. average loss 52

From Table V we see that two months after the second cervical nerve had been cut in a rat twelve days old the corresponding spinal ganglion had lost about one-half its cells, and that this occurred with striking uniformity in five different specimens. Indeed, we find that the smallest number of cells in the operated ganglia, 3764, differs from the largest number 4497 by only 19 per cent. of the smaller number, while in the normal ganglia the greatest variation amounts to 21 per cent. Hence there can be little doubt but that the numerical differences which the operated ganglia show among themselves are due to normal individual variation present in the ganglia before the operation. We repeat, therefore, that this table shows an altogether striking uniformity in the number of cells in the operated ganglia, and that the number of cells dropping out of a ganglion must represent a certain constant percentage of the cells it originally contained. There must be some very definite reason for this constant reaction; but our knowledge of the architecture of the spinal ganglion is at present so vague that it is not possible to say what are the responsible factors.

If it is desired to know the percentage of cells that disappear, this may be determined by taking the average normal number of cells, 8451, as the base number, of which 4412, the average number of cells destroyed, constitutes 52 per cent. Here again we are totally at a loss for an explanation. We know of no anatomical relations which would justify the expectation of such a result.

The number of medullated afferent nerve fibers cut in the operation on a twelve-day old rat is about 1500. [The average number of medullated fibers in the dorsal roots of twelve-day old rats was found to be 1568 (p. 274); to this must be added a 10 per cent. "distal excess" to find the number of medullated afferent fibers in the nerve (p. 274); and from this result 13 per cent. must be subtracted for the afferent fibers running in the uninjured ramus anterior (p. 275). This calculation gives 1500 medullated afferent fibers which would be injured at the operation.] And were all the cells associated with these 1500 fibers to drop out, the loss would only amount to 17 per cent. Or, expressed in other words, nearly three times as many cells have disappeared as can be accounted for in terms of medullated axons injured at the time of the operation. Even if we assume that all the axons ever to develop are present (partly as non-medullated fibers) at the time of the operation on the young rat, and if we let this be represented by the number of medullated afferent axons in the adult nerve, we find that even this number, which does not exceed 2500 (see p. 274) is inadequate to account for the number of degenerated cells. For the explanation of these results we are, therefore, forced to fall back upon the existence of some as yet unknown relations within the spinal ganglion.

There was not sufficient disturbance of the blood supply to account for the degeneration, since the artery and vein accompanying each root were not in any way injured. The objection that the degeneration was due to a septic infection has been answered in connection with the discussion of the technique, and against such an objection there also speaks the fact that infection could not produce such uniform results.

It might be supposed that the fact that only the dorsal branch was cut and the ventral branch left intact explained the occurrence of a partial degeneration, and that if both branches had been cut all the cells would have disappeared. This supposition is, however, manifestly incorrect since the intact ventral branch did not contain more than 13 per cent. of the afferent fibers (see footnote, p. 275), and hence cannot be responsible for the 48 per cent. of the cells which survive.

The results obtained by the enumeration of the medullated nerve fibers in the ventral and dorsal roots of young rats surviving two months after the section of the second cervical nerve are much less constant. The percentage of loss is much smaller than in the case of the ganglion cells, scarcely greater than the percentage of individual variation, so that the latter tends to render the former less evident. But this consideration only in part explains the lack of uniformity in the results; it seems that the degenerative processes in the root fibers are more variable than those in the ganglion cells and more directly dependent upon such conditions as reunion of the central and peripheral stump of the nerve.

TABLE VI.

Showing the Decrease in the Number of the Medullated Nerve Fibers in the Ventral and Dorsal Roots Two Months After the Section of the Ramus Posterior of the II C. Nerve in Rats Twelve Days Old.

(Normal and "Operated" Material from Different Animals.)

	Ventral Root.		Dorsal Root.	
	Normal.	Operated.	Normal.	Operated.
	689	523	2,472	2,641
	660	537	2,394	1,236
	590	506	1,959	1,983
	591	431	2,217	1,607
Sum........	2,530	1,997	9,042	7,467
Average.....	632.5	499.2	2,260.5	1,866.7
Average loss..................	133.3		393.8	
Average (%) loss............	21		17	

The ventral roots show a fairly uniform loss of fibers. The smallest number of fibers in the normal roots (590) exceeds by 53 the largest number in the operated roots (537). Moreover, the average of the operated roots falls 133 behind the average for the normal roots, making an average loss of 21 per cent. This loss is, however, by no means so uniform as that in the number of spinal ganglion cells. The loss of fibers in the ventral root is in harmony with the results reported by numerous investigators who found, as a result of cutting the peripheral nerve, fibers present in the ventral root which gave the Marchi reaction (p. 268). It is also a necessary result of the degeneration of the cells of the ventral cornu of the spinal cord so constantly found after the section of nerves (p. 270).

Even more variability is shown in the column of Table VI representing the operated dorsal roots. The first operated dorsal root that was subjected to an enumeration contained 2641 nerve fibers, a number even greater than the normal average for rats of that age. The other three roots fall below the normal; in one case the number goes as low as 1236. The average loss is 393 fibers or 17 per cent.

The deficiency of fibers in the dorsal roots, associated with the injured nerves, finds its counterpart in the degenerating fibers which may be recognized by the method of MARCHI (see p. 267). According to recorded observations the degenerating fibers constitute only a fraction of the total number. To what extent degeneration occurred in our specimens can only be determined by study of the roots with the MARCHI method, because it is not possible to say what part of the fibers, enumerated in this investigation have been formed since the operation as an attempt to repair the damaged root.

TABLE VII.

Showing the Relation of the Number of Dorsal Root Fibers to Spinal Ganglion Cells in the Operated II C. Nerve of the White Rat.

SPECIMEN.	SPINAL GANGLION CELLS.	DORSAL ROOT FIBERS.	RATIO.
Rat 8...........	3,845	2,641	1:1.4
Rat 10...........	3,764	1,236	1:3.0
Rat 11...........	4,193	1,983	1:2.1
Rat 12...........	4,497	1,607	1:2.7
Average of 3 normal rats (Table II)	8,153	2,485	1:3.2

Table VII shows that in every case there are more than enough spinal ganglion cells to account for the dorsal root fibers, although in one case the excess of cells is not very great. By comparison with the average normal ratio taken from Table II, it will be seen that the ratio of cells to fibers is reduced in the operated nerves, and that while in the normal nerve it is approximately constant at one fiber to 3.2 cells in the operated nerves it shows much greater variation. The table also shows that there is no constant relation between the number of spinal ganglion cells destroyed by the operation and the number of dorsal root fibers which are found two months later; and that, therefore, the loss of dorsal root fibers cannot, without some qualification, be attributed to the degeneration in the spinal ganglion. The possible factors which may complicate the result are given in the footnote, on p. 275.

II. *The Influence of the Length of the Post-operative Period upon the Results.*

After the changes just described had been found in the rats that had survived the operation for two months, the question arose whether the degeneration had come to an end before the animal was killed, and whether if the rat were allowed to live for a longer period of time, further changes might not take place. It was thought possible that the number of spinal ganglion cells might further decrease, and that the roots might either continue to lose fibers, or perhaps show a tendency to repair.

TABLE VIII.

Showing the Numerical Relations in the II C. Nerve in Rats which Lived Four Months after Section of the Ramus Posterior of that Nerve when the Animals were Twelve Days Old.

	SPINAL GANGLION CELLS.	VENTRAL ROOT FIBERS.	DORSAL ROOT FIBERS.
	4,020	515	1,455
	4,516	646	2,357
		562	1,987
Average	4,268	574	1,933

TABLE IX.

Showing the Influence of the Lapse of Time upon the Effect of Cutting the II C. Nerve.[1]

AVERAGE NUMBER OF	2 MONTHS AFTER THE OPERATION.	4 MONTHS AFTER THE OPERATION.
Ganglion Cells.	(5) 4,039	(2) 4,268
Ventral Root Fibers.	(4) 499	(3) 574
Dorsal Root Fibers.	(4) 1,866	(3) 1,933

[1] The figures in parentheses indicate the number of cases from which the averages were obtained.

From Table IX we see that the number of spinal ganglion cells, although still far below the normal, is a little greater in the specimens removed after four months than in those removed after two months. According to our present knowledge there is no reason to expect any regeneration of the spinal ganglion cells. This statement is based in part on HATAI's ('02) study of the growth changes in the spinal ganglia, but more particularly on the negative results of a series of investigations undertaken for the purpose of testing the regenerative capacity at one time supposed to belong to these structures (TIRELLI '95, MONTI and FIESCHI '95). The slight excess of cells in the four-month specimens is probably of no significance, representing nothing more than the individual variation of which so much has already been said. Further support is given to this view by the fact that of the two specimens enumerated the first gives a figure close to the average for the two-month specimens while the second runs much higher and in all probabilty represents a large ganglion which originally contained over 9000 cells.

The point of importance is not that there is a slight excess of cells in the four-month specimens, but that there is certainly no decrease, and that, therefore, the process of cell-destruction runs a rather rapid course and is completed during the first two months, after which there is no further change. This is of interest in connection with the usual doctrine that in chromatolysis the phase of reaction is followed by a phase of restitution, which may result in the complete restoration of the cell, or may in turn give place to a phase of degeneration, resulting in the gradual disappearance of the injured neurones. It is obvious that in this case the phase of degeneration (if it can properly be separated as a distinct phase at all) must have been a rapid one which came to a definite termination. It did not result in the destruction of cell after cell until all had disappeared. According to recent observations of KÖSTER ('03), who cut the sciatic nerve in cats, rabbits and dogs, the cell destruction in the spinal ganglia is only slightly noticeable after 100 days, but is very marked after 284 days. There can be no doubt that in my experiments on rats the degeneration was complete before the end of the first sixty days. That my animals were very young and of a different zoölogical order from those of KÖSTER, may in part explain the discrepancy in the results. It should be mentioned, however, that KÖSTER did not control his observations by an actual enumeration of the cells.

By reference to Table IX it will be seen further that the number of ventral root fibers is greater in the animals which survived four months than in those which were killed at an earlier date. The difference, howeve amounts to only 15 per cent. of the smaller number, and this can readily be accounted for in terms of normal growth. There seems, therefore, to be little if any tendency to repair the ventral roots in the sense of an acceleration of the normal rate of fiber formation to compensate for a previous loss. Of course the neurones represented by the degenerating fibers in the root undergo complete destruction (p. 270) and no regeneration of the injured axons could be expected. But it was deemed possible that some reserve cells might be located in the ventral cornua, which might take part in a reformation of the ventral root after the neurones whose axons originally entered into its formation had been destroyed. There is no evidence that such a compensatory process occurred in this set of experiments; and if reserve cells are present in the ventral cornua of the spinal cord, they certainly failed to respond to the demands placed upon them by the conditions of this experiment.

The excess of fibers in the dorsal roots four months after the operation, as compared with those at the two-month period, amounts to less than 1 per cent. This is less than would be expected on the basis of normal growth processes, and it is certain that during the second two of the four months intervening between the operation and the autopsy there was no tendency for the small latent cells to increase their normal rate of development in an attempt to restore the atrophied dorsal roots to their normal condition.

The fact that both the ventral and dorsal roots show more fibers four months after the operation than at an earlier period, indicates very clearly that there can be no slow progressive degeneration going on in these localities. This fact is of interest, since retrograde degeneration has usually been regarded as a chronic progressive process. In this case it ran a rather rapid course and came to a definite termination.

III. *Significance of Differences in the Ages of the Animals.*

It has been shown what the effects of cutting the second cervical nerve are in the young rat and what influence is exerted by the lapse of a greater or less length of time between the operation and the autopsy. It is now our purpose to inquire how far these results are dependent upon the immaturity of the animal used for the experiment. It was anticipated that the section of the nerve would not be nearly as destructive of spinal ganglion cells in the adult, as it had been in the younger animals; and the results expressed in Table X came as something of a surprise to the writer.

TABLE X.

Showing the Effect of Cutting the II C. Nerve in Adult Rats (140 Days Old) which Survived 120 Days.

	Spinal Ganglion Cells.	Ventral Root Fibers.	Dorsal Root Fibers.
	4,215	610	1,983
	4,176	506	2,219
		630	2,176
Average	4,195	582	2,126

TABLE XI.

Showing the Influence of the Age of the Animal and the Length of the Postoperative Period upon the Effect of Cutting the II C. Nerve in the White Rat.[1]

Age at the operation......	12 days	12 days	4 months
Period of survival........	2 months	4 months	4 months
Spinal ganglion cells	(5) 4,039	(2) 4,268	(2) 4,195
Ventral root fibers	(4) 499	(3) 574	(3) 582
Dorsal root fibers	(4) 1,866	(3) 1,933	(3) 2,126

[1] The figures in parentheses indicate the number of cases from which the averages were obtained.

From Tables X and XI it will be apparent that there was found a slightly greater number of cells in the spinal ganglia of the animals operated on when already adult, than in the first set of young rats, but fewer than in the second set. It is believed that the difference is in each case merely a matter of individual variation in the original ganglia, and is, therefore, of no consequence. That the section of the nerve should entail practically the same effect upon the spinal ganglion, whether it is made in the young or in the adult animal, is a matter of a good deal of interest and a result quite contrary to precedent. It is the more difficult to understand because at least 30 per cent. more medullated afferent fibers were cut in the operation upon the adult than in that upon the young rat (p. 274), and it is hard to see how this should have been so exactly compensated for by a greater resistance of the adult neurones. There is a possibility that even in the rat twelve days old all the peripheral fibers ever to develop are present in the nerve, some as medullated, the rest as non-medullated fibers; and this if it should be found to be the case, would help to explain the fact that the reaction is the same in the adult as in the young animals.

Table XI gives only the average number of cells present in the ganglia under each of the three conditions; Table XII shows that the agreement which was found between the averages is just as apparent when all the individual ganglia are brought together. It does not matter whether the animal is young or old or whether it survives for two or for four months; the changes in the spinal ganglion are always the same.

TABLE XII.

Showing the Uniformity in the Cell Destruction in the Spinal Ganglion Resulting from the Section of the Peripheral Nerve.

NORMAL.	OPERATED WHEN 12 DAYS OLD, LIVED 2 MONTHS.	OPERATED WHEN 12 DAYS OLD, LIVED 4 MONTHS.	OPERATED WHEN 140 DAYS OLD, LIVED 4 MONTHS.
—	3,845	—	—
8,116	3,896	—	—
7,721	3,764	—	—
8,624	4,193	4,020	4,215
9,343	4,497	4,516	4,176

By reference to Table XI it will be seen that the number of ventral root fibers is nearly the same in both sets of rats that survived four months, whether the operation was made when they were 12 or 120 days old. This indicates that the same number of ventral root fibers dropped out in each case, after which the nerve fibers continued to develop at the normal rate in the immature animal. Hence, since the number of medullated fibers was smaller in the young rat, those that degenerated must have constituted a larger proportion of the entire number than in the case of the adult rat. And this is in accord with the general belief that immature neurones succumb more readily to an axonal lesion than do the fully developed ones. This variation in reaction, according to the age of the animal, is very pronounced in the case of the fibers of the corpus callosum (RANSON '04). In a rat twelve hours old in which the corpus callosum was injured, the injured fibers underwent complete degeneration, both Wallerian and retrograde; in a rat of three months the retrograde degeneration affected only the part of the fiber in the immediate vicinity of the lesion.

The dorsal roots show distinctly more fibers in the animals operated on at four months of age than in either of the other cases (Table XI); since, as Table IV clearly indicates, these older animals do not possess as much regenerative capacity, and since it is certain that at least one-third more medullated fibers were cut in operating upon them, it seems altogether probable that the large number of fibers in the dorsal roots in the adult rats is to be explained as in the case of the ventral roots on the basis of a greater resistance of the adult neurones.[1]

The interpretation of the numerical results obtained for the spinal ganglion and dorsal root is exceedingly difficult. A final statement can only be made when we have the results of the MARCHI test and the NISSL stain to assist us in drawing conclusions, since in these ways we can tell what proportion of the fibers degenerate and whether the large or the small cells are chiefly concerned in the changes going on in the ganglion. Investigations along these lines are now in progress.

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[1] At first sight it seems a contradiction to say that the dorsal roots show varying degrees of resistance, but that there is no difference in the degree of degeneration seen in the spinal ganglion. If, however, it were the small cells not directly associated with medullated fibers that had disappeared from the ganglion it would be easy to understand how the dorsal root fibers, associated as they are with the large cells, would be quite independent of the decrease in the number of the ganglion cells. These large cells with their medullated processes would then suffer varying degrees of injury, usually not resulting in the destruction of the perikarya, but in a certain proportion of the cases bringing about a degeneration of the associated dorsal root fibers. The more mature the animal, the less seriously would the large neurones be injured, and the fewer would those be that could not maintain their dorsal root fibers intact.

The possible causes of variation in the dorsal roots may be stated as follows:

1. While the total number of cells destroyed is constant, the proportion of large and small cells affected may vary, and accompanying a greater destruction of large cells, there may be a greater degeneration of the dorsal root. This supposition is very improbable.

2. All the large cells may drop out in every case, the variation in the dorsal roots depending upon the extent of the compensatory development of the small cells.

3. Most of the large cells may pass through the stages of reaction and repair, while the small cells drop out in large numbers. In this case the medullated nerve fibers associated with a varying number of large neurones might degenerate although the perikarya of these same neurones survive. This is the most probable explanation of the results, as will be shown in another paper. At the present moment it seems probable that the key to the explanation of all these conflicting results is to be found in the existence in the nerve of many non-medullated fibers which are the axons of the small cells. This would furnish an explanation for the degeneration of the small cells after the section of the nerve.

IV. *Effect of Reunion of the Cut Ends of the Divided Nerves.*

It is clear from Table IV that, so far as the survival of spinal ganglion cells is concerned, it is a matter of indifference whether regeneration of the nerve occurs or not. In four cases no regeneration occurred at all; in the other six cases the extent of the regeneration varied considerably; in one case (14) an almost perfect nerve was found, with only a slight thickening to indicate the point of division. But with this wide range in the degree of the restoration of the peripheral nerve, there is no difference in the condition of the spinal ganglion. This shows very clearly that the degeneration of spinal ganglion cells is not markedly influenced by the regeneration or lack of regeneration of the peripheral nerve. MARINESCO ('98) states that unless there is union of the divided ends of the nerve, the motor cells of the ventral cornua do not pass from the phase of reaction to the phase of restoration, but atrophy and disappear. The entrance upon the phase of restoration is, according to him, an indication that regeneration has begun in the nerve. VAN GEHUCHTEN ('99) and FOA ('99) have been unable to confirm these observations of MARINESCO for the motor nuclei, and my results would indicate that for the spinal ganglia the restoration of the cells is entirely independent of the restoration of the peripheral nerve.

CONCLUSIONS.

As a result of dividing a peripheral nerve, there occurs not only the typical Wallerian degeneration of the distal portion but also various changes in the proximal portion of the nerve, the spinal ganglion, the ventral and dorsal roots and the spinal cord. In all these regions there take place both a simple atrophy and a true degeneration. The atrophy results in a decrease in the size of the fibers, many of which entirely lose their medullary sheaths. Many of the cells of the ventral cornua and of the spinal ganglion are markedly atrophic. The degeneration in the fibers proximal to the lesion begins some weeks later than Wallerian degeneration, from which, however, it cannot be distinguished histologically. This retrograde degeneration affects only a part of the fibers and can be found not only in the central stump and the ventral and dorsal roots but also in the intramedullary continuations of the root fibers. This results in a distinct diminution of the number of nerve fibers in these regions and helps to increase their atrophic appearance. The degeneration of nerve cells results in the disappearance of a certain, apparently variable, number of ventral horn cells and a very considerable and constant number of spinal ganglion cells.

It has been shown by careful enumeration that after cutting the second cervical nerve of the white rat, one-half of the cells in the corresponding spinal ganglion degenerate and disappear. This reaction is very constant and uniform; in the nine ganglia studied the percentage of variation is no greater than the percentage of individual variation in the normal ganglia. This is peculiar in that many more cells disappear than can be accounted for in terms of medullated fibers cut at the time of the operation; and while it is not possible at present to give a satisfactory explanation of the results they point to some as yet unknown relations in the ganglion.

The number of fibers in the dorsal root is open to much greater variation; but there is on the average a loss of about 17 per cent. The dorsal roots seem more susceptible to the degenerative changes in the young than in adult animals.

The degeneration of ganglion cells is constant, that of the dorsal root fibers is variable and is much less extensive than would be expected from the number of cells which disappear. This shows that the degeneration in the dorsal roots cannot without some qualification be attributed to the degeneration in the spinal ganglion. It is hoped that an investigation now in progress will supply the necessary data for the interpretation of these results.

Contrary to the usual conception, the degeneration of fibers and cells was not progressive; it had been completed before the end of the first two months, after which there was no further change.

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THE PRIMITIVE PORES OF POLYODON SPATHULA

BY

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WITH PLATE XVIII.

This work was undertaken with the view of determining the character and significance of these remarkably numerous organs, about which there is very little in the literature. The nomenclature of COLLINGE (1) has been used in designating these structures as primitive pores.

The material used was obtained from fishermen, who frequently catch the fish on set lines. Those studied in this case were from 80 cm. to 90 cm. long and weighed from twenty-six kilos to thirty-three kilos. They were brought to the laboratory alive and the desired structures placed immediately in various fixing solutions. For the purpose of general histological study picric-sulphuric-acetic acid, corrosive sublimate-acetic acid, and 10 per cent. formalin were used. These tissues were embedded in paraffin and stained with DELAFIELD'S hæmatoxylin, HEIDENHAIN'S iron hæmatoxylin and acid fuchsin. For the study of the distribution of medullated nerves, 1 per cent. osmic acid gave the best results. To bring out the neuro-fibrillæ and their terminations a number of methods were employed, among which were APATHY'S aftergilding gold chloride method and the GOLGI method after both formalin and potassium bichromate-osmic fixation.

The method which gave the most precise differentiation of the neuro-fibrillæ was the following: The pieces of bill, head and gill-flaps were placed in 10 per cent. formalin for two weeks. They were then transferred to 10 per cent. formic acid for twenty to thirty minutes, then to 1 per cent. gold chloride for fifteen to twenty minutes Following this they were placed in a 2 per cent. formic acid solution, in the dark, for twenty-four to forty-eight hours, or until the tissue acquired a rich purple color when viewed with the unaided eye by reflected light. The tissues were then washed for one hour in distilled water, run rapidly through the different grades of alcohol and embedded in paraffin. Sections from 3 μ to 5 μ were cut and mounted in balsam.

On casual examination, the head, bill and gill-flaps of Polyodon appear to be profusely covered with irregular dark spots (Fig. 1), which are much lighter on the gill-flaps than on the head and bill. When these spots are examined more closely, they are seen to contain small pin-point holes which are the openings of primitive pores. The pores are exceedingly numerous, there being as many as fifty in most of the spots. No spots, however, are found in a strip 1 cm. to 2 cm. wide which extends along the mid-dorsal surface of the head and bill, and also in a similar strip of the mid-ventral surface of the bill, as shown in Fig. 1.

The pores are arranged in small groups of from three to twenty each. From the counting of some fifty of these groups, they were found to contain an average of about eleven pores. From two to ten of these smaller groups are collected into larger groups which measure from 2 mm. to 12 mm. in diameter and correspond to the above-mentioned spots. These larger groups are usually circular or ovoid, except on the gill-flaps where they become more or less linear. Close around the eye and nose, where the pores are very numerous, the larger groups are not well defined, but the smaller ones are as distinct as elsewhere. The smaller groups of one fish were counted and found to be distributed as follows: On the dorsal surface of the bill, 1845; on the ventral surface of the bill, 1648 ; on the head, 760; on the gill-flaps, 926. Taking 11 as the average number of pores in each of the smaller groups, the approximate total number is 57,365.

The pores usually open singly, but in some instances, two or even three pores have a common opening. The form of the opening when single is circular or oval with a diameter of from 0.3 mm. to 0.5 mm. Sections show that the depth of the pores is from three to five times the thickness of the epithelium, instead of being no deeper than the epithelium as shown by COLLINGE (1, Pl. 39, Fig. 5). Serial sections show that the general form of the pores is cylindrical. In some the lumen diminishes toward the base of the pore, becoming conical, while in others it increases toward the base of the pore becoming flask shaped. Occasionally a pore has a lateral sacculation.

The primitive pores are frequently in close proximity to the lateral line canals and their branches, yet in no case has the writer observed a connection between the two, and is consequently unable to confirm the statement by COLLINGE (1, p. 512) that many of the branches of the lateral line canal end in primitive pores. COLLINGE (1, p. 510) expressly states that his material was in poor condition for histological study and it is probable that herein lies the explanation of his error.

The epidermis consists of from twelve to fourteen layers of cells which at the surface are of the squamous type. These change gradually into the deeper lying low cuboidal cells and finally into the columnar cells of the basal layer (Fig. 3). At the margin of the pores, the epidermis becomes thinner and as it passes over into the neck of the pore it is further reduced to four or five layers. On the sides of the pore the superficial epithelial cells are elongated and have finger-like processes, which project freely into its lumen (Fig. 3, *m.c.*). The processes do not extend into the lumen of the pore at right angles to the surface of the epithelium, but slant toward the opening of the pore. These cells, which may be spoken of as marginal cells, stain similar to those in the deeper layers of the epidermis.

The bottom of the pore is covered by a single layer of epithelium, which is composed of two entirely different types of cells (Fig. 3). The cells of the first type (*sup.c.*) are the more numerous and resemble low columnar cells, excepting that in most instances they present an oval or oblong profile with the nucleus well out toward the distal end (Fig. 6). These cells lie frequently in close contact and sometimes in small groups. Scattered among these cells at more or less regular intervals are the cells which belong to the second type (*sen.c.*) and which in profile appear much like inverted Indian clubs (Fig. 6). The expanded portions of the cells are mostly superficial to the cells of the first type, while the slender portions lie between them. The distal extremities of these cells are drawn out into slender conical processes which are quite unlike the finger-like processes of the marginal cells in that they are more slender and have no granules in them. The bases of these cells are broadly expanded where they come in contact with the basement membrane. Their nuclei are small and lie in the expanded distal portions. The most striking peculiarities of these cells are their form, deeply staining capacity and clear processes. Because of these peculiarities, the arrangement of the cells and the distribution upon them of nerves, soon to be described, the writer has concluded that these last described cells are sensory, and those first described are supporting.

According to VAN WIJHE (2) and COLLINGE (1) the nerves supplying the sensory canal system of Polyodon are the trigeminus, the facialis and the vagus. The findings of these men differ as to some of the smaller branches of the nerves. The writer has found them in general to be as described by COLLINGE, but because of the complexity and communication of the nerve groups more work must be done upon them to determine the exact distribution of each.

In the regions where primitive pores are found, there are many medullated nerve trunks which in the immediate vicinity of a group of pores send off branches to it (Fig. 4). These branches contain only a few fibers which separate from each other, divide once or twice, then lose their myelin sheaths and immediately enter the bases of the primitive pores (Fig. 4). The axis cylinder after losing its myelin sheath appears as a dense strand of neuro-fibrillæ which divide and subdivide many times forming an end-brush (Fig. 5). As the branches of this end-brush enter the epithelium at the base of a pore they spread out and end in minute filaments upon both the sensory and supporting cells, as represented in Fig. 6.

In closing, the writer must emphasize the fact that the structure of the primitive pore is entirely unlike that figured and described by COLLINGE (1). Whatever the function of these numerous organs may be, it is certain that from a structural standpoint they possess the characters of a sense organ.

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LIST OF ABBREVIATIONS

c.t.c.—connective tissue cells.
e.—epidermis.
m.c.—marginal cells
n.—nerve.
n.f.—nerve fiber.
n.f.'—neuro-fibrillæ.
p.—pigment.
p.p.—primitive pore.
sen.c.—sensory cells.
sup.c.—supporting cells.

Fig. 1. The ventral surface of the bill of the Polyodon spathula, photograph, A. H. Cole. $\times\frac{3}{5}$.

Fig. 2. Two primitive pores (*p.p.*) seen in transverse section. The figure shows their relative width and depth, the deep staining capacity of the epithelium of their bases, a nerve (*n*) in cross-section, and strands of neuro-fibrillæ (*n.f.'*) entering the base of a pore. This section was made from a specimen taken from the dorsal surface of the bill and stained with gold chloride as above described. ×27.

Fig. 3. A primitive pore in transverse section, showing the character and thickness of the epithelium (*e*) upon the surface of the bill, the marginal cells (*m.c.*) of the sides of the pore, the supporting cells (*sup. c.*) and sensory cells (*sen.c.*) of the base of the pore, and pigment (*p.*) in the connective tissue about the pore. ×150.

Fig. 4. A large group of primitive pores, viewed from its deep surface. It shows the variation in size of the pores, the arrangement of them into smaller groups, the branching and distribution of the medullated nerve fibers to the group, and the accumulation of pigment among the pores.

Fig. 5. The base of a primitive pore cut so as to show the deeper portions of the sensory and supporting cells, and strands of neuro-fibrillæ (*n.f.'*) approaching and breaking up among them. ×90.

Fig. 6. Three sensory cells (*sen.c.*) and two supporting cells (*sup.c.*), with the termination of neuro-fibrillæ (*n.f.'*) upon them.

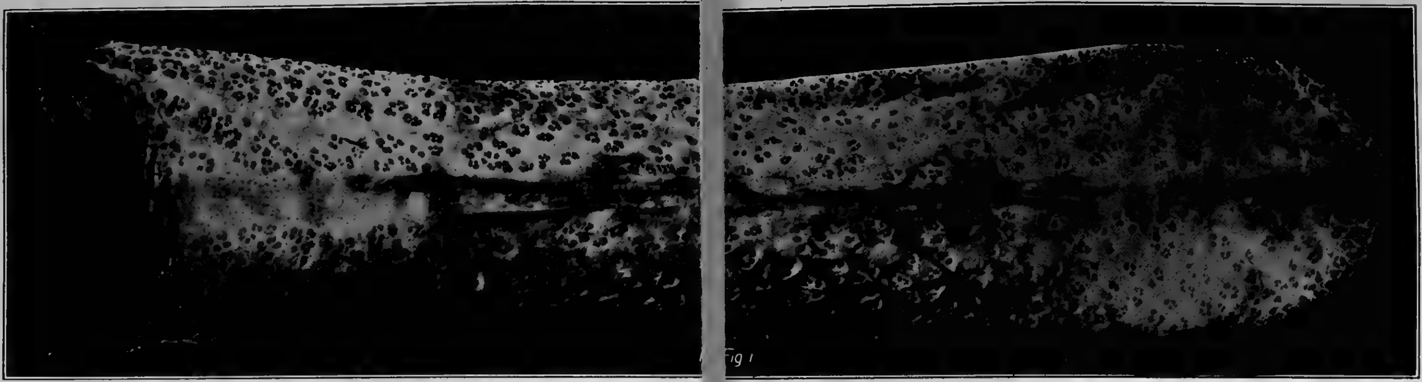

Fig 1

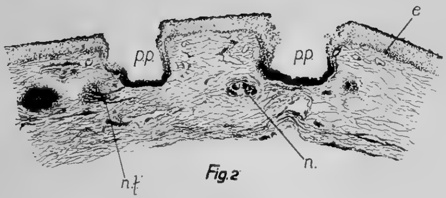

Fig. 2

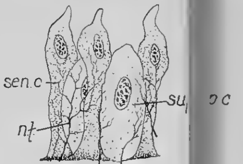

Fig. 6

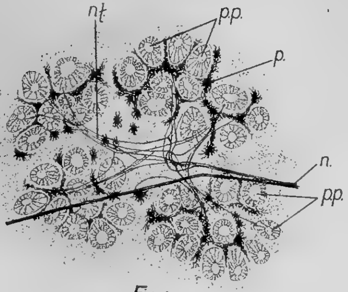

Fig. 4

Fig. 5

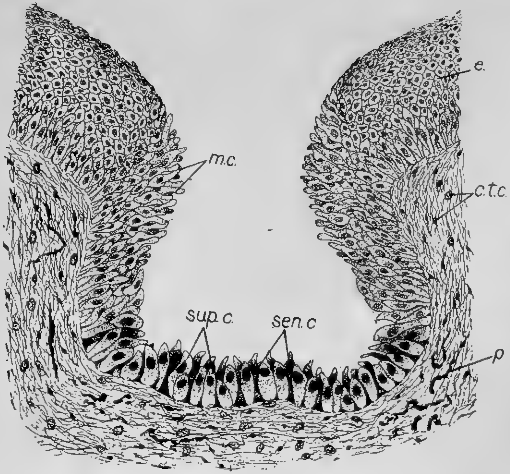

Fig. 3

J. S. Jones del.

THE REACTIONS OF CRAYFISH TO CHEMICAL STIMULI.[1]

BY

JAMES CARLETON BELL.

CONTENTS.

HISTORICAL.

1. *Reactions to Chemical Stimuli.*—HUXLEY, in his work on the crayfish, states that they seek calcareous waters, and are not found in streams flowing through granite regions. As to food, he says, they are not particular, eating almost any kind of animal or vegetable matter that they can get hold of, and perhaps giving preference to that which is tainted and decaying. They are frequently caught by hanging a piece of meat over a net and pulling

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[1] The following observations on the reactions of the crayfish to chemical stimuli were made in the Harvard Psychological Laboratory and are abridged in part from a thesis presented in fulfillment of the requirement for the degree of Doctor of Philosophy at Harvard University. Grateful acknowledgment is made to Dr. ROBERT M. YERKES for kindly criticism and helpful suggestions throughout the course of the work.

it up when the crayfish have had time to gather. ABBOTT[1] says that they lie in wait under stones for ethestomoids or "darters," which they seem to be very skillful in catching with their chelæ.

PUTNAM[2] contrasts the reaction of Combarus bartonii to food with that of Cambarus pellucidus, the blind crayfish.

> The moment the water in its jar is disturbed the eyed species rears itself upon its tail, throws out its large claws, seizes the piece of meat, or bread, and hastily conveying it to its mouth, generally holds on to the morsel until it is all eaten; though sometimes this species will take but a bite or two and then drop the food, and I do not think it will touch the same piece again. The blind species, on the contrary, darts back as soon as the food is dropped into the water and then extends its antennæ and stands as if on the alert for danger. After a long while, sometimes from fifteen to thirty minutes, it will cautiously crawl about the jar with its antennæ extended as if using them for the purpose of detecting danger ahead. On approaching the piece of meat, and before touching it, the animal gives a powerful backward jump and remains quiet for a while. It then cautiously approaches again, and sometimes will go through this performance three or four times before it concludes to touch the article, and when it does touch it, the result is another backward jump. After another quiet time it again approaches, perhaps only to jump back once more, but when it finally concludes that it is safe to continue in the vicinity of the meat, it feels with its antennæ for awhile, and then it takes the morsel in its claws and conveys it to its mouth. I have twice seen the meat dropped as it was passed along the base of the antennæ, as if the sense of smell, or more delicate organs of touch seated at that point, were again the cause of alarming the animal. When the jaws once begin to work, the piece of meat, or bread, if very small, is devoured, but if too large only a few bites are taken and the food is dropped and not again touched, though the animal then crawls over it and rests upon it without being in the least concerned.

GRABER[3] experimented upon various animals with chemicals, and found that Pagurus and Palinurus pay no attention to oil of roses, which is extremely disagreeable to most animals. Pagurus reacted to asafœtida by sinking one of its long eye-stalks every two to four minutes, and wiping it with its maxillipedes. Sometimes both eyes were lowered at once. The antennæ and the tail fan showed no reaction.

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[1] ABBOTT, C. C. Notes on the Habits of Certain Crayfish. *American Naturalist,* Vol. 7, pp. 30–34. 1873.

[2] PUTNAM, F. W. Remarks on the Mammoth Cave and some of its Animals. *Proceedings of the Society of Natural History, Boston,* Vol. 17, pp. 222–225. 1875.

[3] GRABER, V. Ueber die Empfindlichkeit einiger Meerthiere gegen Riechstoffe. *Biologisches Centralblatt,* Vol. 8, pp. 743–754. 1889.

BATESON[1] says that prawns and shrimps when blinded find pieces of food quite as quickly as when uninjured. Shrimps find their food more quickly than prawns. They hunt with their heads down like hounds, whereas prawns hunt with their heads up as usual. If a worm is just buried in the sand the shrimp will dig it out whether blinded or not. If worms are put into one tank and the water allowed to flow into another where the shrimps are, they become very restless and hunt about for the food. If a worm be hung in water about eight inches from the bottom, prawns will first hunt about on the bottom, but on coming directly under the booty they will rise to it at once.

NAGEL[2] has performed some very interesting experiments on Crustacea. The reactions of Pagurus, Astacus and Carcinus to chemical stimuli were observed, and the opinion is expressed that the chemical sense is not of as much value as sight and touch in localizing food. A blinded Pagurus was very much excited by meat but could not find it even when it was close to him. If the animal chanced to touch it the meat was seized at once. There seemed to be evidence that the antennules were the most sensitive to chemical stimuli, but when these were destroyed the reactions, though reduced, were by no means eliminated.

Astacus reacted to bits of Limburger cheese by moving their antennæ and antennules slightly and waving the filamentous endopodites of the maxillipedes vigorously. One would suppose that the latter might carry chemical sense organs, judging from the reaction, but this is not the case, for all the hairs are plumed and none have an opening at the base to admit the nerve. The animals would go to the cheese, touch it with their chelipedes, and then leave it without eating. Saccharine caused movements of the antennules different from anything ever observed under other conditions. Lavender water and 1 per cent. and 2 per cent. solutions of hydrochloric acid caused reactions which were interpreted as disagreeable. The former caused the antennules to be stuck down toward the mouth parts, while the acid made the animal wipe its antennules, then its antennæ, and finally but

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[1] BATESON, W. Notes on the Senses and Habits of some Crustacea. *Journal Marine Biological Association (Plymouth)*, Vol. 1 (N. S.), pp. 211–214. 1889.

[2] NAGEL, W. A. Geruchs- und Geschmackssinn. *Bibliotheca Zoologica, Leuckart und Chun*, Vol. 18, pp. 1–207. 1894.

invariably its eyes with the maxillipedes and chelipedes. This action seemed to indicate pain.

Experiments on Carcinus showed that a piece of meat, held one centimeter from the animal's head, caused a violent movement of the antennules but the meat was not grasped unless it touched the mouth parts. This was no sign of taste, for the same thing occurred with tasteless objects. Other reactions went to show that the antennules are organs of touch as well as of taste, a condition which does not seem to prevail in Pagurus and Astacus. NAGEL is in doubt as to how much Carcinus is guided by the chemical sense in procuring food. He often saw children catching them with strings without any bait, and thinks they were caught by touch and sight rather than by taste, or at least not solely by taste. In shallow water Carcinus seizes whatever touches or comes near him, but is never observed to hunt up bait at a distance.

BETHE[1] cannot agree with NAGEL regarding Carcinus. He thinks that in the search for food it is the chemical sense upon which the animal depends almost altogether, and that the eye plays a very insignificant rôle. If a Carcinus sees a bit of meat fall into the aquarium, he does not react at all at first and only after some seconds, when the juice has diffused to him through the water, do the antennules begin to wave vigorously. Seven or eight vessels were arranged one above the other with a small Carcinus in each. Water was conducted into the upper vessel and allowed to flow down through the others in succession. If a piece of meat was placed in the upper vessel the animal in the one below was seen to grow excited and reach upward, and this was repeated at a definite interval by each of the others in turn. When a piece of meat is thrown into an aquarium the animals begin to move soon after the stimulus reaches them, and proceed in a rather direct line to the food. Blinded animals do the same, even at a distance of half a meter or more. Therefore the chemical reaction is of most importance in the search for food. The mouth parts seem to be more sensitive to chemical stimulation than the antennæ or the antennules, since the animals react when the latter are removed. The threshold for chemical stimulation is extremely low, for the animals react vigorously to the trail left in

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[1] BETHE, ALB. Das Nervensystem von Carcinus maenas, I. *Archiv für mikroskopische Anatomie,* 50, pp. 460–547, 589–640. 1897.

the water by a finger that has been in contact with meat, and greedily devour filter-paper which has barely touched meat, but to really clean filter-paper they pay no attention.

HERRICK[1] experimented with ammonia gas and clam juice on various parts of the lobster. "All or nearly all the appendages react strongly to chemical stimuli, and in many cases the surface of the body is capable of receiving and responding to stimuli of various kinds." Ammonia gas on the telson sometimes caused violent flexion of the abdomen, on the swimmerets it occasioned scratching movements of the walking legs to remove the disturbance, on the mouth parts it produced violent chewing movements, and on the back it induced movements of the legs. The walking legs were most sensitive at their tips, and the chelæ closed vigorously when stimulated with the gas at the tip. The mouth parts were especially sensitive to clam juice, and active chewing movements were set up. Other portions of the body gave little or no response. It should be noted that HERRICK's method of experimentation was the rather crude one of laying the animal on its back on a table, sprinkling it now and then with sea-water, and applying the stimulus directly.

DEARBORN[2] thinks that the third maxillipedes are the organs of taste in the crayfish since they would sometimes remain extended a few seconds over a bit of meat and then seize it and press it to the mouth. One animal seized and chewed a piece of sheet rubber cut to represent a leech, but none of the rest would notice it. DEARBORN also experimented with three odors both in and out of the water but got no reactions whatever.

SPAULDING[3] found that the chemical stimulation of Pagurus with fish meat produced a reaction that was sufficiently strong to overcome a marked positive phototaxis, and in connection with the sight of the screen which darkened that portion of the aquarium where the food was placed, set up an association which even without the chemical stimulus was sufficient to overcome the avoidance of the dark.

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[1] HERRICK, F. H. The American Lobster: A Study of its Habits and Development. *Bulletin U. S. Fish Commission*, Vol. 15, pp. 1–252. 1895.

[2] DEARBORN, G. V. N. Notes on the Individual Psychophysiology of the Crayfish. *American Journal of Physiology*, Vol. 3, pp. 404–433. 1900.

[3] SPAULDING, E. An Establishment of Association in Hermit Crabs (Eupagurus longicarpus). *Journal of Comparative Neurology and Psychology*, Vol. 14, pp. 49–61. 1904.

2. *Organs for the Reception of Chemical Stimuli.*—There has been considerable difference of opinion as to the structure and nerve supply of the setæ in Crustacea, and a still greater difference of opinion as to their function. The confusion is intensified by the fact that many investigators generalize about "sensory hairs" without specifying just what hairs they mean, some contrast them with "ordinary hairs" others distinguish ordinary hairs, touch hairs, taste hairs, olfactory bristles, and auditory hairs, while still others contend that all hairs are sensory and reduce them to two types, tactile and chemical. A brief résumé of the more important of these views will be in place here.

The first careful work on the sensory hairs of crustacea was that of LEYDIG[1] in which he called attention to modified setæ on the distal half of the outer antennules and to these setæ he gave the name of olfactory tubes. Their walls are described as being thick at the base and growing thinner, more delicate at the end. Above the basal portion there is a slight nick in the walls, and above this the tube enlarges and, tapering somewhat toward a point, ends in a sort of button, which is either covered with a thin membrane or is perforated. Near these bunches of olfactory hairs there are feathered bristles of the ordinary heavy kind, and also lighter feathered bristles or "touch" hairs. The inner antennules and the antennæ present the same appearance except that the olfactory setæ are lacking. In a later work[2] LEYDIG examined the antennules of Cambarus pellucidus, the blind crayfish, and found that the outer ones were composed of about 36 segments, and that olfactory setæ occurred from the 15th segment to the end.

On the basis of this WRIGHT[3] claimed that C. pellucidus is better supplied with olfactory setæ than the crayfish with eyes, since C. propinquus, the most closely allied species, has only 18 or 19 segments, and only the distal 9 of these bear olfactory setæ. FAXON,[4] however, found C. propinquus may have as

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[1] LEYDIG, F. Ueber Geruchs- und Gehörorgane der Krebse und Insekten. *Müller's Archiv für Anatomie und Physiologie,* Jahrgang 1860, pp. 265–314, 1860.

[2] Untersuchungen zur Anatomie und Histologie der Thiere. *Bonn.* 1883.

[3] WRIGHT, R. R. Comparison of the So-called Olfactory Organs of Cambarus pellucidus with those of Cambarus propinquus. *American Naturalist,* Vol. 18, pp. 272–273. 1884.

[4] FAXTON W. Revision of the Astacidæ. *Memoirs of the Museum of Comparative Zoölogy, Harvard College,* Vol. 10, Part 4, pp. 1-186. 1885.

many as 35 segments, 15 or 16 of which may bear olfactory setæ. C. affinis may have 33 segments with 19 bearing olfactory setæ, and C. blandingii has as many as 50 segments, 29 with olfactory setæ. Thus WRIGHT'S contention is not supported by the facts. FAXON states, however, that the olfactory setæ of C. pellucidus are longer than those of most species of Cambarus.

In his study of the otocyst of decapod crustacea HENSEN[1] states that the auditory hairs differ from the touch hairs found in the otocyst in that the former do not spring directly from the walls but are raised on a small thin spherical membrane which permits great delicacy of movement. Three classes of auditory hairs are distinguished: (1) Otolith hairs, which surround the otoliths, and are more or less completely plumed; (2) free hairs in the otocyst, also called hooked hairs on account of being bent at a right angle near their middle, heavily plumed; (3) free auditory hairs on the surface of the body. These are also plumed. Besides these there is a little clump of hairs in the otocyst which are short and unplumed. HENSEN thinks the auditory hairs are rather sharply differentiated from the tactile hairs, chiefly by the spherical membrane at the base. In all sense hairs he finds a peculiar process, the lingula, extending into the central portion of the base, and to this the nerve is attached.

CLAUS,[2] discussing sense hairs in general but referring to olfactory setæ in particular, disagrees with LEYDIG in two points: (1) he affirms that the sense hairs are never open at the tip, and that any such appearance is due to their being broken off; (2) he asserts that the sense hairs are supplied with a single nerve each and that this nerve can be shown, in favorable specimens, to enter the hair—a thing which LEYDIG had denied. VOM RATH[3] confirms CLAUS' view that sense hairs are penetrated by the nerve, but is unable to say whether they are always closed by a membrane or not. In any case he showed by immersing the animals in methylene blue that the liquid gradually penetrated the interior of the olfactory setæ even when closed. VOM RATH distinguishes between

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[1] HENSEN, V. Studien über das Gehörorgan der Dekapoden. *Zeitschrift für wissenschaftliche Zoologie,* Vol. 13, pp. 319–412. 1863.

[2] CLAUS, C. Ueber das Verhalten des nervosen Endapparates an den Sinneshaaren der Crustaceen. *Zoologischer Anzeiger,* Vol. 14, pp. 363–368. 1891.

[3] VOM RATH, O. Zur Kenntniss der Hautsinnesorgane und des sensibeln Nervensystems der Arthropoden. *Zeitschrift für wissenschaftliche Zoologie,* Vol. 61, pp. 499–539. 1896.

sense hairs and ordinary ones by the criterion that the former have sense cells at the root, the latter have not. Like LEYDIG, he notes that the hair shaft consists of two parts, a proximal which is thick and strongly chitinized, and a distal which is paler and more delicate. He says that the only way to distinguish between different kinds of sense hairs is by their position and their mode of attachment. Besides the olfactory hairs on the antennules there are many unplumed touch hairs, which are stiff and sharp and situated on a strongly chitinized bulbous membrane. Touch hairs may also be half plumed or plumed, but plumed hairs attached to a delicate bulbous membrane are auditory hairs, whether they occur in the otocyst or on the free surface of the body. There is not one but several sense cells at the root of each hair, and the nerve fibrils, after passing through these, unite again into a terminal bundle which extends sometimes almost to the tip of the hair.

In Astacus RETZIUS [1] was unable to find any nerve entering the hairs on the broad parts of the maxillæ or of the abdominal appendages. He is inclined, therefore, to disagree with CLAUS and VOM RATH (in his earlier publications) regarding the innervation of sense hairs in Astacus and Palæmon, but admits that Cyclops shows the entrance of nerves into the antennular hairs.

BETHE [2] agrees that for most of the hairs on the mouth parts and pleopods of Astacus it would be impossible for the nerve to penetrate the hair, since there is no place for it to get through the chitinous membrane on which the hair sits. But *in certain places* on the mouth parts he finds hairs where the nerve does ramify on the inside of the hair. The chief places are on the edge of the endopodite of the second maxillipede, the edge of the larger palp of the first maxillipede, and the edges of both palps of the first maxilla. These, as well as the rest of the mouth parts, are also thickly covered with hairs which admit no nerve into their interior. These are always plumed, while the innervated hairs are never plumed.

GULLAND,[3] whose paper on "The Sense of Touch in Astacus"

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[1] RETZIUS, G. Das sensible Nervensystem der Crustaceen. *Biologische Untersuchungen*, Vol. 7, pp. 12–18. 1895.

[2] BETHE, A. Ein Beitrag zur Kenntniss des peripherischen Nervensystems von Astacus fluviatilis. *Anatomischer Anzeiger*, Vol. 12, pp. 31–34. 1896.

[3] GULLAND, G. L. The Sense of Touch in Astacus. *Proceedings of the Royal Physiological Society, Edinburgh*, Vol. 9, pp. 151–179. 1886.

seems to have escaped the notice of the German investigators, divides the setæ of the crayfish into two classes according to whether the lumen receives a nerve fibril into it or not. The hairs that have such an entering nerve fibril he calls "sensory setæ," those that have not are denominated "fringing setæ," since they usually form the fringes on the various appendages and segments of the body. The sensory setæ are tactile, auditory, or olfactory, and he devotes himself at once to the consideration of the tactile. These, he says, are rather long, smooth, hollow, and very elastic, partly on account of their substance and partly due to the mode of their attachment. This is as follows: "The lumen is widest at the base, as a general rule, and the walls thickest; suddenly the thick cylinder formed by the walls widens out, and the walls become thinner and more membranous, and roof in a dilation of the canal which pierces the integument; while the membrane itself passes up to become continuous with the cuticular thickening or 'areola' which surrounds the base of the seta, and rises slightly above the level of the cuticle." A little less than half way up the seta there is a joint-like appearance, and from here the hair tapers to a point, or swells out again into a small knob which has a slight depression at the tip like an elephant's proboscis. The lumen extends almost to the point, but there is no opening. The nerve fiber enters the lumen but does not pass all the way up the seta; rather it is attached or opposed to an oval surface a very short distance from the base of the seta, but distinctly within the lumen. As to the nature of this attachment to the oval surface, GULLAND could give no further account. The fringing setæ, on the other hand, have the lumen closed near the proximal end by a thick chitinous ingrowth, and there is no nerve supply. The fringing setæ are invariably plumed. GULLAND gives a minute and extended account of the distribution and arrangement of the tactile setæ, to the effect that they are found on almost all parts of the body, except the eye-stalks and the carapace. He says that only the setæ on the middle segments of the antennules are olfactory, those at the distal end being tactile. The arrangement of tactile setæ on the mouth parts agrees quite closely with that of BETHE indicated above.

The most recent as well as the most lucid account of sensory setæ in decapod Crustacea, so far as my knowledge goes, is that of PRENTISS[1] who, although he is primarily interested in the study of the otocyst, gives some attention to sensory hairs in general. As a result of extended physiological experimentation both he and BEER[2] deny an auditory function to any setæ, whether within the otocyst or without. In other words they assert that the animals give no response to true auditory stimuli, that the otocyst is an organ of equilibration more properly called "statocyst," and therefore that no setæ can rightly be called auditory. PRENTISS says, "All sensory bristles of decapod Crustacea can be divided into two general types: (1) Tactile bristles, having typically a long, straight, plumed, attenuate shaft, attached at the base by a thin spherical enlargement, which allows great freedom of movement. Auditory hairs, so-called, are merely modifications of these, for all gradations between the two exist. Tactile hairs are found on nearly all the appendages, and on some parts of the body. (2) Olfactory bristles, which are short, cylindrical or slightly tapering, and firmly attached as compared with tactile hairs, there being no marked basal enlargement. At the tip the chitin is either pierced by a pore, or ends in a thin, permeable membrane, which allows substances in solution to enter the cavity of the hair. If found on the first or second antennæ, they are termed olfactory hairs; when on the oral appendages, taste or gustatory bristles, though their functions are probably the same." Thus the term "chemical hairs" would include both classes, olfactory and gustatory, and in view of the practical difficulty of distinguishing between olfactory and gustatory reactions in aquatic animals, would be the better term to apply. It is to be noted that all chemical hairs, according to PRENTISS, are smooth, or unplumed. In regard to the innervation, all the tactile hairs examined (otocyst and mouth parts) showed the same form, a single nerve fiber running to the base of the hair and terminating in the spherical enlargement without branching, and in no case entering the lumen of the hair proper. The chemical hairs, on the other hand, present quite a different appearance. Here the number of ganglion cells and peripheral fibers going to each hair varied from ten on the

[1] PRENTISS, C. W. The Otocyst of Decapod Crustacea. *Bulletin of the Museum of Comparative Zoölogy at Harvard College,* Vol. 36, pp. 165–251. 1901.

[2] BEER, T. Vergleichend-physiologische Studien zur Statocysten function. I. Ueber den angeblihen Gehörsinn und das angebliche Gehörorgan der Crustaceen. *Archiv für die gesammte Physiologie,* Vol. 73, pp. 1–49. 1898. II. Versuche an Crustaceen. *Ibid.,* Vol. 74, pp. 364–382. 1899.

mouth parts to over a hundred on the antennules. There was no spherical membrane separating the nerve from the lumen of the hair, and the terminal strand entered the hair and ended freely along the lower two-thirds. HENSEN'S group of short unplumed hairs in the otocyst is not mentioned by PRENTISS in his discussion of Palæmonetes, Crangon and Cambarus. In the otocyst of Carcinus he speaks of "group hairs," 200 in number, which are "short, thick, and blunt, without a trace of fringing filaments." These, however, have the same sort of innervation as all the other hairs observed in the otocyst, and PRENTISS considers them "degenerate tactile hairs" which have lost their plumage.

From this review it will be seen that our knowledge of the setæ of decapod Crustacea is anything but satisfactory. All of the authors discuss sense hairs and speak of different kinds of sense hairs, leaving it to be inferred that there are other kinds of hairs not sensory in function. GULLAND distinguishes sharply between sensory setæ and fringing setæ, but his criterion is the presence or absence of a nerve fibril in the lumen of the hair. Moreover, his sensory setæ are all smooth hairs, whereas HENSEN, VOM RATH, and especially PRENTISS have shown conclusively that at least some plumed hairs have a sensory function. VOM RATH, on the other hand, admits the possibility (though his preparations did not seem to support it) that all setæ are sensory, and PRENTISS, though he does not say so, seems to incline to that view. If, then, we follow PRENTISS' account and say that all hairs are sensory, that plumed setæ supplied by a single nerve which does not enter the lumen are tactile, and that smooth setæ which are supplied with nerve bundles entering the hair and ramifying along its lower two-thirds are chemical, we must assume that LEYDIG failed to observe those nerve ramifications owing to faulty impregnation, that all of the hairs studied by HENSEN were tactile, and that CLAUS and VOM RATH selected only smooth, chemical hairs for histological examination, neglecting the tactile altogether. Moreover, GULLAND'S description of "tactile" hairs and their innervation tallies very well indeed with PRENTISS' account of chemical setæ, so that we may assume the latter were what GULLAND was describing. In that case, however, we shall have to assert that chemical hairs are found in considerable profusion all over the body, just as HERRICK[1] has found that some fishes have chemical sense organs all over the body.

It is hoped that the following observations may throw some light on this question from the physiological side.

EXPERIMENTAL.

The investigations of GRABER and NAGEL on the reactions of Crustacea to chemical stimuli are open to the objection that no details are given to indicate how the stimuli were applied. The observations of HERRICK on the lobster, while much more definite, suffer from the highly abnormal position in which the animals were kept. In all of the following experiments upon the crayfish, Cambarus affinis, the animals were placed singly in a small, white enameled pan in about four centimeters of water. This water was changed and the pan rinsed out after every three or four stimulations. To make the stimulation, a little of the chemical substance to be tried was taken up in a fine pointed pipette and was pressed out in the immediate vicinity of the part to be stimulated. In order to follow its diffusion through the water, the substance was colored with a little eosin, or in the case of some substances with carmine. In this manner only a reaction which took place immediately after the diffusion of the substance to the part to be stimulated was counted as a reaction to the substance. Check tests were made on many of the animals with pure water and with water colored with eosin and with carmine. With pure water the only reaction ever obtained was from the pleopods of the abdomen, and with care in pressing the bulb of the pipette so that no current was set up in the water this was avoided. With the colored water there were slight reactions in many cases from the anterior portions of the animals. The reactions obtained with the various stimuli, however, were so decided and characteristic that the slight effects of the coloring matter could be discounted.

1. *Meat Juice.*—A piece of fresh beef was left overnight in just enough water to cover it and the juice then pressed out. To this the animals reacted very decidedly and with a positive chem-

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[1] HERRICK, C. J. Organ and Sense of Taste in Fishes. *Bulletin U. S. Fish Commission*, Vol. 22. pp. 237–272. 1903.

otaxis that was surprising when compared with their behavior toward a bit of meat itself. The contrast was doubtless due to the fact that here the stimulus was applied directly and in a concentrated form. As soon as any considerable quantity of the juice diffused through the water to the animal, the latter would face about and move toward the source of the stimulus, making vigorous chewing movements with the maxillæ. Fifteen animals were subjected to systematic tests for their response to meat juice. and each animal was stimulated in eleven different places, with the following results:

(1) The distal portion of the antennæ. Reactions were obtained from twelve out of the fifteen animals. The typical reactions were a slight movement (usually a quick jerk) of the antenna, vigorous chewing movements of the mouth parts, and in seven cases the quick orientation of the animal so that the mouth parts came in contact with the stimulus. In one case there was a vigorous snapping with the chelæ toward the source of the stimulus.

(2) The ends of the chelæ. Here the reactions were very prompt and decided. All the animals reacted except one. The typical reaction was an energetic grasping with the chela toward the source of the stimulus, accompanied frequently by chewing movements, and bringing the chelæ and first chelipedes to the mouth as if they held a bit of meat. In five cases the animal brought the mouth to the stimulus.

(3) The antennules. All but two animals responded, though the reactions were in general not so vigorous as those from the chelæ. The chief reactions were twitching the antennules, dropping the antennule stimulated and drawing it through the maxillipedes, in eight cases approach of the mouth to the stimulus, in three cases chewing movements and in two cases snapping with the chelæ.

(4) The mouth parts. Here of course the typical reaction was the chewing movements. These occurred in every case and were usually very vigorous, the animal frequently becoming quite excited. In five cases the chewing movements were accompanied by movements of the chelæ and chelipedes to the mouth with a sort of sweeping or scraping movement, as though they were scraping up food from the bottom of the vessel. In three cases there was a forward movement as if to come into closer contact with the stimulus.

(5) The first chelipedes or first pair of walking legs. Owing to the close proxmity of these with the mouth parts it was difficult to obtain a reaction that was due to the stimulation of these organs alone. Repeated trials were made with each animal, however, and no result was noted unless it was clearly from the stimulation of these members only. These were the most sensitive organs, next to the mouth parts. Every animal responded energetically. The responses were such as closing the forceps of the member stimulated as though closing on a bit of meat, in ten cases bringing the cheliped to the mouth and usually accompanying this with chewing movements, and in four cases the orientation of the mouth to the stimulus.

(6) The second chelipedes. Here the responses were not so vigorous, although they occurred in every case. In eight cases the member was brought to the mouth or moved in that direction, and in five cases this was accompanied by chewing movements of the mouth parts.

(7) The third chelipedes. Here there were six failures to respond, and four of the responses were only by a slight movement of the member stimulated. In two cases the chelipedes were moved toward the mouth, and in four cases the animal turned to the stimulus.

(8) The fourth chelipedes. Out of the fifteen animals experimented upon only four responded to this stimulus, and three of these did so only by a slight movement of the member. One animal reacted with chewing movements and turned toward the source of the stimulus.

(9) The pleopods and the ventral surface of the abdomen. It was not always possible to get at these readily since the animals frequently kept the abdomen tightly flexed, so that the pleopods were covered by the telson. By holding the animal on its back in the air for a few moments, however, it could usually be brought to straighten out. In this way they would remain straight for a few minutes after being put back into the water, and out of the total number eleven animals reacted to the stimulus. In two cases the animals faced about to the stimulus, in another the chelæ were closed and then brought to the mouth, and in still another case there were chewing movements accompanied by a general restlessness. In two cases there was a most interesting reaction. The animal raised itself on the chelæ and telson, bowing up into

an arch, pushed the second and third pairs of walking legs back to the pleopods, then brought them forward to the first pair which in turn were carried to the mouth, just as if they were passing forward a bit of meat. This process was continued four or five times in each case. In three other cases the bowing up on the chelæ and telson was observed but not the pantomimic passing of meat to the mouth.

(10) The plates of the telson. Here there were nine failures to respond. The response was usually a slight movement of the abdomen. In two cases there was a downward stroke of the pleopods and a quick, sharp flexion of the abdomen, while in one case the animal faced about to the source of the stimulus.

(11) The back of the carapace. All the animals but three reacted to this stimulus. The typical reaction was a movement of some sort, sometimes taking the form of a restless moving about and rubbing the chelæ and chelipedes against each other.

From the above experiments it will be seen that crayfish react to the chemical stimulus of meat juice when applied to any part of the body, and therefore we must conclude that there are organs for the reception of chemical stimuli scattered all over the body. These observations confirm the view that GULLAND, in studying the smooth hairs which, he says, are found on all the appendages, had to do with chemical setæ, and not, as he thought, with tactile. His statement, however, that no such smooth hairs are found on the carapace is not in accord with these results, and we must assume that more careful observation would reveal some kind of chemical sense organs there as well. That the stimuli were received by organs on the carapace, and were localized by the animal on a rather definite portion of the carapace, and that the reactions were not due to diffusion to the appendages below, will appear clearly in the later experiments with acids, etc. While it must be said that the crayfish may respond to a chemical stimulus on any portion of the body, it will be observed that the responses are more regular and more decided on the anterior appendages, while the posterior walking legs and the telson are much less sensitive. This agrees with the observation of BETHE and PRENTISS that the smooth hairs are more luxuriantly developed on the anterior appendages. So far as vigor and regularity of response are concerned, there is nothing in the present experiments to indicate that the antennules are specially modified organs for the reception of chemical stimuli. More decided and definite responses were obtained from the chelæ, the mouth parts, and the first and second chelipedes. There was one characteristic reaction, however. The antennule stimulated was frequently lowered to the mouth, clasped by the third maxillipedes, and drawn up through them. Could we hazard the guess that the antennules are a sort of outpost for chemical stimuli, and that when stimulated they are brought to the mouth in order to give the animal opportunity to examine the substance more carefully? If so, it cannot be because they are more sensitive than the antennæ and chelæ but only more mobile. On the other hand, the action may be merely a wiping reflex to clean the organs of the stimulating substance. The most sensitive appendages are decidedly the first and second chelipedes. The general tendency of the reactions was unquestionably to bring the animal into more of the stimulus, in other words a marked positive chemotaxis to meat juice was exhibited.

2. *Lavender Water.*—As stated above, NAGEL experimented on crayfish with lavender water, and interpreted the dropping of the antennules as an indication of a disagreeable experience. In view of the reactions already observed, this interpretation is scarcely justified. A series of experiments was made on five animals in each of the eleven regions mentioned above to determine their exact reaction to lavender water. (1) Three out of the five reacted to the stimulus on the antennæ, one by removing the part stimulated, two by backing off from the spot. (2) Four responded to stimulation of the chelæ, one by removing the member, three by withdrawing from the place. (3) From the antennules there were four responses out of five, three being movements away from the stimulus, and one drawing the antennule through the maxillipedes. (4) Four animals reacted when the mouth parts were stimulated, one with a slight movement, three with a vigorous fanning by the filamentous endopodites of the maxillipedes. This fanning set up a decided current from behind forward which tended to carry the substance away from the mouth parts. Along with this in two cases there was a vigorous pushing outward and forward with the first and second chelipedes and the maxillipedes, as though to ward off and push away the substance. In no case were any chewing movements noticed. (5) All five animals responded very vigorously to stimulation on the first chelipedes,

four showing marked avoidance by retreating or removing the member. In one case the animal pushed outward with the chelæ as though fending off the substance, and in another there were movements of the mouth parts but more as if cleaning off an offending substance than as if feeding, while the cheliped stimulated was brought to the mouth, the forceps closed, the member pushed outward to its fullest extent, and the forceps opened, precisely as if casting something away. (6) The reactions from the second chelipedes of all five animals were of the same sort as those from the first chelipedes, and seemingly were about as vigorous. (7 and 8) Only two animals out of the five reacted to stimulation of the third and fourth chelipedes, and that by a slight movement of avoidance. (9 and 10) Stimulation of the abdominal pleopods affected only two of the animals, causing a flexion of the abdomen, while three responded in the same manner to stimulation of the dorsal surface of the telson. (11) On the carapace only two animals reacted, and that merely with a slight movement.

The striking feature in these experiments with lavender water is the uniform avoidance of the stimulus on the part of all the animals that responded. Again we find the first and second chelipedes apparently the most sensitive, and the reactions from these and the mouth parts especially vigorous and characteristic. Noteworthy is the absence of chewing movements when the mouth parts are stimulated.

3. Acetic Acid.—The same five animals were tested in like manner with a 10 per cent. solution of acetic acid. Owing to precipitation of the eosin in this solution carmine was used as a coloring substance. Here the reactions were more constant and striking than with lavender water. (1) All the animals responded to stimulation on the antennæ, four by moving the organ stimulated, one by a quick jump backward. (2) Stimulation of the chelæ produced vigorous and striking reactions in every case. As soon as the acid diffused to the member violent chewing movements were set up, the limb was drawn in and rubbed vigorously by the first and second chelipedes and the maxillipedes. After the rubbing the chelipedes were also brought to the mouth and rubbed by the maxillipedes. All the while chewing movements were kept up. (3) When the antennules were stimulated three animals jumped back, one of these and the two others dropped the antennule, and one animal rubbed the antennule with the maxillipedes. (4)

When the acid touched the mouth parts three animals jumped back, three rubbed the mouth with the chelæ and the first and second chelipedes, two fanned outward with the filamentous endopodites, and one kept up strong chewing movements. In one case the stimulation of the mouth parts caused a convulsive contraction of all the members, followed by an almost total cessation of movement for eight minutes, except for a few slight tremulous grasping movements of the first chelipedes. On being put back in the aquarium the animal became active again and a few hours later seemed none the worse for the experience. None of the others were affected in this way. (5 and 6) The first and second chelipedes when stimulated were invariably rubbed by the others and wiped by the maxillipedes, and frequently the animals jumped back from the stimulus. Reactions occurred in every instance and were very prompt and decided. (7 and 8) Only four animals responded to stimulation of the third and fourth chelipedes, and the response was a movement of the part away from the stimulus. (9) When the ventral surface of the abdomen was stimulated three of the animals reacted by bowing up on the telson and chelæ, rubbing, pulling and clawing at the pleopods with the chelipedes for perhaps as much as a minute. In the case of the other two animals the abdomen was tightly flexed and the animals sprang away. (10) In every case stimulation of the telson caused a quick, strong flexion of the abdomen, and in one case the animal jumped half way across the pan. (11) In two cases the back of the carapace gave no reaction, in two there was a slight restlessness, and in the fifth case the animal reached up and scratched the stimulated spot with one of the second chelipedes, a feat which was by no means easy to execute, and the like of which was not observed with either lavender water or meat juice. The same animal, when stimulated on the eye, rubbed the spot vigorously with the second cheliped on that side. This animal was decidedly the liveliest of the lot in all the reactions. Once as it was moving around the pan it came upon a drop of the solution diffusing through the water. Immediately the forceps of the chelipedes closed and were brought to the mouth, the mouth was brought over the stimulus, and decided chewing movements were observed, just as if the stimulus had been meat juice. This was the only case where such behavior was observed.

Why chewing movements should be set up by stimulation of the chelæ and chelipedes with acid I cannot conjecture. Sometimes when the stimulus was on the outer and under portion of a chela the contortions of the animal in its efforts to get the spot up to the mouth were violent and even grotesque. Both this and the reaction to the spot on the carapace indicate a tolerably definite localization of chemical stimuli.

4. Hydrochloric Acid.—NAGEL, as already mentioned, states that when Astacus was stimulated with a 1 per cent. solution of this acid the animal wiped its antennules, then its antennæ, and finally but invariably its eyes with its maxillipedes and chelipedes. This action was thought to indicate pain. NAGEL does not indicate in detail the method of experimentation and it is probable that no great care was taken to stimulate particular portions of the animal, and from what we have already learned regarding reactions to acetic acid we can say that the reactions he describes are those we would expect from a general stimulation of the whole anterior surface. To get more accurate data on this point five animals were tested in the manner indicated above with a 1 per cent. solution of hydrochloric acid. (1) Antennæ. Four animals out of the five responded. The most marked response was a quick movement of the organ away from the stimulus. In one case there was a quick spreading of the chelæ as if for the attitude of attack, in another the animal faced sharply about toward the stimulus, and in a third the antennules were wiped by the maxillipedes as the animal moved off. In no case were the antennæ wiped or rubbed. (2) Chelæ. All the animals reacted, two by springing away from the stimulus, two by snapping the forceps of the chelæ and in one case bringing the chela to the mouth and accompanying the action with chewing movements, and one by drawing the antennules between the maxillipedes. (3) Antennules. Three animals drew the member through the maxillipedes, one avoided the stimulus, and one grasped with the chelæ and made vigorous chewing movements. In two cases the animal faced about to the stimulus, and in one case even seized the pipette in its forceps—a thing which had not occurred before. (4) Mouth parts. The reactions were very vigorous in all cases. The chewing movements were naturally the most striking, these being violent in all cases but one. That one animal merely sprang away from the stimulus. In three cases there was grasping with the chelæ and chelipedes, in two the mouth was rubbed by the chelipedes, and in one the animal faced about to the stimulus. (5 and 6) First and second chelipedes. There was a very decided reaction to each stimulus, consisting usually of a quick grasping by the member stimulated and bringing it to the mouth, where it was rubbed by the maxillipedes. (7 and 8) Third and fourth chelipedes. Three of the animals quickly drew the member away, the other two jumped and faced toward the stimulus. (9) Ventral surface of abdomen. Two animals sprang away from the stimulus, one faced toward it, one bowed up on the telson and chelæ, rubbing and pulling at the pleopods with the second and fourth chelipedes, while the fifth bowed up likewise, but rubbed with the fourth chelipedes not the ventral but the *dorsal* surface of the abdomen—a much more difficult feat to accomplish. (10) Telson. The telson was usually folded and the abdomen sharply flexed. (11) Carapace. When the back of the carapace was touched there was a quick start and in one case the spot was scratched with the second, third and fourth chelipedes of both sides at once, the animal meanwhile lying flat on its ventral surface. In another case the animal grasped at the spot with the second cheliped as if to pull something away.

In one case where the left eye was stimulated the animal rubbed and dug at both eyes with the second and third chelipedes; in another case when a first cheliped was stimulated the eye on the same side was rubbed with the first and second chelipedes, while in a third case the stimulation of the antennule was followed by rubbing the eye with the second cheliped. In the latter case, however, the eye may have been stimulated directly by the diffusing liquid. The manner in which the animals rubbed the part stimulated seemed quite human in a way, and reminded one of the instinctive fashion in which we rub a slight bruise or burn.

One animal was tried with a 50 per cent. solution of hydrochloric acid. When the antennæ were touched they were jerked away quickly, and the antennules when stimulated were clawed at vigorously. Touched on the chelæ the animal writhed and struggled as if in great pain until the solution diffused. Stimulated on the mouth, the animal scratched and clawed and dug and scraped both the back of the carapace and the abdomen, drew in its eyes (a thing which had not occurred before in any of the chemical experiments) and rubbed them violently, and in general exhibited every sign of intense pain. The faintest trace on the telson caused the animal to roll up in a ball digging furiously at the spot.

It was not expected that the animal would survive, but it remained as active as ever, and was still alive when the whole lot was disposed of four months after the trial.

5. Saturated Salt Solution.—After the preceding experiments had been performed it was thought that it might be of interest to observe the reactions of the crayfish to substances which on the human tongue give the three other principal tastes, salt, sweet, and bitter. For the first a saturated solution of common salt was used, and five animals were experimented on as before. (1) Stimulation of the antennæ caused a quick movement of those organs and a general restlessness of the animal, accompanied in one case by a grasping with the chelipedes. (2) In every case the forceps of the chelæ were opened or closed, and the member was withdrawn. The animals became restless and moved away from the stimulus. One even stuck up its chelæ in the attitude of attack. (3) When the antennules were stimulated the animals grew restless, moved away, and invariably thrust the antennules down and wiped them with the maxillipedes. Only the member stimulated was lowered, never both at once. In one case there was grasping with the chela. (4) All the animals responded to stimulation of the mouth parts with restlessness, movement away from the stimulus, chewing movements in all cases but one, grasping with the chelipedes in two cases, and bringing them to the mouth in four. (5) The first chelipedes closed with a snap in four cases and were brought to the mouth in three. In all cases there was great restlessness and movement away from the stimulus. One animal rubbed the cheliped stimulated with the opposite one and with the second chelipedes. (6) Stimulation of the second chelipedes also caused decided restlessness and withdrawal from the stimulus in all cases. In three cases there was grasping with the member affected, and in one there was vigorous spreading of the forceps and rubbing with the other members. (7 and 8) On the third and fourth chelipedes the chief reactions were slight movement and increased restlessness. In two cases the first chelipedes were brought to the mouth, and in two the member stimulated was rubbed by others. In one case on stimulation of the right third cheliped the whole ventral surface was vigorously rubbed by the second, third and fourth chelipedes, then the right third was rubbed by the left fourth reaching under, and finally the member stimulated was thrust up to scratch the dorsal portion of the carapace. (9) Stimulation of the pleopods caused a sharp flexion of the abdomen at first, then in four cases the animal bowed up on the telson and pulled madly at the pleopods with the chelipedes. In one case even a chela was stuck back as if to assist in the work. (10) The telson was merely folded together, in one case the abdomen was flexed, and in one there was inhibition of a restless movement of the anterior members. (11) On the carapace only four animals reacted, usually with increased restlessness. In two cases there were vigorous attempts to rub the posterior portion of the carapace with the chelipedes. (12) Stimulation of the eyes caused retraction of those organs in every case but one, and in every case the animal rubbed and scraped and dug at the eyes with one, two, or even all the chelipedes on that side, and in one case even with the chela. One animal, in addition to this, pulled at the antennæ with the chelæ.

On the whole the reactions to salt were remarkable for their promptness, definiteness and vigor. They were in some respects even more marked than those with acids. Particularly the reactions from the chelipedes, the pleopods, the carapace and the eyes showed distinctive characteristics. The general nature of the reactions was such as might be considered to indicate that the experience was disagreeable, in contrast with that to meat juice, for instance.

6. Sugar.—To test the reactions to a sweet stimulus a 40 per cent. solution of sugar was used and five animals were experimented on as above. (1 and 2) To stimulation of the antenna all the animals responded but usually only with a slight movement of the organ. This was also the prevailing result from the chelæ. In one case the chelæ were spread, and in another the forceps were closed and the animal grew very quiet. (3) In every case the antennules were lowered and drawn through the folded maxillipedes, but sometimes this reaction was very slow. (4) The mouth parts showed chewing movements in four cases, and in three cases, the chelipedes were brought to the mouth, drawn through and wiped off by the maxillipedes. (5) From the first chelipedes the typical reactions were slight movements, chewing in one case, and in three cases the member stimulated was brought to the mouth and wiped by the maxillipedes. (6, 7 and 8) The second, third and fourth chelipedes responded in every case with slight movements. Some of these were so insignificant as to be almost imperceptible.

In the case of one animal, however, the stimulation of the third chelipedes on either side called forth the characteristic flight reflex caused by the sudden flexing of the abdomen. (9) To stimulation on the abdominal pleopods all animals responded, four by slowly flexing the abdomen, one by flattening the abdomen on the bottom of the pan and slowly spreading and contracting the telson. This flattening was observed in one other case before the abdomen was flexed. (10) The telson responded in only two animals, and that by a slight folding of the plates on each other. (11) No reaction was gotten from the carapace, except perhaps a slight restlessness in two cases. (12) Three animals reacted to stimulation on the eyes by drawing them in.

It is evident from all this that the reactions to sugar were less marked and definite than those to the other stimuli thus far used.

7. *Hydrochlorate of Quinine.*—In determining the reactions of the crayfish to a bitter substance a 2 per cent. solution of hydrochlorate of quinine was employed, and five animals were tested in the usual manner. Here the most striking result was the effect of the stimulus upon an active, more or less restless animal. In quite a number of cases such an animal would become suddenly quiet and remain so for as much as half a minute. This was never noted for any of the other stimuli. Aside from this characteristic reaction the responses were usually slight movements. The antennules were always lowered to the mouth, but very slowly and in a hesitating manner. When the mouth parts were stimulated the maxillipedes were slowly rubbed together, and in one case the antennules were lowered. None of the chelipedes responded with more than a slight movement. On the abdomen and telson the substance caused a cessation of all movement in four cases, a flexure of the abdomen in three, and folding of the telson plates slightly in three. From the carapace there was no reaction that one could be certain of. The most vigorous responses were from the eyes. Four animals reacted to this stimulus, one by slightly twitching one of the eyes, another by withdrawing the right eye but not the left, the other two by first digging fiercely at the eye with the second and third chelipedes, then drawing in the eye but continuing the scraping and digging.

The results of these experiments with chemicals upon the crayfish are in complete accord with HERRICK's observations on the lobster, to the effect that all parts of the body are receptive of chemical stimuli. This indicates that there are chemical receptive organs on all parts of the body. Whether these organs are more numerous on the anterior appendages or not, more decided and definite reactions are obtained from the stimulation of these members. All the observations are in agreement with BETHE's statement that the mouth parts are more sensitive than the antennules. Indeed both the chelæ and the first and second chelipedes respond more readily to chemical stimulation than the antennules. The accuracy of localization of a chemical stimulus on various parts of the body is considerable, as is evidenced in the experiments with acids and salt, where not only the member but even the very spot stimulated was frequently rubbed. Characteristic reactions were dropping the antennules and wiping them with the maxillipedes, quickly orienting the mouth to a meat juice stimulus, grasping with the chelæ and chelipedes and bringing them to the mouth as though holding food, bowing up on the telson when the ventral surface of the abdomen was stimulated and pantomimic passing of food to the mouth in the case of meat juice or digging at the pleopods with the chelipedes in the case of acids and salt, and vigorous retraction and rubbing of the eyes from salt and acids.

8. Feeding.—More important in the ordinary life of the organism than mere reactions to chemicals is the question to what extent and in what manner does the animal's reception of chemical stimuli assist it in obtaining food? In other words, how quickly and accurately does the animal orient itself to a chemical stimulus whose source is some distance away? What part does the chemical sense and what part do sight and touch play in procuring food?

(1) Reactions to Meat. In the air no reactions whatever were obtained to meat. The animal paid no attention to a bit of meat swung near it, and when the piece was touched to the antenna or antennule the only movement was one of avoidance. If held between the forceps of the chela the meat would sometimes be grasped but more often the chela would be withdrawn. When grasped the bit of meat was carried to the mouth in one case only and then soon discarded. This is what was to be expected, as the animal probably never eats anything in the air.

When first brought into the laboratory the animals will not eat anything even in water. It usually requires some two or three weeks for them to become sufficiently accustomed to their environment to take food readily. An interesting case of "learning," *i. e.*, modification of reaction, developed in this connection. The animals were regularly given their meat from a pin, bent slightly at the end to prevent the meat slipping off until it was given a little pull, and attached to a string. When the animals were first put into the aquarium they could not be got to notice this arrangement, but in a few weeks several of them learned to reach up for it quite vigorously.

After the animals have become accustomed to their surroundings, when a bit of meat is thrown into the aquarium in which they are lying quietly two or three minutes usually elapse before there is any movement. Then they begin to exhibit a vague general restlessness which increases until finally they start to move about. These movements seldom have any great definiteness, and it is only in the rarest cases that an animal is observed to move directly toward the meat. Usually the movements seem vague and undetermined, but the restlessness increases and frequently the vague movements gradually lead the animal nearer to the source of the stimulus. If the meat be suspended about five centimeters above the bottom of the aquarium the animal frequently passes directly under it without seeming to notice it. Often, however, the animal will return and pass back and forth under the meat, seeming to be vaguely attracted to the spot but not able to locate the source of the stimulus exactly. In case the antenna touches the meat the animal grasps at it at once with the chela, usually very accurately. In a few cases as the animal was passing to and fro under the meat it seemed to reach upward somewhat with the chelæ and if by chance one of these touched the morsel it was very quickly and accurately seized. This was especially observed of animals that had been kept in the aquarium for some time and fed in this manner. Moving the bit of meat slightly seemed to increase the tendency to reach upward, but did not materially increase the accuracy of these movements. Only when the meat was touched was there an accurate response.

From these observations we must conclude that sight plays little or no part in procuring food, and at best only serves to direct the animal's actions in a general way toward a moving object. The reaction to chemical stimulation is more important, and is seen in a general restlessness resulting in rather indefinite movements, which, nevertheless, usually bring the animal nearer the source of the stimulus. The ability to locate the source of chemical stimulation appears to be rather poorly developed. The chief dependence seems to be upon touch stimulation for the accurate localization of the food and the certainty of seizing. The great part which touch plays in obtaining food is still more clearly brought out in the following experiments with objects which, to the human tongue at least, are practically tasteless.

DEARBORN speaks of the avidity with which one animal seized a piece of sheet rubber cut to represent a leech, implying thereby that it was deceived by the appearance of the object. I find that almost all my animals will take a piece of rubber of whatever shape or color as soon as it is touched to the antennæ, chelæ or mouth parts, will press it to the mouth and chew at it for from thirty seconds to five minutes, and will then cast it aside. A piece of cotton batting was rolled into a wad and tied to the end of a string. This of course would not sink, but as soon as it was touched to an antenna that extended up to the surface of the water the animal reared on its telson, seized the wad, pressed it to its mouth, and chewed at it for two minutes. Not all of the animals would react to the cotton, but about half of them did, and some of those that did not would not react to meat either at the time. A more conclusive experiment was one with a small white pebble washed perfectly clean and suspended by a clean white silk thread, so that there might be no coloring matter to afford a chemical stimulus. When this was lying on the bottom of the aquarium or hanging quietly suspended in the water the animals paid no attention to it. If it was moved about in the water the animals did not make for it but rather moved away. When it was touched to the antennæ or mouth parts, however, it was seized in 60 per cent. of the cases, pressed to the mouth, and chewed from one to eight minutes. From this we conclude that the feeding reflex may be called forth by a touch stimulus as well as by a chemical stimulus, and we are strengthened in the conclusion that the animal depends largely on touch stimuli for localizing and capturing food. ABBOTT's statement that crayfish capture ethestomoids must be accepted on the assumption that the animals are borne directly against the chelæ of the waiting crayfish and then snapped at and seized.

(2) Reactions to Vegetables. Experiments were made with bits of apple, potato, turnip, carrot and onion. As the reactions to all of these were practically alike, a detailed account of the

experiments will not be given. When the piece of vegetable was suspended in the water it occasioned no restlessness of the animals, such as was produced by meat. Even when it was held within a centimeter of the antennules there was no response unless it happened to be touched by an antenna. As soon as it was touched to any part of the body, even the telson, the animal responded vigorously, seized the bit accurately and devoured it greedily. The gusto with which the animals chewed at and devoured the vegetables was even greater than that exhibited with meat. Onion especially seemed to be a favorite delicacy.

SUMMARY.

1. Crayfish react to meat juice very quickly and definitely with a positive chemotaxis. To lavender water, acids and salt the reactions were rather indicative of a negative chemotaxis. The reactions to sugar and quinine were on the whole less definite, and quinine in general seemed to have a quieting effect upon the animals.
2. The animals react to chemical stimulation on any part of the body, and therefore we must assume that there are chemical sense organs all over the body, just as in some fishes. Nevertheless for all stimuli the anterior appendages show the greatest sensitiveness, either because they are better supplied with chemical sense organs or because these appendages are more used in food getting.
3. There is no evidence that the antennules are specialized organs for the reception of chemical stimuli. It is true that the characteristic reaction of those organs is dropping to the mouth and being wiped by the maxillipedes, but more definite and more vigorous reactions were obtained from stimulation of the mouth parts and the first and second chelipedes.
4. There was a rather definite localization of the stimulation, as indicated by rubbing the outer portion of the chela, pulling at the abdominal appendages, digging at the eyes, and scratching and grasping at a limited spot on the carapace.
5. When the abdominal appendages were stimulated with meat juice some of the animals bowed up on the telson and made as if to pass the stimulus along to the mouth with the chelipedes. Stimulated with acid or salt the pleopods were merely pulled or scraped.

6. Acid, salt, sugar and quinine when applied to the eyes all caused retraction in some cases, the acid and salt producing the most vigorous reactions. Both before and after retraction the eyes were rubbed and dug at by the chelipedes.

7. To a strong solution of hydrochloric acid the reactions were such as to give every indication of pain.

8. Chemical stimulation with meat caused general restlessness and vague movements toward the source of the stimulus, but the animals seem to depend chiefly on touch for the accurate localization of food.

9. Vegetables do not seem to stimulate the animals at a distance but when touched to the appendages they are seized and devoured eagerly.

EDITORIAL.

ABNORMAL PSYCHOLOGY.

We take this opportunity to announce to our readers the appearance of two noteworthy contributions to the literature of Abnormal Psychology, namely, JASTROW'S[1] discussion of the subconscious and PRINCE'S[2] book on the dissociation of personality, as well as of a new journal devoted to the materials of one division of Comparative Psychology, *The Journal of Abnormal Psychology.*[3]

In his book on the subconscious Professor JASTROW has assembled a large number of observations concerning normal and abnormal subconscious states. The author's discussion of the facts of subconsciousness makes clear their importance in life and suggests many problems concerning the genesis of subconsciousness and its relations to consciousness. Aside from its value as a source of materials, this book is important because it shows that the subconscious is always with us, as much a part of our mental life as is consciousness proper and scarcely more likely to be abnormal or morbid. There is no reason for regarding it as mysterious; there is every reason for the recognition of its fundamental importance for life.

Dr. PRINCE'S book is the result of prolonged observation and experimental study of a case of multiple personality, which, as the author remarks, has proved to be a mine of psychological material. Miss BEAUCHAMP, the individual in question, exhibited, in addition to four fairly well organized and distinctly different personalities, certain phenomena of amnesia, aboulia, impulsion, automatism and subconscious activity which are of great interest to both neurologists and psychologists. The patient, natur-

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[1] JOSEPH JASTROW. The Subconscious. *Houghton, Mifflin and Company, Boston.* Pp. ix + 549. 1906. ($2.50.)

[2] MORTON PRINCE The Dissociation of a Personality. *Longmans, Green and Company, New York.* Pp. x + 569. 1906. ($2.80.)

[3] Published by the Old Corner Book Store, 27-29 Bromfield Street, Boston, Mass. Subscription price three dollars a year. Editorial communications should be addressed to Dr. MORTON PRINCE, 458 Beacon Street, Boston, Mass.

ally highly unstable nervously, subject to hallucinations and extremely suggestible, experienced a number of severe nervous shocks, the influence of which was to cleave her mind in various directions. One of the most interesting and important features of the case is the existence of a subconsciousness from early childhood. This subconsciousness claims that she never sleeps and she apparently knows everything that the primary self does or thinks, even to her dreams.

The book is written in the form of a biography of the case. It is fascinatingly interesting and of quite unusual value for the problems which it suggests as well as for its material of fact.

One result of the interest in abnormal psychology which Dr. PRINCE has acquired during his study of the case of Miss BEAUCHAMP is the establishment of *The Journal of Abnormal Psychology.* This is a bi-monthly publication under the editorship and management of Dr. PRINCE, with whom are associated as editors HUGO MÜNSTERBERG, JAMES J. PUTNAM, AUGUST HOCH, BORIS SIDIS, CHARLES L. DANA and ADOLF MEYER.

It is announced that the journal is "primarily intended for the publication of articles embodying clinical and laboratory researches in abnormal mental phenomena. It will also publish observations in the field of psychiatry proper, though it is intended that clinical and laboratory studies shall be given precedence over routine reports of cases or theoretical discussions."

In the first number of the new journal, which appeared in April, 1906, we find "The Pathogenesis of Some Impulsions," by PIERRE JANET; "What is Hypnosis?" by W. v. BECHTEREW; "Recent Experiences in the Study and Treatment of Hysteria at the Massachusetts General Hospital," etc., by JAMES J. PUTNAM, and "The Psychology of Sudden Conversion," by MORTON PRINCE.

We believe, and in this Dr. PRINCE heartily agrees, that the interests of our science and of individual investigators will be promoted by journalistic specialization, and we therefore propose to recommend *The Journal of Abnormal Psychology* for the publication of such articles submitted to us as are within its field. Dr. PRINCE likewise will suggest that articles in the fields of Comparative Neurology and Animal Psychology which are sent to him be submitted to *The Journal of Comparative Neurology and Psychology.*

ROBERT M. YERKES.

LITERARY NOTICES.

Loeb, Jacques. The Dynamics of Living Matter. Columbia University Biological Series. VIII. *The Macmillan Company, New York.* 1906. xi + 233. $3.00.

In the twelve lectures which constitute this volume the author deals rather summarily with the chemistry, physical constitution and manifestations of living matter. Living organisms are considered "as chemical machines, consisting essentially of colloidal material, which possess the peculiarities of automatically developing, preserving, and reproducing themselves. . . . . It is the purpose of these lectures to state to what extent we are able to control the phenomena of development, self-preservation, and reproduction" (p. 1).

After the introductory lecture, which is devoted to the presentation of the author's general point of view and aims, come five lectures on the chemical and electrical phenomena in living matter. The author's purpose is to indicate the present status of our knowledge of the physical chemistry of protoplasm rather than to discuss facts or problems. Three lectures treat of the influence of heat and light on living matter and of heliotropism and the tropisms in general, and the remaining lectures present certain facts of development, especially those of fertilization, heredity and regeneration.

Scarcely any of the material of the book is presented for the first time, and it is therefore unnecessary for us to attempt to restate the facts which the author has assembled. Still less is it necessary to restate his aims, his theoretical positions and his interpretation of the recent progress in bio-chemistry. It will suffice for this review that we note the general make-up and characteristics of the book and the content of those portions of it which deal with the nervous system and animal behavior.

The property of irritability, for example, is described as follows: "the normal qualities, especially the normal irritability, of animal tissues depend upon the presence in these tissues of Na-, K-, Ca-, and Mg-ions in the right proportion; that these ions are at least partly in combination with colloids (proteids or higher fatty acids or possibly carbohydrates), and that any sudden change in the relative proportions of these ion lipoids or ion proteids or ion carbohydrates alters the properties of the tissues and gives rise to an activity or an inhibition of the activity, according to the sense in which the change takes place." And further concerning other organic processes: "I believe that the natural rhythmical processes, such as heart-beat, respiration, etc., are due to a substitution of certain metal ions for others, these substitutions being caused by the enzymatic processes going on continually and by which, among others, metal ions are freed from certain combinations, and rendered available for others, as seems to be the case in the action of rennet in the coagulation of milk" (p. 95). The above quotation will serve to indicate the use which Loeb makes of bio-chemistry. It is of interest to note that he now believes that the toxic effects of electrolytes are due to chemical reactions and equilibrium conditions and not to the electric charges of the ions.

That the present stage of our knowledge of the chemistry of living matter is anything but satisfactory could hardly be more clearly indicated than by the following sentence from the pen of this enthusiastic seeker for physical-chemical descriptions of vital phenomena: "It appears. . . that by the word 'stimulation' we mean a process which is unknown to us, which, however, seems to consist . . . . . in the substitution of Na- or K-ions for Ca, or *vice versa*, in some colloidal (proteid or lipoid) compound of the muscle or nerve, whereby some physical qualities of the colloidal substances are changed" (p. 105). This sentence and many like it proves that he who at present attempts to describe life phenomena in terms of chemical processes must necessarily speculate as to the proper filling for numerous gaps in his descriptions.

In the lecture on heliotropism, we find for the most part the facts, as well as the explanatory theory, which the author has discussed in his several papers on reactions to light. The lecture has the striking merit of stating clearly and in readable form certain of the most important facts thus far discovered in this field.

A later lecture gives an equally lucid restatement of the author's orientation theory. From one point of view it is rather surprising that LOEB did not give more attention to facts, apparently not in accord with his theory, that have been brought to light by other investigators. In several of this series of lectures he has noted briefly the results of the work of a considerable number of investigators, but in this particular field it seems as if he were clinging to his past rather than moving forward either with or in advance of the progress of research. In this lecture on the tropisms a sentence occurs which seems to contain one word too many: "I have repeatedly pointed out that it is superfluous, and often in direct contradiction to the facts, to assume the existence of human sensations in lower animals, and to put these hypothetical sensations as a necessary link between the external stimulus and its motor effect" (p. 146). If the author really means to use the word human, it would seem that his statement is superfluous. This is a trivial matter apparently, merely a word more or less! yet if it is not a typographical error it suggests a lack of attention to distinctions which is disastrous for the progress of science.

The interesting materials of the lectures on fertilization, heredity and regeneration might be discussed more appropriately in a journal of experimental biology than in this *Journal*. It should be noted, however, that they present a considerable number of recently discovered facts in these fields, and point out in a stimulating way further possibilities of progress.

In criticising LOEB's book, we should not fail to consider the occasion of the preparation of these lectures. They were delivered in Columbia University. As a result of adaptation to this end they lack exhaustiveness and are somewhat dogmatic in statement.

ROBERT M. YERKES.

King, Willis P. Perjury for Pay; an Exposé of the Methods and Criminal Cunning of the Modern Malingerer. *The Burton Co., Kansas City, Mo.* 1906. $2.00.

Considerable psychological interest attaches to these detailed records of cases of malingering observed by the author while acting as Assistant Chief Surgeon of the Missouri Pacific Railway System.

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THE IMITATIVE TENDENCY OF WHITE RATS.[1]

BY

CHARLES SCOTT BERRY.

(*From the Harvard Psychological Laboratory.*)

CONTENTS.

I. PROBLEM AND METHOD.

This paper is an account of some experiments made for the purpose of determining to what extent white rats learn by imitating one another.

The animals studied were ten white rats, whose ages and sexes were as follows:

No.		*Sex*	*Date of Birth*
1	Albino	male	July 15, 1905
2	Albino	female	July 15, 1905
3	Albino	female	August 29, 1905
4	Albino	female	August 24, 1905
5	Albino	male	August 30, 1905
6	Black and white	male	August 30, 1905
7	Albino	female	August 30, 1905
8	Black and white	male	September 25, 1905
9	Black and white	—	September 25, 1905
10	Black and white	—	September 25, 1905

Nos. 9 and 10 died soon after the experiments were begun.

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[1] This investigation was carried on under the direction of Dr. Robert M. Yerkes, to whom I am greatly indebted for the suggestion of the problem and general method.

It was important in connection with the experiments to make the conditions such that the rat would make the greatest effort of which it was capable to perform the required act.

To get this result it was found necessary to fulfill three conditions. In the first place the animal must be entirely free from fear, otherwise its attention is diverted from the act to be performed. When the white rats first came under my care they were so timid that they could not be induced to perform the simplest acts. It was only through careful handling, and feeding them from my hand that their fear gradually disappeared. They were also frequently placed in the experiment-box, so that they were thoroughly familiar with it before the experiments were begun.

In the second place the experiments must be of such a nature that the rat is not required to perform any movements that are not natural to it. Pushing with the nose, climbing, digging, and grasping with the teeth and forepaws are movements that a rat naturally makes. No experiment was used that could not be performed by one or more of these movements.

In the third place the inducements for the rat to perform the act must be made as great as possible. The desire for food and companionship produced the most vigorous action. It was very difficult, however, to regulate the diet of the rats satisfactorily. If they were under-fed in order to induce them to make vigorous efforts to get the food placed on the outside of the experiment-box, they declined in strength and vigor; if they were given plenty of food they would not make any great effort to perform the required act. The best results were obtained by giving them enough food that they liked fairly well to keep them in good condition, but using as an inducement to the performance of the required act food of which they were particularly fond. Cheese and "Egg-O-See" came in this latter class.

The experiments were generally conducted in the morning, from nine to ten o'clock. The rats were fed once a day, and the time of feeding was immediately after the experiment.

II. EXPERIMENTS.

Experiment I. Climbing a Wire Ladder.

Method.—A glass jar 40 cm. in height and 15 cm. in diameter was fitted with a cover, in the center of which a large hole had been made. From a wooden bar placed across this hole a string hung down to within 5 cm. of the bottom of the jar. The purpose of the experiment was to discover whether the rats would climb out of the jar by means of the string. Rats Nos. 1, 2, 3 and 4 were tested, each being put in alone and left in the jar until he ceased to make any particular effort to get out. Every rat tried to get out by climbing up the side, and every rat took hold of the string with his forepaws, but not one made any attempt to climb it.

I now substituted for the string a wire ladder made of wire netting of a centimeter mesh. The ladder was 5 cm. wide and long enough to reach from one side of the bottom of the jar to the top of the opposite side. A small box containing food was placed on top of the jar beside the ladder. Food was also placed at frequent intervals on the ladder.

Results.—No. 1 when put into the jar ate all the food on the ladder that he could get by standing on his hind legs. After a few attempts he ceased trying to get the food that was just out of reach. He was in the jar twelve minutes in all.

No. 1 was now taken out and No. 2 put in. No. 2 climbed the ladder and entered the box in less than five minutes.

The next day No. 1 was again put into the jar by himself. As before, he ate the food within reach but made no effort to climb the ladder. After fifteen minutes No. 2 was put in with him. No. 1 looked on while No. 2 climbed out, and in less than five minutes followed him to the top of the ladder. He then returned to the bottom of the jar, but in about two minutes he again climbed the ladder, this time entering the box at the top of the jar.

No. 4 when put into the jar by himself climbed out in less than a minute; No. 5 got out in fifteen seconds; No. 6 in three minutes; and No. 7 in seven minutes. No. 3 ate the food within reach but made no effort to climb the ladder, although he was left in the jar twenty minutes. No. 4 was now put in with him. He saw No. 4 climb out but made no effort to follow him. The next day No. 3 was again put in by himself. He ate all the food within reach and stretched to the extent of standing on one leg in his vain efforts to seize the food that was just out of reach. He soon gave up and remained quiet. After sixteen minutes I put No. 4 in with him. But No. 4 would not climb the ladder. Both rats seemed to be cold and refused to make any particular effort to get out. No further trials were made with them.

Experiment II. Pushing Open a Swinging Door.

Method.—A wooden box, whose length was 96 cm., breadth 37 cm. and depth 14 cm. was covered with wire netting of a centimeter mesh. The box was divided into two parts by a wooden partition, and in the middle of this partition was a swinging door 10 cm. wide and 6 cm. high, which was made of the same material as the top of the box.

The act to be performed was to push the swinging door open and get the food placed in plain sight just beyond the door.

Results.—No. 4 was put into the box alone for ten minutes, but before the end of the time he had ceased to make any effort to get out. No. 3, who had already been taught to go through the door, was now put in with him. Although No. 4 saw No. 3 go through the door repeatedly, he did not succeed in getting through. The next day the experiment was repeated but the results were negative, as No. 4 would watch No. 3 go through the door but would make no effort to follow him through. No. 3 was now taken out and No. 1 and No. 2 were put in with No. 4. They went through the swinging door at once and No. 4 followed them through in less than two minutes.

Nos. 5 and 8 got through the swinging door in less than two minutes when put into the box alone; No. 9 got through in fifteen seconds. No. 7 did not get through although he opened the door part way. No. 5 was now placed in an apartment beyond the food in order to make the inducement greater for No. 7 to get out. Although he tried the door repeatedly he did not succeed in getting through in ten minutes. No. 5 was now put in with him. No. 5 passed through the door seven times, and No. 7 saw him go through three times. The first time that No. 5 went through the door No. 7 followed him to the extent of pushing the door part way open. The other two times that No. 7 saw No. 5 pass through he made no effort to follow him.

No. 6 was now put in with No. 7. No. 7 followed him part way through the door but jumped back the moment the door struck him. However, he succeeded in getting through in nineteen minutes. When put back he went through in fifteen seconds.

Experiment III. Digging Through Sawdust.

Method.—A wooden box 33 cm. long, 33 cm. wide and 14 cm. deep was covered by wire netting of a centimeter mesh. The box was divided into two parts by means of wire netting of the same mesh as the top. In the lower part of the wire partition a hole was made large enough for a rat to pass through. The hole was completely concealed by sawdust, packed along the entire side of the wire partition.

The task for the animals was to find the hole by digging in the sawdust and get through to the food which was placed in plain sight on the other side of the partition.

Results.—The time it took the different rats to perform the act was as follows:

No. 8 got through in 3′
No. 2 got through in 2′
No. 4 got through in 2′
No. 3 got through in 3′
No. 5 got through in 7′
No. 6 got through in 4′

No. 9 tried to get out by climbing, but made no attempt to dig, although he was left in the box by himself for ten minutes.

No. 7 after thirteen minutes gave up trying to get out; No. 1 gave up in fifteen minutes. After No. 1 had ceased to try to get out No. 2 was put in with him. No. 2 dug out at once and No. 1 followed him through. Put back by himself No. 1 dug through in thirty seconds.

After No. 7 gave up trying to get out No. 5 was put into the box with him. No. 5 dug out at once. The hole was immediately filled but No. 7 made no effort to dig through. In a few minutes No. 5 dug his way back to No. 7 and then No. 7 passed through the open hole. No. 7 was put back, the hole was filled, and No. 5 taken out, then No. 7 went at once to the right spot and dug through.

After No. 9 had ceased to make any effort to get out No. 7 was put in with him; No. 7 dug out at once and was followed out by No. 9. The hole was filled and No. 9 was put back. He made no attempt at digging. No. 7 dug his way out and in six times before No. 9 made any effort to dig, and then he did not dig enough to get through, although he did dig in the right place. No.

7 was put in with him two more times, but still No. 9 refused to make any further efforts to get out by digging. As he was cold and inactive no further trials were made.

Experiment IV. Pushing Open Door in Top of Box.

Method.—The apparatus consisted of a wire box 30 cm. long, 20 cm. wide and 12 cm. high. It was made of wire netting of half inch mesh. In the top of the box near one corner a wire door was made that opened upward. A rat could easily open this door by pushing up against it with his nose or forepaws. A small glass dish containing "Egg-O-See" was placed at one side of the closed door. To get the food it was necessary for the rat to raise the door and climb through.

First, one rat was taught to raise the door and climb through and then he was used to teach the others. The untrained rat being put into the box with the trained one had an opportunity to see him raise the door and climb out. If the untrained rat followed the trained one out he was allowed to eat a little food and then he was put back in the box by himself and kept there until he got out or ceased to make any particular effort to get out. The trained rat was then put in with him as before.

The tables used in the following experiments are largely self-explanatory. The first column represents the number of times the trained rat got out when put in with the untrained one. The second column represents the number of times the untrained rat saw the trained one open the door. The third column shows the number of times the untrained rat followed the trained one out. And the fourth column represents the number of times the untrained rat got out when put back in the box by himself, after having followed the trained one out. The last column is a record of the time it took the untrained rat to get out when put in the box by himself. If he did not get out by his own efforts no time record was made.

No. 2 IMITATING NO. 1.

No. 2 was put in the cage by himself for ten minutes. He tried very hard to get out but did not succeed.

In following No. 1 out No. 2 crowded through the swinging door while it was held partly open by the body of No. 1.

Date	*No. 1 gets out*	*No. 2 sees*	*No. 2 follows No. 1 out*	*No. 2 gets out*	*Time*
Nov. 8	8	8	2 (5, 8)	1	1'
Nov. 9	—	—	—	1	2'
Totals	8	8	2	2	

NO. 6 IMITATING NO. 1.

No. 6 was first put in the cage alone for ten minutes. He did not get out.

Date	*No. 1 gets out*	*No. 6 sees*	*No. 6 follows No. 1 out*	*No. 6 gets out*	*Time*
Nov. 9	16	5	0	—	—
Nov. 10	7	7	6	—	—
Nov. 10	—	—	—	1	5'
Nov. 11	1	1	1	—	—
	—	—	—	1	3'
	—	—	—	1	15"
Totals	24	13	7	3	

Each time that No. 6 followed No. 1 out he squeezed through the door as it was held partly open by the body of No. 1.

NO. 7 IMITATING NO. 6.

Date	*No. 6 gets out*	*No. 7 sees*	*No. 7 follows No. 6 out*	*No. 7 gets out*	*Time*
Nov. 11	19	15	9	—	—
Nov. 13	10	10	7	—	—
Totals	29	25	16		

Each time No. 7 followed No. 6 out he got through before the door fell; at first he did not follow No. 6 closely but after No. 6 got out a few times he followed him all about the cage. He soon discovered the location of the door so that he went to it when put back into the cage by himself; yet he did not learn to push it open with his nose as No. 6 did. At first he was quite energetic when put back, after having followed No. 6 out, but he soon reached a point where he made little or no effort when put into the cage alone but quietly waited until No. 6 was put in, when he became very active and followed him closely.

NO. 5 IMITATING NO. 6.

No. 5 was first put in by himself for a few minutes. He tried to get out but did not succeed.

Date	*No. 6 gets out*	*No. 5 sees*	*No. 5 follows No. 6 out*	*No. 5 gets out*	*Time*
Nov. 13	13	3	3	—	—
	—	—	—	1	—
Nov. 14	—	—	—	1	2′
Totals	13	3	3	2	

No. 5 saw No. 6 open the door only three times, yet he saw him several other times before he was entirely through the door, and two of these times he followed him out, getting to the door before it had completely closed.

NO. 8 IMITATING NO. 6.

No. 8 was first put in the cage by himself for five minutes. He did not get out.

Date	*No. 6 gets out*	*No. 8 sees*	No. *8 follows No. 6 out*	*No. 8 gets out*	*Time*
Nov. 14	7	7	5	—	—
Nov. 14	—	—	—	1	—
Nov. 14	—	—	—	1	1′
Totals	7	7	5	2	

No. 8 in following No. 6 out of the cage passed through the door while it was held open by the body of No. 6. In two cases, however, only the tail of No. 6 was in the door.

NO. 3 IMITATING NO. 1.

No. 3 was put in the cage by himself for ten minutes. He saw and apparently smelled the food but did not make any very strenuous effort to get out.

Date	*No. 1 gets out*	*No. 3 sees*	*No. 3 follows No. 1 out*	*No. 3 gets out*	*Time*
Nov. 15	2	2	2	—	—
	—	—	—	1	2′
Totals	2	2	2	1	

After following No. 1 out the first time, No. 3 was put back by himself for five minutes. During these five minutes he found the door and raised it a little, but then gave up and did nothing during the last two minutes. Previous to this experiment I had been allowing the rats to remain in the cage from one to five minutes when put back after following the leader out. The point was to let them try until they gave up, which was generally not longer than two or three minutes.

NO. 4 IMITATING NO. 1.

No. 4 was put in the box by himself for eighteen minutes. At first he made vigorous efforts to get out, but gave up before the end of the time.

Date	*No. 1 gets out*	*No. 4 sees*	*No. 4 follows No. 1 out*	*No. 4 gets out*	*Time*
Nov. 15	3	3	1 (3)	—	—
Nov. 16	2	2	1 (2)	—	—
Totals	5	5	2		

No. 4 was left in the cage five minutes each time after No. 1 got out. After he had followed No. 1 out the first time he tried the door when put back and raised it partly. The trouble seemed to be that he was not hungry enough to make any great effort to get out.

Experiment IV. Modified.

I now modified the experiment by changing the top of the cage in such a way that the door was no longer near the middle but to one side of the top, and the food instead of being placed near the door, as before, was removed as far from it as the size of the cage would permit. The purpose of the change was to discover how the rats would proceed to find the door in its new position. The following table shows the time it took the different rats to get out.

No. 1	6′
No. 6	3′
No. 8	5′
No. 2	3′
No. 5	1′
No. 3	15′
No. 4	24′

For some of the rats the center of attraction was the place where the door had been, and from that point they gradually worked outward until they found the door. Other rats started from the place where the dish containing the food was and gradually radiated out from that place until they found the door. When the rats found that the door was not in its former position they proceeded to examine the top of the cage until they found it.

If reference is made to p. 339, it will be seen that No. 7 did not get out of the cage, although he saw No. 6 pass out twenty-five times. When first put in, after the position of the door had been changed, he showed no preference for any particular part of the top of the cage. After ten minutes he gave up trying to get out. I then put into the cage a small piece of wood attached to a string and drew the piece of wood through the door fifteen times in about twelve minutes. The first few times No. 7 smelled of it and watched it go through the door. Once or twice he smelled of the door, but most of the time he paid no attention to the piece of wood. Not once did he attempt to follow it through the door. He was next given an opportunity of getting out by watching No. 6 and No. 8.

No. 7 was given five minutes in the cage by himself each time after No. 6 or No. 8 got out. The interesting feature was the way that he followed No. 6 or No. 8. In each case he tried to get through the door before it fell, but was a little too late until the seventh trial.

No. 7 IMITATING NO. 6 AND NO. 8.

Date	*No. 6 gets out*	*No. 7 sees*	*No. 7 follows No. 6 out*	*No. 7 gets out*	*Time*
Nov. 19	4	4	0	—	—
Nov. 21	1	1	0	—	—
	No. 8 gets out		*No. 7 follows No. 8 out*		
Nov. 21	2	2	1 (2)	—	—
Nov. 21	—	—	—	1	2′
Nov. 21	—	—	—	1	1′
Nov. 21	—	—	—	1	45″
Nov. 21	—	—	—	1	20″
Nov. 21	—	—	—	1	25″
Nov. 2		—	-	1	15″
Nov. 21	—	—	—	1	15″
Totals	7	7	1	7	

SUMMARY OF EXPERIMENT IV.

	Rat	*Chances to Imitate*	*Sees*	*Follows*	*Imitates*
	No. 2	8	8	2	yes
	No. 6	24	13	7	yes
	No. 8	7	7	5	yes
	No. 3	2	2	2	yes
	No. 7	36	32	17	yes
Average		15.4	12.4	6.6	
	No. 4	5	5	2	no

Experiment V. Pulling a Wooden Bar.

Method.—The apparatus consisted of a wire box with wooden floor. The lengths of the sides were 17 cm., 26 cm., 21 cm., and 13 cm.; height, 15 cm. In the small end of the box and about 5 cm. above the floor a door was made that was large enough for a rat to pass through easily. This door, which opened out, was held shut by a small wooden bar. To the end of the bar a string was fastened which passed up over the middle of the box and hung down into it. To the lower end of the string a white, horizontal wooden bar about 4 cm. long was fastened. It was 13 cm. from the door and 4 cm. below the top of the cage. A slight pull on the bar caused the door to fly open. Food was placed in front of the door in plain sight.

After a good deal of trouble No. 1 was taught to open the door by pulling the bar with his teeth and forepaws. Then the other rats were given opportunity to learn to get out by watching No. 1 open the door. In every case the untrained rat was fed when he followed No. 1 out. Then he was put back into the box alone for five minutes, his conduct being carefully noted. If he got out in less than the five minutes he was fed and put back again. This was continued until he thoroughly understood how to open the door. But if he did not get out within five minutes, No. 1 was put in with him again.

NO. 2 IMITATING NO. 1.

Date	*No. 1 gets out*	*No. 2 sees*	*No. 2 follows No. 1 out*	*No. 2 gets out*	*Time*
Dec. 2	1	0	1	—	—
	—	—	—	1	4′
Dec. 2	7	6	7	—	—
Dec. 4	1	1	1	—	—
Dec. 4	—	—	—	1	2′
Dec. 4	—	—	—	1	1′
Dec. 4	—	—	—	1	2′
Dec. 4	5	5	5	—	—
Dec. 5	1	1	1	—	—
Dec. 5	—	—	—	1	5′
Dec. 5	4	3	4	—	—
Dec. 6	—	—	—	1	4′
Dec. 6	—	—	—	1	3′
Dec. 6	—	—	—	1	1′
Dec. 6	—	—	—	1	15″
Dec. 6	—	—	—	1	40″
Dec. 6	—	—	—	1	10″
Dec. 6	—	—	—	1	30″
Totals	19	16	19	12	

At first when No. 2 was put in with No. 1 he paid but little attention to him. But after he had seen No. 1 open the door a few times he followed him all about the box. And finally he reached a point where he ran back and forth to the door while No. 1 was pulling on the bar.

NO. 3 IMITATING NO. 1

Date	*No. 1 gets out*	*No. 3 sees*	*No. 3 follows No. 1 out*	*No. 3 gets out*	*Time*
Dec. 6	—	—	—	1	5′
Dec. 6	2	0	1	—	—
Dec. 6	—	—	—	1	5′
Dec. 6	—	—	—	1	4′
Dec. 6	—	—	—	1	3′
Dec. 6	—	—	—	1	4′
Dec. 7	—	—	—	1	4′
Dec. 7	—	—	—	1	13′
Dec. 7	—	—	—	1	7′
Dec. 8	—	—	—	1	5′
Dec. 8	—	—	—	1	6′
Dec. 8	—	—	—	1	4′
Dec. 8	—	—	—	1	2′
Dec. 8	—	—	—	1	1′
Dec. 8	—	—	—	1	3′
Dec. 8	—	—	—	1	1′
Dec. 8	—	—	—	1	1′
Dec. 8	—	—	—	1	45″
Dec. 8	—	—	—	1	30″
Dec. 8	—	—	—	1	25″
Dec. 8	—	—	—	1	15″
Totals	2	0	1	20	

The interesting feature in connection with No. 3 was the way he learned to get out. At first he accidentally touched the bar; then his attention was attracted to it. After he had learned that pulling the bar was connected with opening the door he did not go directly to the bar from the door when put in the box, but first he smelled of the floor in various places and finally when he came almost under the bar, and his attention was attracted to it, he stood upon his hind legs and pulled it at once. It was not until the last three or four trials that he went directly to the bar from the door. Several times after he had opened the door by pulling the bar he did not go out at once, but began to gnaw the string; twice he gnawed it in two, and would have done so repeatedly if he had not been prevented.

NO. 4 LEARNS TO GET OUT.

Date	*Gets out*	*Time*
Dec. 9	1st time	7′
Dec. 9	2d time	6′
Dec. 9	3d time	3′30″
Dec. 9	4th time	1′30″
Dec. 9	5th time	1′
Dec. 9	6th time	1′30″
Dec. 9	7th time	20″
Dec. 9	8th time	20″
Dec. 9	9th time	30″

The total time it took No. 4 to learn how to get out was one hour, and his method of learning was similar to that of No. 3. At first he tried different places at random until he found the bar. After opening the door two or three times he went directly to it after pulling the bar. If he found the door closed he returned to the bar and pulled it again.

Experiment VI. Pulling a Knot With the Forepaws.

Method.—A wooden box 45 cm. long, 39 cm. wide and 13 cm. deep, inside measurements, was covered with wire netting of a centimeter mesh. The door (6x5 cm.) was in the middle of one end of the box. It opened outward and was held shut by a wooden bar on the outside. A string of black thread fastened to the end of the bar extended up and over the box, terminating in a knot about a centimeter above the top of the box, 13 cm. from the nearest side of the box, and 38 cm. from the door.

In order to open the door it was necessary for a rat to stand on his hind legs, reach up through the top, grasp the knot with his forepaws and pull it down. The knot was too far above the top of the box for him to seize it with his teeth without first using his forepaws.

It was my purpose to make the act so difficult that no rat would learn to do it by himself.

No. 2 was first taught to open the door. The knot was lowered until he could seize it with his teeth. Then it was gradually raised until it was too high for him to grasp it with his teeth without first seizing it with his forepaws and pulling it down.

Results.—The rats were now tested to see if they could learn to get out of the box without being taught. Not one succeeded. The following table gives the time that each rat had for learning to get out.

Date	*No. 3*	*No. 4*	*No. 5*	*No. 6*	*No. 7*	*No. 8*
Dec. 21	30′	30′	—	—	—	—
Dec. 22	60′	60′	60′	60′	60′	60′
Dec. 23	60′	60′	60′	60′	60′	60′
Jan. 1	60′	60′	60′	60′	60′	60′
Jan. 2	—	—	30′	30′	30′	30′
Totals	3½ hrs.	3½ hrs.	3½ hrs.	3½ hrs.	3½ hrs.	3½ hrs.

NO. 3 IMITATING NO. 2.

Date	*No. 2 gets out*	*No. 3 sees*	*No. 3 follows No. 2 out*	*No. 3 gets out*	*Time*
Jan. 2	5	5	5	—	—
Jan. 3	7	7	7	—	—
Jan. 4	7	7	7	—	—
Jan. 5	6	6	6	—	—
Totals	25	25	25		

It is to be noted that in all the trials in Experiment VI, the rat that is learning is put into the box by himself for a period of five minutes each time he follows the trained rat out.

The first time that No. 2 pulled the knot No. 3 pulled it after him and then followed him out. It was not until No. 3 had followed No. 2 out four times that he showed any marked preference for the knot-spot when put back. He would then go to the knot, smell of it and run to the door. This he did two or three times, but he made no effort to seize the knot. The next time No. 2 was, put in with him he ran back and forth from No. 2 to the door, while No. 2 was pulling at the knot.

After having followed No. 2 out nine times No. 3 made his first attempt to get hold of the knot with his teeth, and then ran directly to the door. This was the only time that he tried to seize the knot when alone in the box. Three or four times he pulled the knot after No. 2 had opened the door before he followed him out. Frequently he would stand beside No. 2 and try to get hold of the knot when No. 2 was reaching for it. After he had followed No. 2 out about ten times he became much less active when put back by himself, but was all attention and activity as soon as No. 2 was put in with him. He would then run back and forth from No. 2 to the door until No. 2 opened it, when he would not infrequently beat him out.

Once I put in No. 4 with No. 3 to see what No. 3 would do. He followed No. 4 all around the box for a little while, but as No. 4 did not get out he soon gave up following him closely.

NO. 4 IMITATING NO. 2.

Date	*No. 2 gets out*	*No. 4 sees*	*No. 4 follows No. 2 out*	*No. 4 gets out*	*Time*
Jan. 6	5	5	5	—	—
	—	—	—	1	3′
Jan. 6	1	1	1	—	—
Jan. 8	8	8	8	—	—
Jan. 9	7	7	7	—	—
Jan. 10	3	3	3	—	—
Totals	24	24	24	1	

No. 4's single success in getting out was due to the fact that the knot hung low enough for him to reach it with his teeth. I raised the knot so he could not get it except by using his forepaws.

Out of the twenty-four times that No. 2 pulled the knot, No. 4 stood up beside him twenty-one times. Twice No. 4 tried to get hold of the knot as No. 2 was reaching for it. Thirteen times No. 4 stayed behind long enough to pull the string before following No. 2 out.

Of the twenty-four times that No. 4 spent five minutes in the box by himself after having followed No. 2 out, he tried eleven times to get hold of the knot, sometimes making several attempts during the five minutes. The interesting point to be noted is that the first two or three times he was put into the box alone he paid no attention to the knot. After two more trials he began to smell of the knot and tried to get hold of it with his teeth. After having followed No. 2 out six or seven times, he became most active in his efforts to grasp the knot when put back by himself. This activity continued for several trials and then rapidly decreased. This was not because he was not hungry or did not want to get out, for when No. 2 was put in with him he became very active, standing up beside him and running back and forth to the door. Only once, however, did I see him try to get hold of the knot by grasping for it with his paw. He always used his teeth, hence his failure to get out.

NO. 6 IMITATING NO. 2.

Date	*No. 2 gets out*	*No. 6 sees*	*No. 6 follows No. 2 out*	*No. 6 gets out*	*Time*
Jan. 13	1	0	1	—	—
Jan. 13	—	—	—	1	2′
Jan. 15	6	4	6	—	—
Jan. 16	1	1	1	—	—
Jan. 16	—	—	—	1	2′
Jan. 16	4	3	4	—	—
Jan. 17	8	6	8	—	—
Jan. 18	7	2	7	—	—
Totals	27	16	27	2	

The two times that No. 6 got out he succeeded in seizing the knot with his teeth without using his forepaws to pull it down. When it was raised so he could not grasp it with his teeth, without first using his forepaws, he did not once succeed in getting hold of it. No. 2 always seized the knot with his forepaws and pulled it down until he could also get hold of it with his teeth.

Out of the twenty-seven times that No. 2 opened the door by pulling the knot, No. 6 stood up beside him at the knot sixteen times and tried to get hold of it eight times. Much of the time that No. 2 was trying to get hold of the knot No. 6 was running back and forth from him to the door.

Out of the twenty-seven times that No. 2 opened the door, No. 6 pulled the string twelve times before following him out.

Nearly every time that No. 6 was put back after following No. 2 out he made an effort to get hold of the knot with his teeth. After such an attempt he generally would run directly to the door but finding it closed he frequently would go back and try the knot again.

When first put in with No. 2 he did not follow him so closely as he did after No. 2 had got out a few times. It was also noticeable that he did not try as hard to get out when put back, after having followed No. 2 out fifteen or twenty times, as he did at first. He seemed to depend more and more upon No. 2 to open the door for him. Once I put No. 8 in with him. At first No. 6 followed him very closely, but soon gave it up, as No. 8 did not get out.

NO. 8 IMITATING NO. 2.

Date	*No. 2 gets out*	*No. 8 sees*	*No. 8 follows No. 2 out*	*No. 8 gets out*	*Time*
Jan. 19	6	2	6	—	—
Jan. 20	9	7	9	—	—
Jan. 22	9	6	9	—	—
Jan. 23	5	3	5	—	—
Totals	29	18	29		

I first put No. 8 in the box by himself. He tried hard to get out but showed no preference for any particular spot. The first time that No. 2 was put in with him they paid no attention to each other. No. 8 finally followed No. 2 out. But when No. 2 was put in the second time, No. 8 followed him very closely, standing up beside him while he was working at the knot.

Not once in the twenty-nine times that No. 8 was in the box alone did he try to get hold of the knot. He spent nearly all of his time licking a certain spot in the bottom of the box; but as soon as No. 2 was put in with him he quit licking the spot, followed him, and twelve or fifteen times stood up beside him as he was working at the knot. During the trials he spent most of his time running back and forth from No. 2 to the door. Part of the time he would stand halfway between him and the door, looking from one to the other, and the moment No. 2 got the door open he would dash through it in front of him.

Before beginning the experiment with No. 2 and No. 8, I put No. 1 in with No. 8. Neither paid much attention to the other. Again at the conclusion of the experiments with No. 8 and No. 2 I put No. 1 in with No. 8. No. 8 followed No. 1 quite closely but No. 1 paid little attention to him. When No. 8 was not following No. 1, he was running back and forth from him to the door.

NO. 5 IMITATING NO. 2.

Date	*No. 2 gets out*	*No. 5 sees*	*No. 5 follows No. 2 out*	*No. 5 gets out*	*Time*
Jan. 24	7	4	7	—	—
Jan. 25	8	6	8	—	—
Jan. 26	6	3	6	—	—
Jan. 27	6	1	6	—	—
Totals	27	14	27		

The first time No. 2 was put in with No. 5, No. 5 paid little or no attention to him, but after No. 2 had got out twice No. 5 began to follow him, stand up beside him at the knot, and run to the door and back. In all the trials, not once did No. 5 try to pull the knot. When put in by himself he frequently would smell of the knot, or near the knot, and then run directly to the door. He finally became very dependent upon No. 2, and made but little effort to get out when put in alone.

NO. 7 IMITATING NO. 2.

Date	*No. 2 gets out*	*No. 7 sees*	*No. 7 follows No. 2 out*	*No. 7 gets out*	*Time*
Jan. 29	7	6	7	—	—
Jan. 30	7	7	7	—	—
Jan. 31	7	6	7	—	—
Feb. 1	6	2	6	—	—
Totals	27	21	27		

In this experiment No. 7 followed No. 2 from the first, standing up beside him and getting in his way when he was pulling at the knot. After No. 2 had opened the door, by pulling the knot, No. 7 generally would stay behind long enough to pull the knot himself before following No. 2 out. He did this sixteen out of the twenty-seven times that No. 2 opened the door. When put back alone No. 7 did not once try to get hold of the knot. He went to the spot where the knot was and smelled of it and then ran to the door. Apparently he did not see the knot for he acted similarly in respect to the other parts of the cage.

Experiment VII. Pulling a Bent Wire with the Teeth and Forepaws.

Method.—In place of the knot used in the previous experiment, a small piece of wire of the same size and color as the wire top was used. The wire was bent at the end to make it easy for the rat to grasp it with his teeth and paws. After being thoroughly washed to remove all odor, the wire was suspended in the opposite (not diagonally opposite) corner of the box to that where the knot had been. It hung just on a level with the netting of the top, or just low enough so that a rat could grasp it with his teeth without first using his paws. In other respects the apparatus was just the same as that used in the preceding experiment.

Results.—February the second No. 2 was put in the box alone. He first went to the spot where the knot had been and examined it thoroughly. Then he began to try other places. In two minutes he had found the wire, pulled it, opening the door, and passed out. Put back he first went to a spot halfway between where the knot had been and where the wire was; then he went directly to the wire, pulled it and passed out. Time, fifteen seconds. Put back again he got out in ten seconds, although he first went to the knot spot. The next two times he got out in eight seconds and yet each time he first went to the spot where the knot had been before going to the wire. The last time, since he went directly from the door to the wire, he got out in three seconds.

Nos. 3 and 4 were now put in the box together for fifteen minutes. They did not get out, neither did they pull the wire, although they examined almost every other place in the box.

NO. 4 IMITATING NO. 2.

Date	*No. 2* *gets out*	*No. 4 sees*	*No. 4 follows* *No. 2 out*	*No. 4* *gets out*	*Time*
Feb. 6	3	2	3	—	—
Feb. 12	4	3	4	—	—
Feb. 12	—	—	—	1	4′
Feb. 12	—	—	—	1	2′
Feb. 12	—	—	—	1	45″
Feb. 12	—	—	—	1	35″
Feb. 12	—	—	—	1	90″
Feb. 12	—	—	—	1	45″
Feb. 12	—	—	—	1	45″
Feb. 12	—	—	—	1	15″
Totals	7	5	7	8	

The first time that No. 2 pulled the wire No. 4 did not see him. The second time that No. 4 was put back after following No. 2 out, he smelled of the wire; the third time, he went to the wire and smelled of it and then ran to the door. He did this five times during his five minutes. Once he took hold of the wire with his fore-paws but it was not until he had followed No. 2 out six times that he actually pulled the wire when put back, and then he did not pull it hard enough to open the door.

NO. 6 IMITATING NO. 2.

Date	*No. 2* *gets out*	*No. 6 sees*	*No. 6 follows* *No. 2 out*	*No. 6* *gets out*	*Time*
Feb. 13	3	3	3	—	—
Feb. 13	—	—	—	1	3′
Feb. 13	—	—	—	1	4′
Feb. 13	—	—	—	1	2′
Feb. 13	—	—	—	1	20″
Feb. 13	—	—	—	1	15″
Feb. 13	—	—	—	1	5″
Feb. 13	—	—	—	1	4″
Feb. 13	—	—	—	1	5″
Totals	3	3	8	8	

No. 6 was first put in alone for fifteen minutes. During that time he found the wire and pulled on it a little but not hard enough to open the door. After pulling it he ran to the door. No. 6

made no effort to pull the wire when put back after having seen No. 2 pull the wire twice. He went to the wire and smelled of it. But the third time when put back he went to the wire, pulled it hard and then ran to the door; the door being only partly open he went back and pulled the wire again.

NO. 1 IMITATING NO. 2 AND NO. 4.

Date	*No. 2 gets out*	*No. 1 sees*	*No. 1 follows No. 2 out*	*No. 1 gets out*	*Time*
Feb. 15	4	4	4	—	—
Feb. 16	8	5	8	—	—
Feb. 16	—	—	—	1	3′
Feb. 16	—	—	—	1	30″
Feb. 16	—	—	—	1	1′
Feb. 16	—	—	—	1	5″
Feb. 16	—	—	—	1	15″
Totals	12	9	12	5	

No. 1 was first put in alone for ten minutes. He struck the wire with his nose but made no effort to pull it. The first time he was put back after having followed No. 2 out he went to the wire and pulled it and ran to the door, but he did not pull it quite hard enough. He made no further effort to pull the wire until put back for the sixth time when he pulled it a little with his teeth. After the ninth trial I used No. 4 in place of No. 2. No. 1 followed No. 4 even more closely than he had followed No. 2.

NO. 3 IMITATING NO. 2 AND NO. 4.

Date	*No. 2 gets out*	*No. 3 sees*	*No. 3 follows No. 2 out*	*No. 3 gets out*	*Time*
Feb. 17	4	4	4	—	—

No. 3 was first put in the box alone for one hour. He made no effort to pull the wire. No. 3 followed No. 2 quite closely, but when put back he made little or no effort to get out. After No. 3 had followed No. 2 out twice I put in No. 4 once in place of No. 2. No. 3 followed him just as readily as he had followed No. 2. I made only the four trials because No. 3 was unwell, since he coughed almost constantly. A few days later I tried No. 3 again but with no positive results; his coughing and sneezing seemed to rob him of his spontaneity.

No. 5 was put into the box alone. He soon found the wire and pulled it three or four times, running to the door after each attempt. At the end of fifteen minutes he succeeded in getting out. The following table shows the time of learning.

1st time	15′
2d time	3′
3d time	15″
4th time	90″
5th time	15″
6th time	15″
7th time	15″

NO. 7 IMITATING NO. 6

Date	*No. 6 gets out*	*No. 7 sees*	*No. 7 follows No. 6 out*	*No. 7 gets out*	*Time*
Feb. 19	6	5	6	—	—
Feb. 21	6	6	6	—	—
Feb. 23	—	—	—	1	3′
Feb. 23	—	—	—	1	30″
Feb. 23	—	—	—	1	15″
Feb. 23	—	—	—	1	30″
Feb. 23	—	—	—	1	20″
Feb. 23	—	—	—	1	15″
Feb. 23	—	—	—	1	60″
Feb. 23	—	—	—	1	10″
Totals	12	11	12	8	

No. 7 was put into the box alone. He succeeded in getting out by pulling the wire after thirty minutes. When put back he went to the wire, touched it and ran to the door; again he returned to the wire, pulled it a little and ran to the door. This he did several times and then gave it up, making no further effort to escape, although left in the box for forty minutes. I then put No. 6 in with No. 7. No. 7 followed him very closely, stood up beside him at the wire, and took hold of the wire after No. 6 had opened the door. When No. 7 was put back he tried the wire and ran to the door. The next two times when put back he pulled on the wire and then ran to the door, but after that he made no further effort to get out. The next day he got out in three minutes when put in alone.

III. DISCUSSION OF RESULTS.

MORGAN says that "in the case of an imitative action the stimulus is afforded by the performance by another of an action similar in character to that which constitutes the response."[1] It is in this sense that we shall use the term "imitation" in this paper. He distinguishes two kinds of imitation, voluntary and involuntary instinctive. By the latter term he designates what is imitation only from the standpoint of the observer. As an illustration of this kind of action he cites the case of a hen pecking on the ground and the chicks imitating her action. The pecking of the mother acts as the stimulus that calls forth the instinctive action on the part of the chick. MORGAN points out that this action is imitative in its effect but not in its purpose. It is objectively but not subjectively imitative.

Voluntary imitation, on the other hand, is subjective as well as objective. It is conscious, purposive imitation. The action of another is reproduced with a definite end in view. Or, as THORNDIKE says, it is a case of "transferred association." "One sees the following sequence: 'A turning a faucet, A getting a drink.' If one can free this association from its narrow confinement to A, so as to get from it the association, 'impulse to turn faucet, me getting a drink,' one will surely if thirsty, turn the faucet, though he had never done so before."[2]

There is a third kind of imitation which MORGAN does not mention but which he probably would include under instinctive imitation, and that is automatic imitation. An example of this is one person involuntarily whistling the tune he hears another whistling. Here the action is involuntary, yet it is not instinctive.

So much for the different kinds of imitation. Now, let us turn to a discussion of the experimental work along this line that has the most direct bearing upon our investigation.

SMALL, in his study of the white rat, made a few experiments to determine to what extent they learn by imitation. In summing up the results of his work he says: "My conclusion from all this experimental work, and from much other observation of rats is that they do imitate, but that imitation with them is relatively simple. They imitate simple actions; but I have seen no case of

[1] MORGAN. Habit and Instinct, p. 168. London. 1896.

[2] THORNDIKE. Animal Intelligence. *Psychol. Review, Monograph Supp.*, Vol. 2, No. 4, p. 49. 1898.

what may, in lack of a better term, be called inferential imitation. By this I mean merely: learning to do a thing from seeing another do it, the purposive association of another's action with a desired end. For example, not one of the eight rats that might have learned to open the door of Box II by seeing another rat do it, ever thus profited by such experience. Each rat learned the task for himself, and learned it by doing it. On the other hand, imitation of simple actions is of frequent occurrence. Very often if one rat begins digging all are eager to dig in the same place; if one runs over the box, over the box they all go . . . . This simple form of imitation depending on the immediate functional connection between sensory and motor centers in a lower level—like the frown of a three months baby when the nurse frowns—covers all the cases of imitative action I have observed in the course of these experiments."[1]

THORNDIKE, after a study of the cat, chick and dog under experimental conditions, arrived at the same conclusion as SMALL, namely: that all the cases of supposed voluntary imitation in these animals are nothing more than instances of instinctive and automatic imitation. At the conclusion of his experiments on imitation he says: "It seems sure from these experiments that the animals were unable to form an association leading to an act from having seen the other animal, or animals, perform the act in a given situation . . . . . . Not only do animals not have associations accompanied, more or less permeated and altered, by inference and judgment; they do not have associations of the sort that may be acquired from other animals by imitation."[2]

Concerning imitation in monkeys, THORNDIKE says: "Nothing in my experience with these animals then favors the hypothesis that they have any general ability to learn to do things from seeing others do them."[3]

KINNAMAN, in his experiments with two *rhesus* monkeys, failed to find any indications of intelligent imitation of human beings. Yet in his study of imitation of one animal by another he succeeded, unlike THORNDIKE, in getting positive results. After he had tried in vain to teach the female monkey to pull a plug out of one end

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[1] SMALL. Mental Processes of the Rat. *American Journal of Psychology,* Vol 11, p. 162. 1900.

[2] THORNDIKE. Animal Intelligence. *Psychol. Review, Monograph Supp.,* Vol. 2, No. 4, p. 62. 1898.

[3] THORNDIKE. The Mental Life of the Monkeys. *Psychol. Review Monograph Supp.,* Vol. 3, No. 5, p. 42. 1901.

of the box in order to get food, he put the male monkey in the box with her. "Knowing the trick perfectly he seized the end of the plug with his teeth and removed it. I set the box again. This time the female rushed to it, seized the plug by the end as the male did, and procured the food. This she repeated immediately eight times in exactly the same way. On succeeding days she removed the plug as a part of a combination lock on the same plan, 130 times. Recalling that she had failed to work the bear-down lever for opening the box. . . I placed it before her. She rushed up, but missing the plug she sat down. The male passed her, pushed the door down and procured the food. When the box was set again she worked the lever and took the food in the same way that he had done. She manipulated the apparatus several times immediately, and 250 times later as a part of a combination lock. Besides these, once when the male peeped under the bottom of one of the trees, the female came and peeped in the same manner."[1]

Commenting on these results, KINNAMAN says: "It seems to me that the two cases with the box are quite as good examples of imitation as could well be gotten even with human beings. While this is an unusual method of learning on the part of the *rhesus*, the above example seems to me conclusive evidence that it is at least a possible method for him."[2]

I entirely agree with KINNAMAN that here we have a clear case of intelligent, voluntary imitation. I also agree with THORNDIKE and SMALL in regard to the interpretation of their results, as I think that all the apparent cases of imitation brought out in their experiments can be explained as automatic or instinctive imitation. From the fact that the results of their experiments were negative so far as voluntary imitation is concerned, it does not necessarily follow, however, that voluntary imitation does not exist in these animals. It may be that the conditions of their experiments were not favorable for imitative action.

So much for what has been done in this field by previous investigators. Now let us turn directly to a discussion of our results.

We found that when two rats were put into the box together, one rat being trained to get out of the box, and the other untrained, at first they were indifferent to each other's presence, but as the

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[1] KINNAMAN. Mental Life of Rhesus Monkeys in Captivity. *American Journal of Psychology*, Vol. 13, p. 121. 1902.

[2] Same article, p. 122.

untrained rat observed that the other one was able to get out while he was not, a gradual change took place. The untrained rat began to watch the other's movements closely; he followed him all about the cage, standing up on his hind legs beside him at the string, and pulling it after he had pulled it, etc. We also saw that when he was put back the immediate vicinity of the loop was the point of greatest interest for him, and that he tried to get out by working at the spot where he had seen the trained rat try.

In the light of these facts it seems to me that imitation in white rats has been conclusively established. The question now is as to the nature of this imitation. Is it voluntary, instinctive or automatic imitation?

We have already seen that SMALL claims that there is no such thing as voluntary, or inferential imitation, as he calls it, among white rats. I readily admit that many of the instances of apparent imitation may be satisfactorily explained as instinctive or automatic imitation, but I wish to maintain that there are cases that cannot be explained in this way. SMALL[1] in connection with his maze experiment states that when two rats met in the maze one seldom followed the other. This is entirely in keeping with the results of my experiments, for I found that when two rats were put in the same box together, one seldom followed the other. It was not until the trained rat had got out a few times that the untrained rat began to follow him. These facts cannot be explained on the basis of instinctive following, as where the young follows the mother, for in these experiments when one rat followed another it was with a knowledge of the end to be attained by that following. When experience of the end was lacking the following seldom took place. For as a rule when two rats were put in the box together they showed no particular tendency to take note of each other's movements until one got out a few times; then the other would follow him all about the cage. If a new rat was now put in with the untrained one, the latter would follow the former just as readily as he had followed the trained rat. Yet, if after a few minutes the new rat did not succeed in getting out, the other would cease imitating his movements. WATSON states that young rats do not track one another by the sense of smell, whereas after sexual maturity is reached, the tracking may occur.[2]

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[1] SMALL. Mental Processes of the Rat. *American Journal of Psychology*, Vol. 12, p. 213. 1901.

[2] WATSON. Animal Education, p. 85. Chicago. 1903.

While maintaining that these are instances of voluntary imitation, I do not maintain that the rats display a grade of intelligence equal to that displayed by the monkey who pulled the plug after seeing the other monkey pull it. The nature of this voluntary imitation is determined by the intelligence of the animal imitating. This means that many of the wonderful stories of the remarkable feats of imitation will have to be taken with the proverbial grain of salt. That this is true is at once evident, when we consider how a rat learns to get out of a box. When put in the box he first tries to get out at the place nearest to the food, but not succeeding there he gradually works away from that spot until he has tried almost every spot in the box, or until he pulls the string that opens the door. Then his attention being attracted to the door by the sound it makes in opening, he runs to it and passes out to the food. When he is put back, take note of what happens. Does he run at once to the string, pull it and open the door? By no means. He first tries the door and finding it closed he makes many random movements before starting in the general direction of the string. After nosing about in its vicinity for a time he finally succeeds in finding it and pulling it, and thus escapes. It is not until he has got out many times that he goes at once to the string, pulls it and passes out, without first making a number of useless random movements.

These facts in regard to the way the rat learns to get out of a box are of vital importance in helping us to decide what we may reasonably expect from the rat in regard to imitation. If, when a rat by chance pulls the string and hears the door open, passes out and is fed, it cannot go directly to that string when put back, why should we expect a rat that has merely witnessed the performance to be able to do it? The rat that opens the door not only sees the string and sees his paw pull it, but he has in addition all the sensations that are connected with the movement of pulling the string, while the rat that looks on has only the visual sensation, no kinæsthetic sensations. It seems to me that in the light of these facts we ought to be able to say *a priori* that no ordinary rat (unless by chance) would be able to open a door by pulling a string, simply from having seen another rat do it, without first making a number of random movements.

All that we can expect one rat to learn from watching another rat get out is, that if he tries the same part of the cage tried by the other rat, he too will be able to get out. It is a case of what THORNDIKE calls "transferred association" meaning by that, that if one rat sees another get food by opening the door, the former realizes that he would get food if he could open the door. It is not through observation alone that the imitating rat learns which movement to make to get out, but it is by observation of another rat plus the experience of practicing the movement. That this is true was shown quite conclusively in Experiment VI. In that experiment the rats learned, from watching and practicing the movements with No. 2, all of the movements necessary to get out, with the exception of pulling down the knot with the forepaws before trying to grasp it with their teeth. This movement was apparently unnatural to most of the rats, hence their failure. They readily learned from No. 2 that pulling the knot would open the door, but they did not learn from him just how they should use their forepaws in order to get hold of the knot. Under ordinary conditions their random movements would have been sufficient to enable them to open the door, but inasmuch as they were not, they did not have sufficient discriminating power to enable them to learn the right movement from No. 2. SMALL[1] has shown that the vision of white rats is defective. This would account in part for their failure to make the required discrimination.

Then to sum up, I think that my experiments have shown that voluntary imitation of a certain type does exist in white rats. While this imitation is not of as high a degree as that discovered by KINNAMAN in his experiments with monkeys, it is not different in kind.

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[1] SMALL. Mental Processes of the Rat. *American Journal of Psychology*, Vol. 12, p. 233. 1901.

APPLICATIONS OF DYNAMIC THEORY TO PHYSIOLOGICAL PROBLEMS.

BY

THE LATE C. L. HERRICK.[1]

The most strenuous and ingenious efforts of foremost biological investigators have been directed for upwards of fifty years to a search for some explanation of vital phenomena upon a purely structural basis. It has been tacitly assumed on all hands that if we could invent some anatomical unit (biophore, gemmule, plastidule, micella, or the like), then it would *ipso facto* become possible to create a geometry of living matter which would *explain* heredity and all other problems of vital activity.

There has been a very general feeling that an appeal to a "vital force" for explanation of such phenomena is at best but begging of the question. Nevertheless, the result of such speculation under the influence of the Daltonian hypothesis of the constitution of matter, including the brilliant work of WEISMANN and NAEGELI, has been so unsatisfactory that the tendency is now apparent to create a neo-vitalism which shall restate the question from a dynamic point of view.

It is the opinion of the writer that the time is approaching when a biologist with a thorough physical and mathematical equipment may hope to formulate a theory which shall prove as helpful in

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[1] Rough drafts of this article and the one which immediately follows were found among Dr. HERRICK's papers after his death. They had not been edited for the press and probably were not intended for publication in their present form. But it has seemed best to publish them substantially as they were written, permitting each reader to make the necessary allowances for the defects of composition naturally found in unrevised notes. This article appears to have been written early in 1904; the one on "Imitation and Volition" which follows dates from an earlier time, perhaps four or five years earlier.

Among Dr. HERRICK's papers is a considerable collection of neurological research notes, from which it was hoped that extracts might be taken for publication. We are disappointed to find, however, that this material is all too incompletely written up to admit of publication. The same is unfortunately also true of much of the large collection of MSS. on psychology, ethics and philosophy. Some fragments from this collection, however, it is hoped can be extracted for early publication in the philosophical journals.—EDITOR.

clarifying our ideas and opening the way for further discoveries as the purely *a priori* theories of WEISMANN. Although disclaiming any approach to such equipment as might justify him in attempting such construction, the writer ventures to offer a few suggestions, relative to the direction along which such effort might be made, and thus to indicate incidentally the views which he has held for nearly two decades as to the general mechanics of organisms.

In view of the revival of interest from a strictly scientific point of view in animal behavior as evidenced in the new departure in the *Journal of Comparative Neurology* and the establishment of the *Journal of Experimental Zoölogy*, it is quite in order to insist on the dynamic interpretation of structure.

In order to condense as much as possible we have chosen an aphoristic form of statement followed by an illustrative commentary.

1. Matter, considered by DALTON to be composed of discrete particles (atoms) more or less loosely connected to form larger composite units (molecules) which are mathematically constant and definitely related to other units, and which has further been analyzed by modern physics into ions (the protons of older speculative writers), is a purely metaphysical concept. For this we substitute that of energy whose sole characteristic as such is that of spontaneous activity (finding expression in our consciousness as the simple element "change"). Energy is the metaphysica postulate of being and is not otherwise definable to the science than as the counterpart of the simple real in consciousness or experience (change).

2. When manifested to human perception energy assumes the form of *force* which is the counterpart of change in terms of motion. As the concept of motion involves that of space and produces it in experience, we may say roughly that force is energy manifested in terms of space or under spacial limitations.

3. Experience recognizes units or individuals making up objects, which units may be unlike among themselves or sensibly similar. Numerous similar elements may be embraced in a greater composite individual. Dynamically these units are expressed as specific forms or modes of motion. Since force always involves a tendency to change, we may say that each such unit may be represented by a locus formula for a single cycle of its motion.

4. Where interaction takes place and units tend to combine, the form of combination and even the possibility of combination may depend on the compatibility of the respective modes of motion (types of activity or locus formulæ). The stability of the resulting complex will be determined by the nature of the resultant. This question of stability may be examined mathematically, but may be illustrated to the eye by the figures produced by compound harmonic motion as seen in LISSAJOUS' figures described beyond.

5. The stability of such a complex may be very great and still permit a wide range of variability within certain critical limits beyond which dissolution will be rapid. Mathematical illustrations of conditions of stability may be derived from the study of the gyroscope and the behavior of vortex rings.

6. In the case of the organic body each individual is the result of the elimination of incompatible types of motion and the establishment of elastic but real limits of variation (heredity and habit) and all this is imperfectly and to a small extent mirrored in structural constants accessible to our examination. One system of coördination involves within it numerous others of a second order and so on indefinitely to an inconceivable degree of complication. From the above it is seen that a study of structure must be supplemented by a still more minute study of behavior (function), and the latter may be used greatly to supplement the information derived from structure rather than simply to be regarded as a result of the latter. MENDEL's laws aptly illustrate the fact that behavior points to mathematical coördinations of activities not indicated in the vaguest manner in the structure of the germ.

7. Of the continuous stream of energy which passes through the organism only such parts are assimilated as can be made to agree with or fit into the locus formulæ already established without too greatly altering them. An entirely antagonistic type of activity may, if sufficiently violent, topple over the equilibrium already established, or to use a different illustration, break up the compound harmonic motion, and such degeneration may be cumulative (poisons).

8. It follows from what has been said that the organism must have all its parts impressed with the effects of the whole in such a way that any part will bear the hall mark of the individual as specific characters. Thus if the integrity of the whole were disturbed, as by mutilation, the tendency would exist to restore the

entire complexly equilibrated system (regulation). The lost part may be restored without specific nervous direction.

9. The nervous system being a special related equilibrated system directly harmonized with and representing the sum of bodily functions, it is particularly impressed by the total locus formula of the entire organism and will be of especial importance in regenerative function as particularly a result of the direct trophic mechanism. Inasmuch as the nervous system is of comparatively late origin in phylogeny, it follows that the nervous control is not specific upon individual cells of the somatic structure but is related to more or less complicated systems of equilibration within the body (organo-taxy not cyto-taxy). The nervous system shares with the body the power of receiving the effect of the total activity but in a greatly exalted degree.

10. The coördinate complex of the adult organism is the mathematical outgrowth of the expansion of a certain simple locus formula representing activities which begin the career under great intensity of action, giving them a powerful assimilative attraction. The single energic units of (say) a germ cell may be most complex and under the conditions afforded it may gather to itself or generate multitudes of other energic units in the formula of each of which are vestiges of the parent cell; or, in other words, traces of the original formula persist. But certain elements so collected do not proceed with the differentiation at once but remain as germ cells capable under suitable conditions of propagating new composite individuals.

Contrasting this with current views, we find that, in the language of what we may call the Darwin-Weismann period: "The dissimilarity in form, size, and arrangement of the micellæ in the idioplasm provides for innumerable combinations of the active forces" (Naegeli, Abstammungslehre, p. 26), and these are responsible for the innumerable varieties of chemical and plastic phenomena *produced* thereby; and thus result the variations in growth, inner organization, external form, and arrangement.

This manifoldness in the constitution of the idioplasm is increased by the fact that each micella may have a different chemical composition. From this point of view structural complexity is the cause of variety of function and the total behavior of an animal is directly a function of an algebraic sum of the structural elements.

The *dynamic theory* proposes to view the organism as a correlation of figures of activity in such a way that the behavior of the animal as a whole is a resultant activity into which the elements enter to a greater or less extent without complete loss of their integrity. Energy or activity is of such nature that it is capable of being individualized without losing the possibility of recombining the whole. As motion may be rectilinear or curvilinear and curvilinear or gyratory motion is capable of acquiring individual modes as rectilinear motion is not, so activities corresponding to elementary parts of the body may be compounded to produce resultants without surrender of their individuality or may be united into a new progressive activity with a complete surrender of individuality, but the resultant will still be a true descendant of the parent motions. Such analogies are important in the study of development.

As to chemical variation, this is but a special case of differences in trajectory or figure among units of activity. Take for illustration familiar instances in organic chemistry which illustrate the grouping of a number of minor complexes (molecules) into an organic radicle forming the base of a series in which this constant appears in varying proportions, groups of atoms behaving like atoms in that they may be transferred from compound to compound. Thus hydrocarbons having the general formula C_nH_{2n+2} may be regarded as hydrides of the radicle C_nH_{2n+1}, so that

methane $(CH_4) - H =$ methyl (CH_3),
ethane $(C_2H_6) - H =$ ethyl (C_2H_5), etc.

The assembling of series formed from such radicles, like the marsh gas or the aromatic series, shows that a regular gradation of physical properties accompanies the changes in proportions. (In our illustration the properties of the members of the marsh gas series are graded in accordance with constant additions of H_2.) If the suggestions offered above as to the nature of chemical union are accepted, then the similarity in diversity giving rise to such series or expressed more generally in the periodic law is not due to the accumulation of different amounts of material bodies (which in itself would, in fact, explain nothing), but to the composition of forces by such constant increments as give rise to rhythmical coincidences in form of such a nature as to produce the effect of similarity in divergence as in the case of chords or octaves in music.

According to the geometrical theories prevailing, which state that the specific peculiarities of idioplasm result from the arrangement and structure of the micellæ composing it, the influence upon heredity would seem to be proportional to the amount of idioplasm present. This, however, it is not necessary to assume upon a dynamic hypothesis. Any portion of an equilibrated system when disturbed will tend to restore the entire trajectory. Especially will this be true if a relation of rhythmical or cyclical motion is involved. No theory of vital activity is complete which fails to take into account the power of a cutting to produce a complete plant or of a medusa to restore mutilations. The *nisus formativus* or *Bildungskraft* is, after all, only a necessity imposed on the mutilated trajectory to complete itself and is lodged in no organ to the exclusion of all others. It is more conspicuous and effective in the germ than elsewhere. The complete separation of germplasm and somatoplasm does not hold as to the possibility of reproduction, and the new plant produced by graft or cutting inherits the type more fully than the seedling in which the function of variation is provided for according to MENDEL's law. It is observed that cells budding from vegetative parts when compared in their development with the germinal individuals overleap the earlier stages in development and this is what might be expected in the case of organic activities already passed the earlier stages of complexity.

The dynamic point of view serves clearly to throw into relief the relation between different factors of evolution and development. As C. M. CHILD well says in the closing paragraphs of his Studies in Regulation:[1] "The relation between form and heredity has never been satisfactorily determined. With the advance of our knowledge the fact becomes more and more evident that the organism is not merely a complex of structural elements ready made by heredity for certain physiological activities, but rather a complex of activities, in consequence of which morphological structure develops." Dr. CHILD insists on the difference between physical and chemical structure of protoplasm and morphological structure, the former representing capacity for activity or functional activity in the broadest sense. According to this view, it is functional capacity that is inherited rather than form. "Heredity

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[1] *Journ. Exp. Zoöl.*, Vol. 1, No. 1.

is, strictly speaking, a physiological and not a morphological problem." In his illustration derived from a study of regeneration in Leptoplana after mutilation, he says: "The regions of the body develop in a characteristic form because they function or attempt to function in a characteristic manner." This is, with certain reservations, a very pregnant statement of the basic principle of dynamic realism as applied to biology. But it must be noticed that the methods involved in the study of multilations present us with little more than a diagram, and a more or less arbitrary one at that, which serves merely to illustrate the principle. The apparent deduction that the reproduced parts are what they are simply because the attempts at locomotion after mutilation tend to focus or direct the growing activity in a certain direction, is probably misleading. This is, as the author himself admits, only a small part of the process.

It would not be claimed that the leg of a newt regenerates in a characteristic form because the growing member kicks or attempts to kick in a characteristic manner. The kicking in a characteristic manner is a late coördination of types of coördinated activity of great complexity which when the organism is complete, form a balanced elastic system whose origin can be traced backward through heredity indefinitely. Structure is simply the way the system reveals itself to one of our methods of research while the gross forms of activity (kicking, etc.) are extreme molar perturbations of the equilibrium along lines marked out by the nature of more subtle coördinations. The structure of a striped muscle fiber is itself the revelation of certain types of (molecular) activities. The leg of a newt regenerates in the characteristic form because the plastic energic system bears the impress of the leg in all its past relations to that system and is adjusted to its trophic activities. Every activity of the remainder of the body after mutilation continues to attempt to react as if the leg were still present and this phase of the locus formula corresponding to the leg part of the whole complex is converted into trophic tendencies. While the leg was present a certain factor in physiological equilibrium was devoted to nutrition of a member of such and such a type. This factor does not cease to operate but, by what might be called physiological inertia, continues this nutritive tendency. Let us figure an elastic bag filled with a viscid fluid from which a tube is conducted. The bag is under pressure and fluid constantly issues from it, so that an avenue of less viscid fluid leads to the tube from within. Now the tube is closed or removed. The jet of fluid still impinges on that point where the tube had been connected and causes the elastic wall to be distended at that point. This might illustrate in a rude mechanical way the idea above expressed. The impinging force would in the case of the mutilation consist of most complex molecular tendencies.

NAEGELI believes that growth (*i. e.*, multiplication of cells) depends primarily on the structure of the idioplasm and secondarily on the amount and method of its mixture with the nutritive plasma, and also that during the development of an organism the idioplasm is continually streaming to the growing parts.

On a dynamic hypothesis we might suggest that in the vast coördinated system of activities (motions) some are by their nature capable of being much more readily affected by activities impinging from without, while others are relatively indifferent to such "stimuli." The nature of the responses will depend also on the nature of the motion or the phase it may be in. In cases where the rhythm of the stimulus and that of the activity of the body are harmonious the latter might be "transparent" to the former, *i. e.*, one would not affect the other. In another case the mode of the bodily activities might be such as to destroy or absorb the extraneous stimulus, being modified or augumented by such absorption. This would be a dynamic explanation of nutrition and growth.

It may likewise be suggested that these elementary activities differ in intensity among themselves and that there will be a necessary relation between complexity of form and intensity in any given case. Thus, the same unit of energy or specialized motion may gradually become more complex and in doing so will lose in intensity (or rate), or by becoming involved in a large complex much of its intensity may be sacrificed to the maintenance of equilibrium. Moreover, the increase in size if a motor unit (amplitude of motion) due (let us say) to absorption of suitable impinging impulses may cause the figure to pass a critical phase and so give rise to a separation into two concordant associated units of motion, such as could be conceived in case of fission of a cell.

Credit is due NAEGELI for making prominent the fact that the specific value of the inheritable substance does not arise from compounding diverse elements representing all organs or characters to be inherited, as seemed to be implied in the gemmule and like hypotheses. He says: "Diese unendliche Mannigfaltigkeit ist in winzigen Tröpfehen von Idioplasma virwirklicht welche durch das Mikroskop, durch chemische und physikalische Hilfsmittel nicht von einander zu unterschieden sind. An der Keimanlage selber ist nicht die Masse, sondern nur die Beschaffenheit seiner kleiner wirksamen Partie von Idioplasm das entscheidende * * *." But he goes on to state that the structure of idioplasm is determined by its molecular composition, particularly by the arrangement of the micellæ with the motions and forces peculiar to them.

For us the structure is but a partial revelation of the equilibrated status of these "peculiar motions and forces." When two types of activity (motion) fuse they form a resultant which is different from either and is by no means an algebraic sum of both. When oxygen and hydrogen unite the result is not an algebraic sum of the qualities (activities) of oxygen and hydrogen but a new quality-complex unlike either and represented by its own locus formula. In like manner, when two heredity bearers unite in a germ cell the resultant is not an algebraic sum of the two formulæ but a new figure. Again, water, under certain circumstances, can be decomposed, as we say, into oxygen and hydrogen, *i. e.*, the composite movement to which the water molecule owes its existence can be resolved into the original two simpler modes.

In like manner, while the germ cell does not contain discrete elements corresponding to the various organs of the future body, it does contain in its complex trajectory elements which under appropriate conditions and with the coöperation of certain external forces or constants may give rise to all of the coördinated activities constituting the organs of the complete organism.

So difficult is this conception that we venture to remind the reader of the simple illustration afforded by compound harmonic traces. In the trace produced, *e. g.*, by a mirror attached to a tuning fork we have the direction of motion in one plane represented by a straight line, the movement in the other plane at right angles to it represented solely by variations in rate of the spot of light which generates the trace. In other words, the harmonic nature of the trace does not appear in the line of light generated by the mirror but is only a question of the law of the motion of the generating spot. This trace is projected on a second tuning fork also in variation and the compound harmonic trace on the screen is a resultant not only of the rectilinear motion of the ray reflected in each case but also of the varying rates of motion of the ray producing the trace. The trace is a projection of a composition of motion in space upon a plane and the curious variations observed are very instructive in assisting us to conceive of such a simple process as the combination of O and H to form H_2O in dynamic terms. From this illustration the dynamic concept is clearly grasped if we admit that whatever type of energy H and O may be respectively (certain directions and rates of motion in our illustration), when these are compounded there results not a something in which these are somehow bound together but a new direction and a rate of motion or a new locus formula.

The objection that may be raised that during the process of growth and consequent increase of size there must be an actual increase of substance (and so of matter) in the body is seen to be inapplicable. It is not claimed that any matter is created during growth. It is simply assimilated, *i. e.*, reduced to conformity with the matter already existing in the body. Dynamically expressed this assimilation simply means that the less highly differentiated types of motion of the surrounding inorganic world are affected by the rhythm of the more highly complex organic forces. Imagine the universe to consist of one homogeneous sea of sluggish activity. Introduce in any way a suitable rhythm at one point and in due course this more vigorous or more rapid rhythm will have imparted itself to the whole universe. It is calculated that, given a suitable medium, the offspring of a single protozoan would in a few years fill the world. We need not contemplate the extreme case but in our own bodies the same law is manifest, the limitations giving rise to an equilibrium between trophism and resistance being more various than in the protozoan.

NAEGELI says that "the configuration of the idioplasm is rather a phylogenetic than a geometric problem. The development of the anlage in the main conforms to this phylogenetic arrangement. By reason of the fact that the organism in its ontogeny successively passes through those stages through which its phylum passed, the idioplasmic anlages appear in the same order in which they originated" (*op. cit.*, p. 50). NAEGELI was also perhaps the only writer of the mechanical school to discuss clearly the possibility of modifications arising in one part of the body being impressed on other parts dynamically without interchange of substance. He says "the communication of idioplasmic peculiarities occurs either in a material or a dynamic manner." The first method suffers from the difficulty of explaining the diffusion of colloid micellæ through living membranes (cell walls). This difficulty he evades by assuming that all cells of the body communicate by means of fine pores, thus forming paths of communication permitting actual exchange of substance between distant parts of the body. In the case of a dynamic interpretation he finds it necessary to assume either that vibrations pass through the cell walls or that they are transmitted *via* the pores above postulated. He remarks, however, that if material mixture and intercourse does occur it is nevertheless probable that equilibrating communication occurs as a dynamic process. This is worthy of careful consideration. No matter how far one may go in the attempt to explain vital function by means of structure, in last analysis, the effect of part on part is always to be construed in dynamic terms.

The communicating avenues which we are daily coming to recognize as existing in and between the reticula of all cells (corresponding to NAEGELI'S *Micellreihen*) are but the evidences of dynamic communication of one order but they do not exhaust the possibilities. Because the molecules are dynamically yoked in constant interaction by chemical combinations this does not prevent the larger groups from being connected by larger (non-chemical) bonds no less real.

Very interesting from a dynamic point of view are recent observations and theories of egg maturation and development. We have progressed very far beyond a purely mechanical theory of the building of the body out of cells as a house may be built out of bricks. The importance of the cytoplasmic elements of localization and differentiation suggested by LANKESTER'S theory of precocious segregation and culminating in ROUX'S mosaic theory of development becomes clear through later observations by WILSON, YATSU, and others.

That a high degree of prelocalization or cytoplasmic organization exists in the unsegmented egg has long been clear. WILSON'S work undertakes to discover whether the prelocalization of the morphological factors exists from the beginning or whether it is a progressive process, for, as he says,[1] "in the latter case * * * prelocalization, even in the unsegmented egg, may be brought under the category of epigenetic phenomena (epigenetic qualities as distinguished from preformed qualities), and falls into harmony with hypotheses that assume the nucleus to be the primary determining factor."

The results of YATSU on Cerebratulus show that the localization of the morphogenic factors is progressive even in stages preceding cleavage. The percentage of normal larvæ obtained from fragments steadily diminished with age and localization becomes progressively more definite. Cleavage and morphological factors may or may not develop cotemporaneously. Such prelocalization exists in Dentalium before the egg leaves the ovary, long before initial stages of maturation and fertilization. By separation of the blastomeres several distinct imperfect individuals may be produced, and, except for readjustment of cells, undergo practically the same development as if unseparated, thus proving a mosaic theory. In Dentalium the clear substance forming the polar lobe is visible prior to cleavage and mutilation experiments prior to segmentation show that this substance has practically the same morphogenic value as the polar lobe itself.

It is evident that, in spite of the recognition given by WILSON to MORGAN'S theory of morphallaxis in the closing and readjustment of the body of an embryo resulting from the development of a fragment of an egg, the former interprets the phenomena in a mechanical rather than a vitalistic way. The regulative capacity of such embryos is very great, however. The same final result may be reached in the case of fragments of unsegmented eggs and separated blastomeres in different ways showing the identical regulative impress of these unlike processes.

We think a dynamic explanation applicable even upon the basis of prelocalization and a mosaic theory of development. As WILSON says: "The early development of egg fragments indicates that the specification of the cytoplasmic regions is primarily qualitative but not quantitative, or if quantitative is still subject to a regulative process that lies behind the originial topographical grouping of the egg-materials" (*op. cit.*, p. 70). But qualitative specification must be dynamic; all qualities are the result of behavior. The smallest part of any "Keimbezirk" is capable of regenerating true

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[1] *Journ. Exp. Zoöl.*, Vol. 1, No. 1, p. 2.

to type so that the mosaic tendency cannot be indefinitely extended, and the regulative process shows that a total equilibrium of the more or less analytically distributed forces still exist.

It is inevitable that in considering any application of dynamics to development we should inquire into its bearing upon WEISMANN'S postulates of the continuity and invariability of the germ-plasm. It will be remembered that, according to WEISMANN, the overplus of germ-plasm not used in individual development is handed over to the custody of the new individual and, in this condition, is capable of growth and multiplication at the expense of nutrient materials supplied by the somatoplasm, and while thus growing it retains its original highly complex structure. This process continues from individual to individual without change as, to use ROMANES' illustration, yeast might be transplanted from vat to vat, the successive vats representing successive generations of progeny.

Now it is plain that certain types of activity are inoperative on other types. Some vibrations will pass through others unchanged. Some bodies are relatively opaque to one set of vibrations but transparent to other kinds or phases of vibration. It is not inherently impossible that the trajectory corresponding to any given germplasm should be transparent to the specific vibrations of its somatoplasm, yet the fact that the germplasm is housed in a medium of activities in which the total activity of the organism is in some sort continually reflected makes it inherently improbable that there should be absolute insulation. Inasmuch as WEISMANN was forced finally to abandon his distinction between germ cells and somatic cells by suggesting that only the nucleoplasm of the former are bearers of the invariable material of heredity and thus the nucleus became the center of interest, it is interesting to observe that non-nuclear parts of the germ cell are found to be capable of multiplication though it might, of course, be suggested in such cases that nuclear materials or forces are diffused throughout the cytoplasm. "Enucleated fragments of fertilized eggs (in Dentalium) pass through alternating stages of activity and quiescence corresponding with the division rhythm of the nucleated half, and form the polar lobes as if still forming a part of a complete embryo."[1]

In answering Dr. VINES' criticism of his theory of the immortality of micro-organisms and the germ plasm, WEISMANN offered a

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[1] WILSON. Experimental Studies in Germal Localization, p. 69.

suggestion, the dynamic interpretation of which may be useful. He says: "If then this real immortality is simply a cyclical movement conditioned on earlier physical properties of protoplasm, why should it be inconceivable that this property, under certain circumstances, should alter to some extent so that the phases of metabolic activity should not exactly repeat themselves, but after a certain number of cycles should come to an end, resulting in death." As so defined the much-mooted law of immortality becomes only the recognition of an equilibrated activity constant only under exactly constant and uniform conditions. But physical conditions are never uniform; yet a vital activity acquires a high degree of egocentric stability by virtue of its activity and is able to resist numerous variations and to return to its regular orbit after mutations. When, however, this disturbance is carried beyond a certain critical angle or degree the equilibrium is destroyed (traumatic death). It is conceivable that in a hostile environment the disturbance might be insufficient to inhibit the activity at once but nevertheless might introduce an antagonistic element which either becomes cumulative, increasing the divergence from the normal in each cycle and so at last pass the critical point or that the change might be insufficient to break up the equilibrium till some nodal point is reached where its effect is for that time adequate.

The above suggestions point to the necessity of expanding the very limited idea we may secure of the nature of vital activity from the study of structure alone by such a study of function as shall note the correspondence, periodicities, incompatibilities, inhibitions, nodal points, and the like, and from these create a science descriptive of vital phenomena in terms of modes of energy. The locus formula of any given vital activity once secured, we may hope to extend our knowledge by leaps and bounds.

IMITATION AND VOLITION.

BY

THE LATE C. L. HERRICK.[1]

Imitation acquires heightened significance for the dynamogenetic psychology, since it has been identified as the source of the will. Professor BALDWIN has most ingeniously and elaborately brought out this connection in his work, "Mental Development," and elsewhere. "The child's first exhibition of volition is found in its repeated effort to imitate something." It is, therefore, most interesting to seek the origin of the imitative impulse—this *avant-courier* of the dominant attribute of mind. But before entering upon this search we may be pardoned for giving a side glance at Professor BALDWIN's distinction between "deliberative suggestion" and will. Professor BALDWIN's waves aside the contradiction implied between the two terms thus yoked together by admitting that the deliberation is in appearance only. Deliberative suggestion is a "state of mind in which coördinate sense stimuli meet, confront, oppose, further one another." "The competition of processes is probably in large measure subcortical." The child at this period of its development, although "motor stimulations have multiplied and emotional life is budding forth in a variety of promising traits and the material of conscious character is present, nevertheless "lacks self-consciousness, self-decision, self in any form." Much here evidently depends on one's notion of the constituents and origin of self.

The illustration given is that of a child who, having acquired the habit of scratching a face whenever brought within reach, is not deterred from doing so, at least at first, by fear of punishment, but seems to deliberate and then, being overcome by the impulse, scratches and immediately bursts out crying in expectation of the punishment. It is assumed in this case that the impulse has acquired the value of a habit after having arisen as a spontaneous

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[1] See the footnote to the title of the preceding article.

reaction or as a result of physiological suggestion. It would be interesting to have further data as to the origin of this habit. Surely there must have been some reënforcement of the originally seemingly aimless impulse; and one could wish to know its nature before excluding the volitional element finally. One would be prompted to ask whether the result of the first accidental scratch was not of a nature to awaken the child's interest. Did it not produce some exaggerated expression of surprise, mock fright, or simulated reproof, such as mother or nurse would naturally indulge? If so, the child would be strongly prompted to repeat an act associated with a highly exciting sensori-motor reaction.

Taking now a still more simple example, we may hope to eliminate the uncertainty and ambiguity. A child, presumably of the age of "H," in the instance recorded by Professor BALDWIN, accidentally places its hand on the window pane. The act was unprompted and would never have been intentionally repeated and could never have formed a habit if no notice had been taken of it. But the nurse, with some ostentation, removes the hand and places it in the child's lap with words of reproof. What does the child then do but repeat the operation, looking into the nurse's face with an air of "I will to put it there." From this point on the phenomena are essentially the same as in the case cited by Professor BALDWIN. Now is this deliberative suggestion or is it will? BALDWIN supposes that "suggestion is as original a motor stimulus as pleasure or pain," and that in the case cited these two classes of stimuli are in direct conflict. It is important, first of all, to be sure that "self in any form" is really absent. What is the basis of self? Is not the ego concept compounded from non-localizable sensory stimuli (stimuli which accordingly have not lost their feeling *quale*) and vestiges of the effort-sense? It is always "I" who suffers and "I" who does. It seems impossible to believe that during the early non-localizing period—the period when feeling is in the ascendancy—the self feeling should not have evolved, even if not clearly expressed. The ego sense must arise in an exceedingly early stage and gradually, as the constant among the fleeting, it usurps the highest associational seat. Every new experience is brought to adjudication here. When the child replaces its hand on the window pane it has merely fused the consciousness of a particular irrelevant "doing" with the autocratic "I." When the attempt is made to divorce these two elements the child is conscious of a sense of loss—of an attack on the self concept—and reacts as violently and persistently as though the particular act had a high potentiality for pleasure or pain. There is no question of habit here nor of impulse with emotional value. Common sense says the child is willful and it would seem that psychological analysis might accept the dictum. But even though we may incline to recognize will in a rudimentary form in a very early stage, there can be no question that for each new voluntary act a pattern must be set and we may recognize with Professor BALDWIN the imitative impulse as the pattern maker. The type of imitation with which we are at first concerned may be called linked repetition, as contrasted, on one hand, with chance repetitions, and, on the other, with intended imitation, where one is conscious both of the imitated act and the imitating effort.

Two types of such repetition are to be distinguished. The first is that related to the accommodation phenomena of sense organs. Imitation is said by PREYER to occur as early as the third or fourth month, while BALDWIN was unable to detect unambiguous instances earlier than in the beginning of the ninth month. But it is known that a moving light is followed as early as the twenty-third day. During the latter part of the first month the child turns the head as well as the eyes. It is plain that visual fixation on a moving object is in so far imitative that it brings into relation outward movements and subjective responses obeying similar laws. I have elsewhere attempted to show that in coördinated passive vision that part of the field of view which is in the macula will seem most brilliant, at least until these differentia are employed in forming local signs, and that the child's unconscious eye-motions will occasion a loss or failure of retention of the image which he will attempt to recover as the power of control is gradually acquired. Now, when a brighter image is seen flitting over the field of view the effect is the same as though the macula image had again wandered and the effort at readjustment is made with this new brighter spot rather than the macula image as the goal. In this way the "seeking" motion of the eyes may have arisen. How powerful and persistent this seeking or following impulse is may be gathered from rotation phenomena. All visual concepts of figure, form, extension, locality, etc., thus lay up great store of dynamic vestiges. When one reads a description there is always a retinue of such dynamic elements in process of unconscious formation so that one is startled to find that he has a spatially distributed field in memory for events in all his novels. So in drawing even an imaginary object the eye foreruns the hand and lays down its course. Such seems to be the origin of one great class of imitative motions. When the stage of consciousness is reached the child already has a large store of ocular vestiges at disposal. It might be suggested that the tendency to imitate is transferred to all other departments of effort from the visual accommodation, but it is possible to detect a simpler law. In the evolution of will we credit the impulsive performance of an act with the power of preparing for its voluntary performance in such way that an impulse to act when associated with a reproduction of the end and form of the act, together with the muscular and other sensations proper to the act, issues in that particular act. By the law of association the repetition of any member of this cycle of processes tends to reproduce all. So the action of another person in a certain way leads to the reproduction in our minds of the entire cycle of inner processes, even if it be but the fingering of a mustache or watch chain. Pleasurable associations have their usual effect in intensifying the concept and so in provoking response in paths thus selected.

Vocal imitation is one of the most remarkable and may be explained in accordance with the above somewhat as follows: First, the basis is afforded by the cry reflex; second, modification of accidental sounds by impulsive mouth motions; third, appreciation of self-agency in the change; fourth, observation of mouth motions in others; fifth, association of mouth motions with the changed sounds of others; sixth, identification in association of certain mouth movements with certain sounds; then finally such sounds produced by others offering the conceptual initiative for the reproduction of the same sound. Nor should we omit the intense stimulation from association of sounds with motions which have already gained a place among the imitative powers of the child. When imitating motions the desire to imitate the associated sounds is undoubtedly enhanced. There may be other roots but these two may be considered foremost among then.

EDITORIAL.

OBJECTIVE NOMENCLATURE, COMPARATIVE PSYCHOLOGY AND ANIMAL BEHAVIOR.

Although it has not come into general use, the objective nomenclature for nerve physiology proposed in 1899 by the German physiologists, BEER, BETHE and VON UEXKÜLL[1] has served a good purpose, for it has stimulated discussion of the methods of description in biology and of the scientific status of comparative psychology.

In following the history of the development and influence of this nomenclature scheme during the past seven years, I have noted that certain facts which would seem to be of primary importance in connection with its use have been wholly neglected. I wish, therefore, after restating briefly the essential features and purposes of the scheme, to call attention to such facts, to discuss the relations of the objective nomenclature to comparative psychology, and to suggest certain considerations which should influence the standpoint from which we view psychic phenomena, and our methods of describing the behavior of animals.

First, by way of restatement, the objective nomenclature had as its chief purpose the avoidance of the implication of subjective phenomena in descriptions of neural processes. Our terms for stimuli, for the neural organs which are affected by stimuli, for processes in the central nervous system and for the responsive movements of the organism in many instances imply some form of consciousness, as the above mentioned physiologists have pointed out. Now, organs which receive stimuli may or may not be sense organs, hence it is obviously more accurate to use the term "receptor," proposed by BEER, BETHE and VON UEXKÜLL, than the term sense organ. We should speak of "photo-receptors" instead of visual organs or eyes, of "phono-receptors" instead of ears, of "tango-

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[1] BEER, BETHE *und* VON UEXKÜLL. Vorschläge zu einer objectivierenden Nomenclatur in der Physiologie des Nervensystems. *Zoölogischen Anzeiger.* Bd. 22, S. 275-80. 1899. *Biologisches Centralblatt.* Bd. 19, S. 517-21. 1899. *Centralblatt f. Physiologie.* Bd. 13, S. 137-41. 1899.

receptors" instead of sense organs of touch, for thus we avoid the implication of sense experience. Even in human (sense!) nerve physiology it is not always possible to prove that receptive organs have a sensory function (witness, the semicircular canal organs of the ear); far greater are the difficulties in justifying the use of subjective terms in the nerve physiology of other animals.

The objective nomenclature scheme provided purely objective terms for processes in the peripheral and central nervous system and for the reactions of the organism. Because of ignorance of the nature of physical processes and the lack of satisfactory physical terms, no terms for stimuli were proposed.

This much will suffice to indicate the nature of the scheme. I do not wish to give the terminology itself unnecessary prominence here, for, in my opinion, it is clumsy, inconvenient and unsuitable for general use; I desire instead to emphasize the convictions which led to the attempt at an objective system of terms: namely, that comparative physiology has nothing whatever to do with subjective phenomena in its descriptions, and that comparative psychology is either valueless or impossible, since we can never directly observe the consciousness of animals.

With the efforts of the advocates of the use of objective terms to the exclusion of subjective in the physiology of the nervous system I am in complete sympathy; with the contention of many of them, that comparative psychology is impossible I heartily disagree. Since the material of comparative physiology is objective phenomena and its goal the accurate and complete description of these phenomena in objective terms, the appearance of a subjective term in a descriptive formula of physiology indicates either ignorance of the nature of the phenomena in question or slovenliness on the part of the scientist. So much one may maintain without affirming or denying the existence of psychic phenomena in connection with the organism whose physiological processes are under consideration.

As a matter of observation, the objective nomenclature of BEER, BETHE and VON UEXKÜLL has not proved satisfactory in practice. It is highly artificial, unnatural and roundabout. Not even its authors have used it consistently, and NUEL'S[1] recent attempt to

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[1] NUEL, J. P. La Vision. Bibliotheque internationale. *Paris*, 1904. Pp. 376. See also, NUEL. La Psychologie comparée est-elle légitime? Repouse à *M. Ed. Claparède*. *Archives de Psychologie*, T. 5, p. 326-343. 1906.

apply it in the description of human visual phenomena resulted in a book which will do much towards preventing its further use. On the whole the results of the use of the system seem to justify the conclusion that clear logical thinking is far more important than the sharp separation of subjective from objective terms.

VON UEXKÜLL argues, however, that since we can describe the functions of the nervous system and the behavior of an animal in objective terms (*an assumption of the possibility of what has not been done, it is to be noted*) there is neither scientific justification nor excuse for the assumption that an animal has sense impressions, feels, thinks or wills. The concluding paragraph of his discussion of this matter is my chief excuse for this paper. "Such in a few words are the problems and aspects of experimental biology. A blossoming of this hopeful science is, however, only to be expected when investigators become impressed with the conviction that psychological doctrines in so far as they relate to the animal mind are worthless and untenable speculations, and when refusing to be led astray by the siren tones of theories of mind, they limit their researches to the facts of experience."[1]

There would be no reason to quarrel with VON UEXKÜLL were it not that he excludes much of the recognized material of human psychology from "experience." In fact, he frankly says that there can be no science of the mental life of animals because we can have no knowledge of their states of consciousness. BEER, BETHE, NUEL and many other writers on the physiology of the nervous system apparently agree with VON UEXKÜLL, and ZIEGLER[2] holds a similar position.

It is not clear that these scientists realize that their denials of the possibility of a science of comparative psychology can be made consistently and logically only if they deny that our inferences concerning the conscious states of our fellow beings, human and infrahuman, influence our actions. It is almost incredible that any thoughtful person should contend that we are not influenced constantly by what we believe to be the feelings, purposes, desires of our fellows, yet precisely this is demanded of those who deny the legitimacy of comparative psychology.

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[1] UEXKÜLL, J. VON. Psychologie und Biologie in ihrer Stellung zur Tierseele. *Ergebnisse der Physiologie*. Bd. 1, Abt. 2, S. 233. 1902.

[2] ZIEGLER, H. E. Theoretisches zur Tierpsychologie und vergleichenden Neurophysiologie. *Biologisches Centralblatt*. Bd. 20, S. 1–16. 1900.

For me the possibility of a science of comparative psychology is established by the observation (a fact of experience!) that we do react differently to what we infer to be conscious and unconscious beings, differently to beings which we infer to have differing grades or kinds of consciousness, differently again to the same being as we infer its states of consciousness to change. Who would deny that our inferences concerning pain in other animals influence our behavior, and who, even among the objectivists, would deny the possibility of validity to our inferences?

For the settlement of this dispute about comparative psychology, far more important than the discussion of an objective nomenclature is the recognition of the differences between the materials of nerve physiology and comparative psychology. The former deals directly and exclusively with objective phenomena, the neural processes, necessarily assuming the existence of consciousness; the latter deals with subjective phenomena as indicated by the structure and behavior of the animal. Both are divisions of biology; neither, so far as I can see at present, can be complete without the other. The physiologist does well to criticise the crudity and inexactitude of the psychologist's methods, as the psychologist does to point out to the physiologist the assumptions upon which his science rests, but neither gains anything by denying the possibility of the other's science.

Comparative psychology rests upon a system of inferences, from objective phenomena to subjective phenomena. Either kind of phenomenon may be a sign or indication of the other. In all natural sciences inferences from such signs are constantly employed. Our inferences concerning consciousness in other beings, it may be pointed out for the benefit of von UEXKÜLL and those who agree with him, are unescapable, for even in the construction of their objective terminology scheme, BEER, BETHE and von UEXKÜLL necessarily assumed that certain other beings are conscious of the objective facts they wish to designate and are capable of using terms as they do. In other words, we affirm the validity and prove the necessity of inferences concerning consciousness in our fellow beings every time we speak. The logical result of the denial of the possibility of comparative psychology is speechlessness. Even those who claim that animals are automata do not treat them as such.

To object to the arguments just advanced that human psychology is legitimate because we directly observe our own mental states introspectively, whereas comparative psychology is illegitimate because direct observation is not possible amounts to a denial of even the possibility of a natural history of mind. That such a denial should come from biologists is surprising, yet the fact remains that to-day the strongest opponents as well as the most able supporters of comparative psychology are biologists. Unfortunately those biologists who dispute the legitimacy of a science of mental life overlook the fact that the human mind is the maker of science.

That there can be no criterion of consciousness in the sense of proof I freely admit. We treat animals as if they were conscious, hence, the reason for a science of mind-in-nature. Merely "acknowledging,"[1] that other animals are conscious does not furnish us with the necessary materials for a genetic formula nor yet for the description of the experience of any particular animal at a given moment. It gives us our starting point, but we must employ signs of mind in the process of gathering together the materials of comparative psychology. The nature of certain of the signs which are available at present I have already discussed briefly elsewhere.[2] We may distinguish two groups: the structural and the functional. Together the facts which we bring under these rubrics constitute the bases for our inferences concerning consciousness.

CLAPARÈDE has expressed much the same view as is here presented, but I disagree with the assumption upon which he bases his discussion, while agreeing with the following conclusion. "Biology should work simultaneously according to two parallel methods each of which has its advantages and disadvantages, but which are mutually complementary; the *ascending* or physiological method, which setting out from the amœba, from the plant, even from the mineral, strives in mounting little by little the ladder of life, to explain the motor manifestations which it encounters by referring them to physico-chemical mechanisms . . . The other method which may be called the *descending* or psychological method, starts from man, from ourselves, in whom conscious states are indisputable, and tries to give account in psychological language of

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[1] MÜNSTERBERG, H. Grundzüge der Psychologie. *Leipzig.* 1900. Bd. 1, S. 98-99.

[2] YERKES, R. M. Animal Psychology and Criteria of the Psychic. *Jour. of Phil. Psy. and Sc. Method.* Vol. 2, pp. 141-49. 1905.

the mental life of animals."[1] CLAPARÈDE believes in the legitimacy of comparative psychology for the present, as is clear from the following, but he suggests that physiology may some time fill the demands which are now made upon the science of mind. "Is comparative psychology legitimate? Yes, as much so as is human psychology. When the physiologist shall have reared beside psychology a brain physiology, I mean a true physiology not the psychological copy which they present to us under that name,—a physiology capable of speaking alone, without failing if psychology does not whisper to it word by word what it ought to say,—we shall see then whether there is any advantage in the suppression of human psychology and, therefore, of comparative psychology. But we are not there yet."[2] It is not clear why psychology should be suppressed by the progress of physiology; rather might we expect it to be extended and developed.

But what is the value of comparative psychology? Granted its legitimacy, how does it justify its existence?

In experience we have a vast assemblage of inferences concerning conscious states beyond ourselves—this is the material of the science of comparative psychology, just as another portion of the experience of the self is the material of physics, another of physiology, another of astronomy. From this point of view comparative psychology is a part of the psychology of the self. The pertinent question is, Can the chemist justify his inferences concerning the existence of matter more satisfactorily than the comparative psychologist can justify his inferences concerning consciousness in other organisms? We have nothing to gain, much to lose, by denying the legitimacy of our inferences. As scientists it is our business to investigate their bases, the materials upon which the inferences rest. The comparative psychologist seeks to discover the developmental history of consciousness. To say at the outset that there is no such history, or that we can never know anything about it is, to put it mildly, unscientific. We may rest assured that comparative psychology will not survive in the struggle for existence among the natural sciences unless it justifies its existence by the perfecting of man's ability to adjust himself to his social environ-

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[1] CLAPARÈDE, E. The Consciousness of Animals. Translated from the French by WM. HARPER DAVIS. *The International Quarterly.* Vol. 8, p. 313. 1903.

[2] CLAPARÈDE, E. La Psychologie comparée est-elle légitime? *Archives de psychologie.* Vol. 5, p. 35. 1905.

ment. I am firmly convinced that it has practical value, and that this value will appear most strikingly in the perfecting of our inferences concerning consciousness which should result from the careful study of those signs of mind which constitute the bases of our inferences. It will do good service in rendering explicit bases of inference of whose existence we are unconscious.

Between nerve physiology on the one hand and comparative psychology on the other stands the study of animal behavior. If we should agree that nerve physiology should use objective terms only and comparative psychology subjective terms only, we should still have to ask what sort of descriptions are appropriate for animal behavior.

At intervals in the development of natural history gross anthropomorphism has appeared; everything was described in terms of human experience; at other times attempts have been made to avoid subjective interpretations by the use of purely objective terms. At present we are in a state of horror of subjective interpretation. Students of animal behavior seem to consider it a sign of weakness on their part to give any hint of an inference concerning consciousness. The odd thing, from my point of view, is that they should continue to treat the animals whose behavior they are describing as if they were conscious.

If there are no such phenomena as we mean to describe by the expressions my pain, your feeling of pleasure, the dog's sensation of sound, then certainly we are not justified in using subjective terms in the description of behavior. It does not follow as a matter of course, however, that we are justified in the use of the subjective form of description if the above phenomena do exist, for it is quite possible, as has been pointed out repeatedly, that the consciousness of the organism may be merely an epiphenomenon, without influence on the animal's action. Clearly then, there are two questions to consider in connection with descriptions of an animal's behavior: first, has the animal consciousness; second, does consciousness influence behavior? The possibility of answering the first is not dependent upon our ability to answer the second. As comparative psychologists we are concerned with the study of the forms and distribution of consciousness as well as with its functions. If it can be proven either that an animal is not conscious or that its consciousness has nothing to do with its behavior, then subjective terms have no place in the description of the behavior of that organism. The evidence in favor of the existence of some form of consciousness in most animals, not to mention plants, is so abundant, however, that it furnishes a grade of certainty upon which we do not hesitate to act; consequently it is fair to say that the burden of proof in this matter rests with the scientist who denies that the earthworm, the fish, the frog, the mouse may feel pain.

When we turn to the second question, we find that no one has ever succeeded in demonstrating that consciousness is unimportant for behavior. We have to admit that we do not know whether it is an epiphenomenon or not. Such being the status of our knowledge, the student of animal behavior is justified, if he chooses, in attempting to describe behavior in objective terms; he is not justified, however, in holding that subjective terms are unnecessary, unless he has succeeded in describing completely all forms of behavior in objective terms. Now, it is just this assumption that the advocates of the objective nomenclature and many other students of animal behavior have made. In opposition to their position, I wish to contend that although extreme anthropomorphism is undesirable because it tends to hide ignorance of objective phenomena with which we should be familiar—to say that the moth has the instinct to fly into the flame no longer satisfies the student of animal behavior—the complete avoidance of subjective terms in descriptions of behavior is impossible in the present state of our knowledge, and undesirable so long as we act as if sense impressions influence an animal's actions. I should further contend that it is wise to extend the use of objective terms in animal behavior as rapidly as possible, but that we lose more than we gain by trying to force our observations into objective descriptions before our knowledge of the objective phenomena warrants such procedure.

As it happens, I am far more deeply interested in the forms and conditions of animal behavior than in the existence of consciousness in connection with that behavior or its relation thereto. It seems to me, however, that the study of behavior will be furthered by the recognition of the fact that we have no right to assume that the subjective state need not be considered by the student of behavior. The investigation of function, as well as of structure, is absolutely necessary for the development of comparative psychology, hence we do well at present to devote ourselves to a study of the facts which constitute the bases of inferences concerning consciousness rather than to the discussion of inferences whose bases we are not able to evaluate. Comparative psychologists too often try to put the cart before the horse, so often in fact that most natural scientists have lost faith in their ability to progress and are inclined to ignore their work.

Practically, we are interested in what an animal feels, it matters not whether that animal be a man, a horse, a dog, only if its conscious state influences its action, for what we must know in order to be able to adjust our life to its life is how it acts and why. If consciousness is a part of the why, it is important that we should know that fact and enough more to enable us to predict the behavior of the animal. Obviously every student of animal behavior must be a comparative psychologist and every comparative psychologist first of all must be master of the science of activity.

The position which I have attempted to defend in this paper may be described summarily as follows. The use of an objective nomenclature in nerve physiology and in animal behavior is both desirable and necessary and the more consistently such a nomenclature can be adhered to the better. In the latter science, however, we are confronted with the question, Is this animal conscious and if so does that influence its behavior? If this question has to be answered in the affirmative in both parts, it is obviously impossible for the student of animal behavior to avoid the use of subjective terms. All natural sciences assume the existence of consciousness; they differ in the limits which they set for it. We treat certain objects as if they were conscious, others as if they were not. It is the business of the comparative psychologist to investigate the reasons for our inferences concerning consciousness in other beings and to evaluate the bases of these inferences. The inferences exist and they are unescapable, hence it is not only legitimate but also desirable to bring into full consciousness the objective facts which condition them. These facts are what may be called structural and functional signs of mind. The thorough study of the form and behavior of an organism is absolutely necessary as a preparation for inferences concerning the experience of the organism. We can never prove the existence of consciousness in any other than our own organism, but we can in certain cases obtain evidence which makes the probability of its existence as great as the probability of many of the facts with which other natural sciences deal. Too often the psychologist speculates as to the existence and form of experience without considering the materials which are the necessary bases of inferences concerning consciousness.

Although there is a general horror of interpretation among zoölogists and students of animal behavior at present, there is some evidence of a reaction against extreme objectivism with its unjustifiable assumptions and self-contradictions, in the writings of such biologists as JENNINGS, BOHN, SHERRINGTON, WHEELER and WHITMAN. ROBERT M. YERKES.

A COMMENT ON "OBJECTIVE NOMENCLATURE."

Mr. YERKES' discussion of the methodological problem in the foregoing article suggests the following questions: (1) Does he not emphasize too sharply the antithesis between the methods employed by the two sciences of nerve physiology and comparative psychology? (2) Might he not make his point, which is an important one, and at the same time advance the interests of comparative psychology, by granting more to the advocatesof the objective method than he does?

All science, we will agree, is study of activity. Comparative psychology, like nerve physiology, is the attempt to describe (and in adequately describing) to explain organic behavior. The phenomena with which comparative psychology deals are identical with those with which nerve physiology deals except that, for purely practical reasons in the convenient division of labor, the latter science stops short in its descriptions and explanations with certain facts and principles which the former science must employ by reason of the wider field which it includes within its scope. There is and can be no antagonism in the methods or points of view of the two sciences, since the one is in principle but the extension of the other; or perhaps it would be better to say that the one proceeds further along the same lines laid down by the other. The two methods are not like parallel lines which never meet—whatever hope there may be of their meeting at infinity where all sciences and philosophies merge in the mist and mystery of a completely rationalized universe. They are rather like different stages in a common process of inquiry, their ulterior starting point and goal being determined by a common motive and end, their difference being methodological only, *i. e.*, differing only by reason of the peculiar demands placed upon method by the greater complication of the phenomena. In this view of the matter comparative psychology finds itself dealing with a certain range of facts, which, like nerve action, are modes of activity and must be interpreted as such, but which in addition pass currently under other names—as conscious behavior, subjective facts, ejective phenomena. The sort of behavior for which these terms stand is a more complex kind of activity than that ordinarily treated under the categories of nerve physiology, but the method of describing them and the point of view from which they must be explained are the same. All the so-called mental facts of the universe can be explained only as they are reduced to terms of this common denominator of action. This is the history of the progressive transformation of the so-called philosophical or normative into exact sciences. This does not mean that these mental or spiritual phenomena *are* nothing more than the chemical and physical processes to terms of which we seek to reduce them. It simply means that we thereby find the bond of identity which therein reveals the two sets of facts as interrelated in a common system. It is simply taking seriously the demonstrable dynamic and organic character of the universe as we have found it up to date. The peculiar permutations and complications which activity exhibits in what are called the subjective or mental phenomena will find specific statement, to be sure, by reason of this greater complexity and this will be the respect in which comparative psychology will find a distinct field and method. But there is to be no schism methodologically corresponding to the ontological chasm between mind and matter which has vitiated so much scientific inquiry in the past. Categories are simply tools; laws and principles are merely the conceptual shorthand for observed uniformities in the behavior of the universe in certain regions and situations. And comparative psychology is distinctive solely by reason of the fact that it is seeking to describe and explain an as yet more ambiguous portion of these observed uniformities than nerve physiology. To seek to restrict this science to the instruments elaborated to deal with a more limited and simpler subject-matter is to prejudge the entire outcome from the start. This, as it appears to the present writer, is the true defense of the independent position of comparative psychology, and a defense which at the same time admits the main contention of the advocates of the objective method.

H. HEATH BAWDEN.

LITERARY NOTICES.

Bing, Robert, and Burckhardt, Rudolf. Das Centralnervensystem von Ceratodus forsteri. *Gustav Fischer, Jena.* 1905. Reprinted from Semon's *Zoölogische Forschungsreisen in Australien und dem Malayischen Archipel.*

This paper, which is dedicated to Professor Edinger, consists of two parts, a purely descriptive part by Dr. Bing and a comparative part by Professor Burckhardt. The first part includes brief descriptions of the external form of the brain, its relations to the surrounding cranial structures, the ventricles the histology of the various regions as revealed by hæmalum preparations, and the embryological development of the brain.

The second part begins with a comparison of Ceratodus and Protopterus. After an exhaustive analysis of their characters, Professor Burckhardt concludes that it is scarcely possible to affirm that either of these brains is more primitive than the other. He rightly dismisses this comparison as of far less importance than the question: Do the structures and relations of the brains of Ceratodus and Protopterus correspond with what we already know of the phylogenetic relationships of these forms in general. Then follows a comparison with Polypterus, Acipenser and Scymnus. The author lays great stress (possibly relatively too great) on growth-strains and other mechanical or non-nervous factors in shaping the forms of the brains of the lower fishes, as opposed to the direct response of the central nervous system to its peripheral sensory and motor functional dependencies. He certainly has made a very important point in emphasizing the necessity of considering in each case the brain in its relation to the organism as a whole. While, therefore, the brain may be taken as a fairly reliable index of phylogenetic values in a group like the selachians where the types follow in closely seried ranks, it is quite otherwise in the ganoid-dipnoid phylum, where we have scattered survivals of a rich fauna now nearly extinct. Here, on account of differences in mode of life and diversity of past phyletic history of the few surviving types, phylogenetic speculations based on the brain can have small value except as controlled by the whole mass of phyletic records—anatomical, embryological and palæontological.

Professor Burckhardt recurs to the thesis which he developed several years ago so forcibly in his "Bauplan des Wirbelthiergehirns," that the broad resemblances from which the phylogenetic relationships of the larger groups are most clearly deduced are to be found in the non-nervous parts of the brain rather than in parts which have been highly specialized for particular functions. But, like most of the other comparative neurologists of Europe, he seems not to have an adequate appreciation of the fact that in evaluating the significance of the positive adaptive differentiations of the nervous substance the real units are not the traditional arbitrary transverse divisions of the brain, but the functional systems. These primitive reflex systems, like the ventricular and ependymal landmarks which Burckhardt uses so effectively, are very constant in fundamental plan; and yet the whole of the evolutionary history of the vertebrate nervous system can be read in terms of their progressive or regressive modifications.

C. J. H.

Wilson, J. T. On the Anatomy of the Calamus Region in the Human Bulb, with an Account of a Hitherto Underscribed "Nucleus Postremus." *Journ. Anat. and Physiol.*, Vol. 40, Part 3, pp. 210-241, and Part 4, pp. 357-386. 1906.

The region of the calamus scriptorius of the medulla oblongata is of great importance morphologically, particularly in connection with the problems connected with the phylogentic relations between brain and spinal cord. This region, it appears, is exceedingly variable, a fact which accounts for much conflict in the literature. In truth, this part of the human brain has never been comparatively studied and minutely described. Professor Wilson here publishes a valuable study designed to supply the desired information regarding this region and the limits of its variation.

He describes three distinct dorsal massive fusions above the fourth ventricle in the calamus region of the human bulb. One is the true obex, another a more extensive fusion of the ala cinereal funiculi ventrally of the obex, which he terms the "intercinereal commissure." Between these two there sometimes occurs a fusion of the areæ postremæ of the two sides. These structures are usually not all well developed in the same specimens. When the most ventral coalescence is large the obex is reduced to scarcely more than a membrane, termed the "false obex." The obex lies above the area postrema, the intercinereal commissure below the latter, connecting the vago-accessorial columns or funiculi of opposite sides. The coalescence of the areæ postremæ may occur independently of both of the other commissures mentioned, or it may be more extensive so as to extend up to and even include within it the obex. A mass of neurones is described in the area postremus, the "nucleus postremus."

The obex is regarded by Wilson as lying in the roof plate (of His), and the intercinereal commissure as connecting derivatives of the lateral zone ("Schaltstück" of His), which Wilson rightly regards (in opposition to the treatment of His in describing these structures) as of equal morphological value with the dorsal and ventral zones. The area postrema of Retzius represents the true dorsal zone (of His) of the embryonic neural tube.

Numerous stereographic illustrations materially assist the author's presentation. He has also studied and figured transections of all the important variant types described.

C. J. H.

Bruce, Alex. Distribution of the Intermedio-lateral Tract of the Spinal Cord. *Trans. Roy. Soc. Edinburgh*, Vol. 45, Part I, No. 5. 1906.

This paper gives the results of an enumeration and study of the cells of the intermedio-lateral tract of the human spinal cord, suggested by the author's previous studies upon the cells of the ventral cornua.

The intermedio-lateral tract may be defined as a tract composed of a special series of nerve cells, situated at the outer margin of that portion of the gray matter which lies between the anterior and posterior cornua. These cells are not necessarily limited to the lateral cornua. Within the spinal cord the tract is found in three regions: (1) in the upper cervical region as low as C. 4; (2) in the lower cervical, the thoracic and the upper lumbar regions; and (3) in the lower sacral region. It is absent in the cervical enlargement from C. 5 to C. 7 inclusive, and in the lumbosacral region from L. 3 to the upper part of S. 3 inclusive. In that portion of the tract which is at present under consideration, viz.: the second of the above mentioned divisions—its component cells are found mainly in two positions: (*a*) in the lateral horn proper, or in analogous positions above the level at which the lateral horn is fully constituted; and (*b*) along the margin of that part of the gray matter which is in immediate relationship to the formatio reticularis, and also among the strands of the formatio reticularis itself. For convenience of description and reference these may be distinguished as the *apical cells* and the *reticular cells*. The apical and reticular cell systems have not a coextensive longitudinal distribution.

The lateral horn is not fully constituted above the lower half of the first thoracic segment. This horn is not a transition from the lateral part of the anterior horn, but a new and independent formation. It is represented in C. 8 and the upper part of D. I by the outlying cells of the intermedio-lateral tract. The middle cells described by WALDEYER do not form any part of the intermedio-lateral tract. The number of cells in the intermedio-lateral tract is vastly greater than has hitherto been recognized. The enumeration shows a total of 88,577 cells on the left side and 89,182 on the right. These figures are certainly below the total number. These cells do not form a continuous column, but occur throughout the tract in groups or clusters. These groups are not symmetrical on the two sides, although they may present a general resemblance to each other. In each segment the cell groups are arranged in a manner which may be regarded as characteristic of that segment. The intermedio-lateral tract has a vascular supply largely independent of that of the anterior cornu. The segmentation of the tract into groups or clusters or cells is not due to the distribution of blood vessels or of the root fibers, but is probably in some way related to their function.

The researches of GASKELL and LANGLEY as to the outflow of the sympathetic fibers show that the distribution of these coincides in a remarkable manner with the distribution of the cells of the intermedio-lateral tract. It is now certain that the column of CLARKE cannot be the source of origin of these fibers, and if there is any spinal center at all it must, by exclusion, be either the "middle cells" of WALDEYER or the intermedio-lateral tract, or both of these. This communication shows that where there is the greatest outflow of sympathetic fibers there is the greatest number of cells in the intermedio-lateral tract. The cervical sympathetic gets its largest supply of fibers from the portion of the cord included between the eighth cervical segment and the fifth or sixth thoracic segments—segments in which the groups are most rich in cells. Then the outflow of the splanchnics is largest in the lower thoracic region, and here again the number of cells markedly increases and the character of the groups changes. The researches of ANDERSON and HERRING, and of ONUF and COLLINS, seem to point with considerable unanimity to the intermedio-lateral tract as being the source of the sympathetic fibers. It must be admitted, however, that other observers have found conflicting, and sometimes unintelligible, results of the experiment of section of the nerves, and further researches are obviously needed.

C. J. H.

Holmes, J. S. The Biology of the Frog. *New York, The Macmillan Company.* 1906. Pp ix 370, 94 figs. $1.60.

What HUXLEY did for the crayfish HOLMES has done for the frog.

In this text-book for college students, which contains the materials of a course of lectures delivered at the University of Michigan, the author has tried to present those facts of structure, function and behavior with which the student of biology should be familiar.

Chapters are devoted in order to the systematic position, habits, natural history, parasites, external and internal characters, development, histology, the anatomy and physiology of the various systems of organs, the reflexes, instincts and intelligence of the leopard frog, Rana pipiens.

Dr. HOLMES has shown good judgment in the selection of his materials from the great mass of literature on the frog. There are many omissions, some of which were necessitated by the limitations of the volume, which are unfortunate from certain points of view, but on the whole the book is well balanced and promises to stimulate students to research while at the same time presenting them with the preeminently important facts concerning the biology of the frog.

There are several minor typographical errors and some verbal omissions which slightly mar the work. The most serious errors noticed by the reviewer occur on p. 331, in the description of the structure of the retina. The passage referred to reads, "The retina is marked by a thickening or papilla where the optic nerve enters, whereas in the higher animals this place is marked by a depression, the *fovea centralis.*" There are two mistakes in the sentence: it certainly is not true of all the higher animals, if of any of them, that the point of entrance of the optic nerve, the blind spot, is marked by a depression. In the human eye there is an elevation, as in the eye of the frog. Further, the *fovea centralis* is the center of the *macula lutea*, not the center of the blind spot. Such errors as these are exceedingly unfortunate.

The chapter on the functions of the brain leaves one with the impression that after all not much is definitely known about the subject. For the elementary student this has both advantages and disadvantages: on one hand it shows him that there is plenty of opportunity for original work even in fields of investigation which have been occupied by many skilled scientists, and on the other it tends to make him feel that too little is known about the subject to enable one to study it to advantage.

Excellent descriptions of many of the commonly observed forms of behavior of the frog are given. It is noticeable, however, that the author has no very definite usage for the word instinct, for on the same page (305) he writes of the clasping reflex and the clasping instinct, while in a later chapter he explains briefly that the instinctive act is probably a chain-reflex. The danger is that a student will be perplexed by the accounts of reflex and instinctive forms of activity which are given.

The book is provided with convenient author and subject indices and with lists of references at the end of each chapter. Undoubtedly the value of the work could be greatly increased by certain changes in the arrangement of materials and in expression, yet there can be no doubt that it will be very valuable as a text-book. The author deserves much credit for bringing together into readable form the mass of material which constitutes "The biology of the frog."

R. M. Y.

Peckham, G. W. and E. G. Wasps Social and Solitary. *Boston, Houghton, Mifflin and Company.* 1905. Pp. xv + 311.

A considerable portion of the material of this volume is revised from the authors' book on the instincts and habits of the solitary wasps,[1] but enough new observations

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[1] On the Instincts and Habits of the Solitary Wasps. *Wisconsin Geological and Natural History Survey.* Series No. 1, Bulletin No. 2. 1898.

have been added to justify republication, even if that were not fully justified by the authors' success in popularizing their work. There are few studies in natural history which combine such admirable accuracy of observation and description with the charm of style which is found in this book.

For several years the PECKHAMS have studied the behavior of the social and solitary wasps with patience, intelligent scientific insight and devotion to truth. They have done well to make the results of their labors accessible to the general reader, as well as to the scientific student of animal behavior, by writing the book which we have in hand.

By far the greater part of the volume is devoted to accounts of the habits of different species of wasps, but a few experimental tests of the sense equipment of the *Vespas* are mentioned in the first chapter. Experiments with colored card-boards proved to the satisfaction of the authors that these wasps can discriminate the spectral colors. Their tests are open to the objection that the influence of difference in intensity was not excluded. It is quite possible, so far as one may judge from the authors' account of their method, that the wasps responded to intensity differences and not to colors.

Other simple tests proved the existence of sensitiveness to chemicals (smell). On the whole it seems fair to say that the value of the observations under natural conditions which are described in the book far outweighs that of the few experiments tried. The PECKHAMS are naturalists, in the best sense of the term, but they are not experimentalists in the study of animal behavior.

Detailed accounts are given of the digging, stinging, cell-storing, cell-closing, nest-finding and several other forms of activity of a number of different kinds of wasps. The value of these descriptions is great because they are based upon a number of observations, not upon a single occurrence of the act.

The various forms of behavior exhibited by the wasps are classified by the authors as instinctive and intelligent. Concerning the first of these classes, the most important conclusion to which one is led by the materials of the book is that acts of this type are far more variable than they are usually supposed to be. Few indeed of those acts of the wasps which are by common consent called instinctive occur in exactly the same way from time to time in either the individual or the species. Indeed, there is such marked variability that the old definition of instinct seems scarcely applicable. The PECKHAMS have rendered the science of animal behavior an invaluable service in proving beyond question that well established instinctive forms of reaction do vary even in the insects. If one were to select the most important contribution which the work of the authors has made to our knowledge of animal behavior, undoubtedly this fact of the variability of instinctive acts would be chosen.

Individual differences appear strikingly not only in instinctive forms of behavior but equally in intelligent acts. The individuals of the same species of wasp differ markedly often in the accuracy, care, skill, and rapidity, with which they perform a certain kind of act. These marks of individuality are indicative of intelligence. Many of the most interesting and picturesque of the descriptions of the book deal with individual peculiarities. The authors came to know intimately and to feel attachments for the members of certain species of wasps because of their attractive ways, their industry, patience, perseverance.

After close attention to the problem of the "sense of direction," observation os the behavior of solitary wasp as they leave and return to the nest and experiments on the social wasps to test their ability to find their way back to the nest after being carried away from it, the authors conclude that there is no special "sense of direction," but that instead the wasps find their way to a particular spot by the aid of memory of the locality. Ordinarily a solitary wasp does not leave its nest until it has carefully examined the surroundings. This it does by walking or flying in constantly enlarging circles about the spot. If by any chance the insect is scared away before this examination is finished it either has difficulty in finding, or is unable to find, its nest. Again, when the surroundings of the nest are changed, the animal is at a loss to locate the spot. These and other observations prove very satisfactorily that the wasps depend upon vision for the locating of a particular spot. Apparently their sense of sight is extremely keen. This suggests the importance of a thorough experimental study of this sense in wasps and other insects.

Thoroughly reliable as well as readable descriptions of the habits of animals are extremely rare. The PECKHAMS deserve great credit for their contribution to the study of the behavior of wasps, for the work which it demanded was by no means a holiday pastime.

R. M. Y.

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Hadley, P. B. Regarding the Rate of Growth of the American Lobster. *Report of the Comm. of Inland Fisheries of Rhode Island*, Vol. 36. 1906.

Watson, J. B. The Need of an Experimental Station for the Study of Certain Problems of Animal Behavior. *Psychological Bulletin*, Vol. 3. 1906.

Boswell, F. P. Irradiation der Gesichtsempfindung. *Zeit. f. Sinnesphysiologie*, Vol. 41. 1906.

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THE MODE OF CONNECTION OF THE MEDULLATED NERVE FIBER WITH ITS CELL BODY

BY

OLIVER S. STRONG.
(*Columbia University.*)

With Plate XIX.

One of the principal lacunæ in our present knowledge of the finer structure of the nervous system concerns the relations between the medullated and non-medullated portions of the nerve fibers—our ignorance of precisely what parts are medullated and what are not. This has been brought out by Nissl in his book on the Neurone Theory, and, while Nissl is doubtless overexacting in his requirements as to what is necessary to practically establish neuro-histological relations, yet he has done a service in calling attention to the somewhat surprising lack of actual observation of certain relations which have been taken more or less for granted. The principal terra incognita is, naturally, that portion of the distal end of the nerve fiber extending from where the sheath ends to the pericellular termination. There is also some deficiency in our actual observation regarding the proximal end of the fiber, especially its acquisition of the sheath. Nissl has also called attention to this fact.

The reasons for these deficiencies lie naturally in the defects of our histological technique. We have precise methods for demonstrating the sheath and also methods for displaying the naked axis cylinder process, but still lack a practical specific axis cylinder stain. We also lack a good method for combining these two pictures and demonstrating at once the medullated and non-medullated parts of the nerve fiber.

The present note does not profess to furnish such a method, nor to fill in the most important of the gaps above mentioned, but simply to give some demonstrations of the relation of the medullated fiber to its cell of origin. These are taken from preparations which were made by means of modifications of the WEIGERT–PAL method which have so far proved rather uncertain and limited in their applicability but are nevertheless here given.

The material used was the lumbar cord of an infant five weeks old. This had been previously fixed and preserved in 10 per cent formalin (4 per cent formaldehyde). Pieces about five mm. long were placed in a neutral developer (ortol without alkali being the one actually used) for two days and then transferred to copper bichromate,[1] 2 to 3 per cent for two days. They were then dehydrated, embedded in colloidin and cut. The sections were stained in one per cent aqueous hæmatoxylin solution, twelve to twenty-four hours, and decolorized with potassium permanganate and weak sulphurous acid in the usual way.

A variation consisted in a repetition of the mordanting. The pieces of cord were treated as follows: Ortol, 3 days; copper bichromate, 1 day; ortol, 4 hours; copper bichromate, 1 day; ortol, 4 hours; copper bichromate, 1 day; dehydrated, embedded, and cut; and sections stained and decolorized as before.

Another variation consisted in staining the sections in DELAFIELD's hæmatoxylin instead of an aqueous solution of hæmatoxylin. These were decolorized as before, the decolorization taking place more rapidly. This variation gave the results somewhat different from the first two, as noted below.

Those who have worked with the WEIGERT-PAL method and its various modifications are aware of the tendency at times for some of the bodies and coarser dendrites of the nerve cells to remain undecolorized. This tendency is usually more pronounced when sulphurous acid is used instead of the oxalic acid-sulphite mixture originally recommended by PAL. It may be diminished by adding potassium chlorate to the mordant, at least when formalin material is mordanted with copper bichromate. This stain of the cell bodies is usually black or brownish-black, and, therefore, apparently different in character from the blue or bluish-black stain of the myelin sheath. The effect of the above treatment is to

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[1] Copper bichromate has been used for some years by the author as a mordant for formalin fixed and preserved material when making WEIGERT–PAL preparations. It usually yields pictures exhibiting all the medullated fibers with great sharpness; its only disadvantage being its tendency to make the material brittle. (See *Journal of Comparative Neurology,* Vol. 13, No. 4. Dec., 1903.)

enhance the tendency of the cell bodies, dendrites, and also of the axis cylinders to remain stained, with the result that in some cases the cell bodies, coarse dendritic branches and axis cylinder processes were stained black, the sheath being stained bluish-black. Often many of the cell bodies were more or less completely decolorized, but in many of these the "axone cone" and the rest of the axis cylinder process retained the stain. Many preparations were filled with small brown granules between cells and fibers which marred their clearness but did not prevent the cells and their processes from being quite easily observed; in other preparations these granules were practically absent.

The sections stained with DELAFIELD's hæmatoxylin presented a somewhat different picture. Here the granules were completely absent and both sheath and axis cylinder were stained blue. The axis cylinders in the white matter were usually more deeply stained than the sheaths. In the cell bodies a considerable variety of pictures was displayed. Often the bodies of NISSL were very clearly defined; in others, the whole body and dendrites were stained a diffuse deep blue with at times a slightly fibrillar appearance. The cells showing only the NISSL bodies stained did not usually, naturally, exhibit the axis cylinder process.

The "axone cone" emerging from the cell body or from a dendrite (Fig. 3), usually either tapers regularly to the narrow portion (neck) of the axis cylinder process (Figs. 3 and 5), or first diminishes gradually and then more abruptly (Figs. 1 and 2). The curves described are so similar to those produced by pulling apart some plastic substance as to suggest that a tension upon this, presumably the weakest, part of the axis cylinder may have been a factor in its production either during growth or as an artefact in fixation, or both.

The diminution of the axone in diameter at a point near the cell body has long been figured (for example, see GERLACH's figure of an isolated cell, copied in many text-books). In the present preparations it is very strikingly shown. In some, this portion is still thinner than indicated in the accompanying figures. Often, too, the cone and the medullated part of the fiber only are shown, this intervening portion not being visible. This is probably usually due to its being decolorized. This extreme attenuation is not improbably an artefact. The cell bodies in these preparations are often not perfectly fixed and exhibit considerable shrinkage. Such a shrinkage of the cell body will naturally, as suggested above, stretch this part, the medullated portion being probably much less plastic. It is hardly probable, however, that all of the diminution in thickness of this portion of the axone is artificially produced, inasmuch as it has been demonstrated by so many methods (isolation, GOLGI, EHRLICH, CAJAL).

With a single exception (see below) no sign of any collateral branch for the naked part of the axone has been noted, but this cannot be regarded as negative evidence of much weight, for the stain is obviously only capable of demonstrating comparatively coarse structures. In the exception noted there is a small process given off from the distal part of the cone which could not be followed far, owing either to its terminating or, more probably, having been decolorized. It is not a termination of some fiber upon the surface. In other imperfectly decolorized sections, however, strands can be seen crossing the pericellular space, similar to those described by NISSL and others. In certain cases these bear some resemblance to the pericellular terminations of AUERBACH.

Beyond the narrow portion the axone expands and at the same place becomes medullated (axis cylinder). This expansion may be rather gradual (Figs. 3, 4 and 5) or quite abrupt (Figs. 1 and 2). At the same time there is usually an apparent deepening of the stain. This is probably due partly to the increase in size and partly to the presence of the stained myelin sheath above and below the axis cylinder. Considering the well known tendency of the axis cylinders to shrink, they would appear to be fairly well fixed in these preparations.

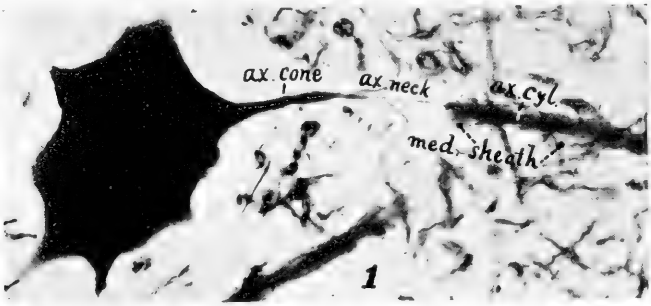
The increase in size of the axone always coincides with the appearance of the myelin sheath. Furthermore, there seems to be often a correlation between its mode of expansion and the appearance of the sheath; when the former expands abruptly, the sheath appears to attain its full size also abruptly. The sheath is often distorted considerably by the fixation, etc., and exhibits alternating contractions and vesicular expansions. This is shown especially in Figs. 1, 3 and 5. In other cases (Figs. 2 and 4), the fixation is better. Owing probably to local contraction, there are places where it is difficult to demonstrate the presence of the sheath, as is indicated in the figures. A close study of the relations at the point of origin of the sheath with the sheath better fixed is still desirable.

The only structures, besides nucleus and nucleolus, to be made out in cell body, dendrites, and axone, are the bodies of NISSL when DELAFIELD's hæmatoxylin was used. The rest of the cytoplasm of the cell body and dendrites and also the axone at times, showed an approach in places to a fibrillar structure; but usually a nearly uniform color with a slight mottling and a slightly alveolar appearance. There appeared no structural differences, consequently, between the cone, the narrow part, or neck and the medullated or axis cylinder part of the axone.

Owing probably to the fact, above mentioned, that the method is incapable of demonstrating very fine processes, the axones of the smaller cells were not available for study. It is to be still more regretted that it was not capable of yielding pictures showing the termination of the distal end of the medullated fibers. In the preparations, especially those stained with DELAFIELD's hæmatoxylin, the gray matter is filled with fine blue fibers, finer than those exhibited in corresponding WEIGERT-PAL preparations, but about equal to the latter in number. These fibers are apparently the axis cylinders of the medullated portions of the fibers in the gray.

All the accompanying figures (Plate XIX) are reproductions of photographs.

Columbia University,
September, 1906.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ax. neck
ax. cyl.
med. sheath
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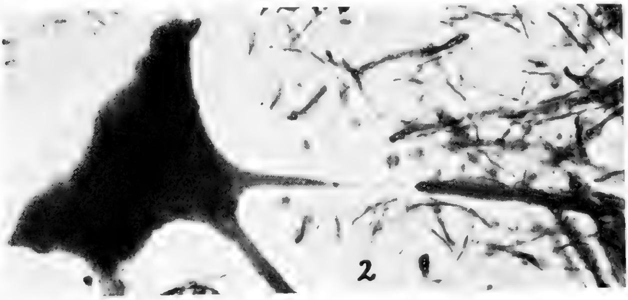
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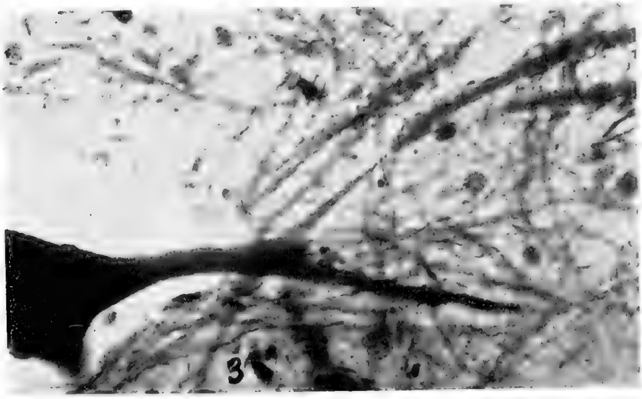
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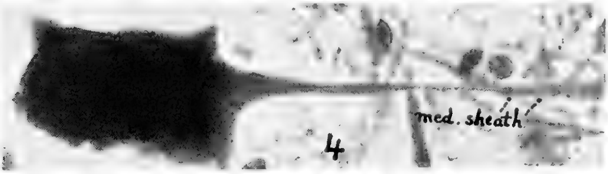
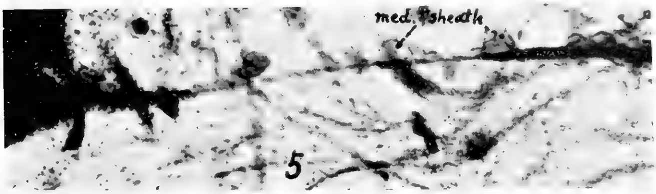

med. sheath
4


med. sheath
5

ON THE CENTERS FOR TASTE AND TOUCH IN THE MEDULLA OBLONGATA OF FISHES.

BY
C. JUDSON HERRICK.

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

WITH FIFTEEN FIGURES

It is now generally recognized that in the medulla oblongata of all vertebrates there is a clearly defined longitudinal differentiation into four zones, somatic motor, visceral motor, somatic sensory and visceral sensory. The somatic sensory is the cephalic continuation of the cornu dorsalis of the spinal cord and includes the funicular nuclei, spinal V tract and its associated substantia gelatinosa Rolandi and sensory V nucleus, the tuberculum acusticum and its derivative, the cerebellum, together with the peripheral nerve roots associated with these structures. The visceral sensory zone includes the fasciculus solitarius of mammals and birds and the associated peripheral roots and gray centers. In the Ichthyopsida the equivalent structure is the fasciculus communis and the associated gray, comprising the facial and vagal lobes and their prolongations caudad into the spinal cord and cephalad into the mid-brain. The somatic sensory column includes the unspecialized centers for touch and their specialized acustico-lateralis derivatives. The visceral sensory column likewise includes unspecialized centers of general visceral sensation and specialized derivatives for taste.

Between these somatic and visceral primary centers there is very little direct anatomical connection, their morphologic independence, in fact, being one of the most striking features of the medulla oblongata, especially in lower vertebrates, where anatomical continuity would be expected if these two systems were phylogenetically related.

Certain fishes which possess functional taste buds in the outer skin, notably the siluroids (Ameiurus) and some gadoids, have been shown (Herrick, '04) to find their food ordinarily by the simultaneous use of both taste and touch, though either sense alone may, upon occasion, call forth the feeding reflexes and the gustatory and tactile factors may be experimentally isolated by training. The primary cerebral centers for both taste and touch in these fishes are now accurately known. They belong, as we have just seen, to entirely different systems of neurones, visceral sensory and somatic sensory, respectively, which throughout the central nervous system are anatomically very distinct. It becomes, then, a question of some interest, where and in what way the peripheral neurones of taste and touch from the outer skin come into physiological relation to serve the ordinary reflex feeding movements of these fishes.

Since both systems of cutaneous nerves are highly developed in Ameiurus, our inquiry will begin with this type, using for control other species in which one or the other member is better isolated. This study is based upon an extensive series of sections of brains of various teleostian fishes, stained with Delafield's hæmatoxylin, and the methods of Weigert and Golgi. The following types have proven especially helpful: Ameiurus nebulosus, which exhibits a high development of both gustatory and tactile centers; Cyprinus carpio, where the gustatory system attains maximal development; Conger conger where the gustatory system is feebly developed and the tactile system strong; and Prionotus carolinus, where the gustatory system is moderately developed and the spinal tactile system is greatly enlarged.

This paper will be devoted to a description of these centers and their connections in the siluroid fish, Ameiurus. The facts here presented have been controlled by a study of the other types mentioned, but the detailed discussion of the comparative data will be deferred.

The spinal cord and region of the funicular nuclei of fishes have never been satisfactorily analyzed, and such analysis is exceedingly difficult if attention is directed solely to fishes of the ordinary type with typical or average development of all of the elements. But by comparing such fishes with various other types showing diverse specialization of the several functional systems, a tolerably precise result can be obtained without resort to the degeneration methods, whose application to fishes proves to be very uncertain.

The ordinary feeding reflexes of Ameiurus are generally total reactions of a simple type, but involving the use of most of the striated muscles of the body. Contact of a barbel or other sensitive part of the outer skin with a morsel of food is followed by a turning of the body in the direction of the food and the movements of the jaws and pharynx necessary to seize and swallow it. The first movement involves practically the entire body musculature and probably requires the discharge of nearly all of the peripheral neurones of the somatic motor type except the eye-muscle nerves. And if the gaze of the fish is simultaneously directed toward the food object, these motor nerves, too, must be brought into play. In a similar way, the movements of seizing, mastication and swallowing require the discharge of nearly all of the peripheral neurones of the head belonging to the specialized visceral motor system—motor V nucleus for the muscles of the jaw and operculum, motor VII nucleus for the muscles of the hyoid and its derivatives, and motor IX and X nuclei for the muscles of the gills and œsophagus.

In the spinal cord of fishes we know from the figures of RETZIUS ('93), VAN GEHUCHTEN ('95), MARTIN ('95), and others, that the ventral horn cells, which innervate the somatic muscles, send their dendrites out to ramify widely in the region of the lateral and dorso-lateral funiculi and adjacent formatio reticularis (funiculus lateralis proprius). Our problem here, then, is to determine the relations of the two primary sensory centers in question to each other and to these longitudinal pathways of the spinal cord.

Similarly in the oblongata, the nuclei of the peripheral motor nerves mentioned above are known to receive their innervation chiefly by way of the formatio reticularis alba et grisea (*cf.* CAJAL, '96, and HERRICK, '05) and we have now to learn the relations of the primary gustatory and tactile centers to this structure and its derivatives.

In the teleosts here examined all of the tactile (general cutaneous) nerves of the head enter the brain by two roots, the sensory trigeminus root and the general cutaneous root of the vagus. The latter is probably always present in teleosts, though often so small as to be distinguished with difficulty. In Prionotus it is very large. Upon entering the oblongata, the sensory trigeminus root turns caudad as a whole to constitute the spinal V tract. There is no appreciable "chief" sensory nucleus at the level of entrance of the nerve, nor have I been able to demonstrate in teleosts a mesencephalic root of this nerve. The spinal V tract just before reaching the region of the funicular nuclei receives the vagal general cutaneous root (Fig. 6). The tract is accompanied by a variable amount of substantia gelatinosa Rolandi within which some of its fibers end. In most teleosts this structure seems to be reduced, possibly by the crowding due to the great development of the tuberculum acusticum and vagal lobes, save in the lower part of the oblongata, so that by far the greater part of the spinal V tract ends in the region of the funicular nuclei or further caudad in the spinal cord. In some teleosts there is a well differentiated nucleus of the spinal V tract in the funicular nucleus region; in others this nucleus and the nucleus funiculi are confused. In all cases a considerable proportion of the trigeminal root fibers pass caudad beyond the nucleus funiculi into the dorso-lateral funiculus of the spinal cord, where they can be separately followed for several segments before being lost among the other fibers of this funiculus.

In fishes where the taste buds are very numerous in the outer skin (cyprinoids and siluroids) the nerves of these cutaneous organs all enter the brain by the communis root of the facialis nerve and terminate in a specially differentiated center, the lobus facialis. In other fishes where they occur these fibers enter the brain by the same nerve root, but end in the vagal lobe along with other gustatory fibers from the inside of the mouth which enter by the VII, IX and X nerves. The vagal lobe in all cases also receives from the IX and X nerves a large number of general or unspecialized visceral fibers which have no peripheral connection with taste buds. These visceral fibers are more numerous in the more caudal rootlets of these nerves, coming from the œsophagus and abdominal viscera, than in the more cephalic rootlets, coming from the gills and palate where taste buds are abundant (HERRICK, '99, p. 246).

The most caudal sensory root of the vagus nerve, immediately after entering the oblongata, turns caudad to end in the commissural nucleus of CAJAL near the median line caudad of the vagal lobes, some of the terminal fibers crossing in the commissura infima to end in the nucleus of the opposite side (Figs. 5, 7, 13, 14, 15). This root is probably chiefly of general visceral function, not gustatory, and in the figures is termed the descending sensory root of the vagus.

In the highly developed teleostean brains which we are here considering, each of the two primary sensory functional zones contains, in addition to the primary terminal nucleus of the related nerve roots, very important coördination centers. In the visceral zone the nucleus intermedius facialis et vagi, as described in Ameiurus (HERRICK, '05) is such a coördination center, putting the primary visceral centers of the facial and vagal lobes into functional relation with the formatio reticularis and thence with the motor cerebral nuclei. It is well known that the primary somatic sensory (tactile) center of this region, the substantia gelatinosa Rolandi, is similarly in functional relation with the formatio reticularis (CAJAL, '96).

There is further a broad connection of medullated fibers, as shown by WEIGERT-PAL sections of Ameiurus, from the spinal V tract to the facial lobe which seems to be unique. These tracts, which appear to be collaterals of the trigeminus root fibers, plunge through the substantia gelatinosa Rolandi to end among the intrinsic neurones of the deeper layers of the facial lobe. When we remember that the facial lobe of Ameiurus receives only those root fibers of the facial nerve which connect peripherally with taste buds in the outer skin (HERRICK, '01), and that the spinal V tract contains root fibers of the trigeminus which conduct tactile sensibility from the same areas of skin in which these taste buds occur, it appears highly probable that the fibrous connection between the spinal V tract and the facial lobe is for the purpose of effecting a correlation of the two diverse modalities of cutaneous sensibility which enter the brain by the V and VII nerve roots. The intrinsic neurones of the facial lobe must be regarded as the coördinating cells.

The facial lobe of Ameiurus, then, is not only a primary endstation for the gustatory root of the VII nerve, but it is also a correlation center for these fibers and for collaterals from the tactile root of the V nerve. Its intermediate nucleus receives neurites of intrinsic neurones which are doubtless in relation with both types of root fibers. It also receives directly a large fascicle of gustatory VII root fibers.

The nucleus intermedius of the vagal lobe is also a coördination center, though not of exactly the same type. The vagal lobe itself receives no direct tactile root fibers from the spinal V tract, nor were any such fibers observed to reach its nucleus intermedius. The latter nucleus does, however, receive unmedullated neurites of intrinsic neurones of the vagal lobe and has broad efferent paths, to the formatio reticularis.

A third correlation center belonging to the visceral sensory column is the nucleus commissuralis. This nucleus, first described in the mammals by CAJAL ('96, p. 46), is very large in all fishes having large gustatory centers. In Ameiurus it is a highly developed structure forming a median protuberance above the caudal tip of the fourth ventricle just behind the vagal lobes, and directly continuous cephalad with the nucleus intermedius of the vagal lobe, some neurites from the latter nucleus terminating here (HERRICK, '05, p. 432). The caudal ends of the vagal lobes fuse in the median line in the region of the n. intermedius and this area of fusion is produced backward into the commissural nucleus (Figs. 7, 6 and 5), which with its commissure lies dorsally of the nucleus ambiguus.

The nucleus commissuralis receives, as we have seen, fibers from the most caudal sensory root of the vagus. That these are not motor fibers is shown by their mode of arborization in GOLGI preparations (Figs. 13 and 14). The motor vagus roots from the nucleus ambiguus lie farther ventrally. The commissural nucleus also receives secondary tracts from the vagal lobe (Fig. 7, *desc. sec. X*). The cephalic end of the commissural nucleus receives slender fascicles of medullated fibers from the descending secondary gustatory tract arising in the facial lobe of the same side. These detach themselves from the inner border of their tract and ascend along the mesial aspect of the substantia gelatinosa, thence plunging directly mesad into the commissural nucleus (Fig. 6, *r.*).

Large feebly medullated and unmedullated tracts pass from this nucleus to the formatio reticularis (Fig. 5), and perhaps also smaller tracts to the cephalic end of the funicular nucleus. Sagittal sections of Ameiurus by the GOLGI method show that the tracts from the commissural nucleus to the formatio reticularis constitute the efferent path from this nucleus. These fibers, having reached the region laterally of the cephalic end of the canalis centralis, give off collaterals and often divide into ascending and descending branches. The cells of the commissural nucleus are small and arranged chiefly along the dorsal surface of the nucleus. The richly branched dendrites ramify throughout the nucleus among the termini of the vagus root fibers, the neurite arising from the dendrite. The arrangement of these cells resembles somewhat that of the chief gustatory cells in the vagal lobe of the carp, though it is much less regular. The commissura infima in this region contains many dendrites of these cells.

Commissural fibers, both medullated and unmedullated, are scattered throughout the substance of this nucleus and these fibers constitute the greater part of the commissura infima Halleri of fishes. The latter commissural complex, however, contains, as we shall soon see, a separate system of somatic sensory fibers in addition to those just described.

In Ameiurus, then, the commissural nucleus of CAJAL receives direct root fibers from the vagus, probably of unspecialized visceral sensation; it also receives secondary tracts from the vagal lobe which may be both visceral and gustatory, and very small secondary tracts from the facial lobe which are quite certainly gustatory. It does not seem to have any somatic sensory connections. Its efferent path is broadly into the formatio reticularis.

These three centers, the nucleus intermedius facialis, the nucleus intermedius vagi and the nucleus commissuralis of CAJAL, are clearly important correlation stations for simple reflexes and seem to form a continuous series. The first receives chiefly gustatory excitations from the outer skin and a far smaller amount of tactile excitation from the same areas; the second receives gustatory excitations from the mouth cavity and general visceral stimuli by way of the vagal lobe; while the third receives direct root fibers of general visceral type and secondary visceral (and gustatory ?) excitations from the vagal lobe and secondary gustatory tracts from the facial lobe, the latter in very small numbers. The main efferent conduction path for all of these centers is the same—to the formatio reticularis of the same and the opposite side, chiefly by short unmedullated tracts. Their connections are, therefore, chiefly with the visceral motor nuclei of the oblongata immediately adjacent, viz: the motor nuclei for mastication, deglutition, etc.

From the lowest of these nuclei, the commissural nucleus of CAJAL, an ill defined visceral area extends caudad on each side into the spinal cord. This is chiefly composed of gray substance and in different fishes contains variable proportions of cells, neuropil and medullated fibers. It can be distinctly followed for but a short distance down the spinal cord and soon is lost in the central gray dorso-laterally of the canalis centralis. This region of the spinal cord of mammals is regarded as a visceral center; the same is probably true for the fishes, though we have no very precise knowledge of the central relations of the visceral components of the spinal nerves in these types.

Figs. 1 to 6 illustrate a series of transections through the brain of Ameiurus stained by the method of WEIGERT-PAL, all drawn to the same scale, extending from the spinal cord as far cephalad as the nucleus intermedius vagi. For the arrangement of the visceral centers cephalad of this point, consult my former paper (HERRICK, '05).

Reviewing now the visceral centers, in the spinal cord of fishes we have not yet clearly demonstrated these centers save at the cephalic end, where we find the central gray dorso-laterally of the canalis centralis related to the cerebral visceral centers. Passing cephalad from this primary visceral zone, we have a series of three visceral sensory centers which seem to have been differentiated successively from the spinal cord cephalad. The commissural nucleus of CAJAL differs in no essential respect from the visceral region in the vicinity of CLARKE's column and the intermediate zone of the mammalian spinal cord save for the greater crowding and more medial position of its cells. In both cases the dorsal commissure contains both root fibers and dendrites of the cells of the nucleus. The condensation of both nucleus and commissure in the oblongata are simply explained on mechanical grounds, as due to the crowding of the commissural elements backward by the opening out of the membranous roof of the fourth ventricle. Another important factor in the condensation of this nucleus is the usurpation by the intestinal, cardiac and œsophageal branches of the vagus of visceral functions which primitively pertained probably to the spinal cord, for this nucleus appears to be the primary end-station for these vagal branches, at least, in part.

We conclude, therefore, that the commissural nucleus of CAJAL and its commissure represent an enlargement of the visceral sensory centers of the spinal cord, but present no evidence of great specialization otherwise.

It is important to bear in mind from the start, that, in addition to the visceral commissural nucleus, or nucleus of CAJAL, to which alone we have referred in the preceding pages, there is in this region another unpaired nucleus, which I shall call the somatic commissural nucleus. Associated with it is a somatic portion of the commissura infima. This nucleus has not, so far as I know, been described. It and its commissure are intimately related to the funicular nuclei and will be more fully discussed in a later article.

Passing forward to the vagal lobe, we find here a second enlargement of the general visceral sensory component correlated with the increase of mucous surface in the gill region, and in addition, an extreme differentiation to provide the terminal nucleus of the fibers from the numerous taste buds found in that same mucous membrane. Still farther cephalad we have in Ameiurus a similar and more recently acquired specialized derivative, the facial lobe, to receive the fibers from the taste buds of the outer skin.

Both the facial and the vagal lobes give rise to long ascending secondary tracts in addition to the short reflex paths just described. These terminate in the superior secondary gustatory nucleus under the cerebellum (nucleus lateralis cerebelli) and will not be further considered in this paper (*cf.* Herrick, '05). There are, moreover, long descending secondary gustatory tracts, to whose consideration, we must next turn. Those from the vagal lobe and commissural nucleus are not well defined and can scarcely be distinguished from the short paths to the formatio reticularis. They are probably of the same tpye, *i. e.*, chiefly visceral and gustatory reflex paths for the visceral musculature. The descending secondary tract from the facial lobe, however, is large, compact and heavily medullated. Its origin from the cephalic part of the facial lobe and its position dorsal to the ascending secondary tract suggest that it has been differentiated in the course of the phylogeny more recently than any of the other secondary gustatory tracts. It passes back ventral to the spinal V tract and closely joined to it and before the level of the funicular nuclei is reached has been enveloped ventrally by the cephalic part of the dorso-lateral funiculus to be described later. It is in fact a part of that funiculus and its further course cannot be described apart from that fiber complex and its associated gray centers. We shall, therefore, next give an account of the somatic sensory centers of the spinal cord and lower part of the oblongata.

The caudal end of the medulla oblongata and the cephalic end of the spinal cord are dominated by the somatic sensory centers in nearly all teleosts. There are two well defined gray centers, as in the mammals, the funicular nucleus and the nucleus of the spinal V tract, whose development varies greatly in different species.

In the lower levels of the spinal cord the cornu dorsalis is feebly developed, as a rule, as is also the funiculus dorsalis, no distinction into fasciculus gracilis and fasciculus cuneatus being possible. The only neurones of the dorsal cornu which are often impregnated in my preparations are small cells whose neurites reach the formatio reticularis of the same side (Fig. 8).

Laterally of the cornu dorsalis there is a large fascicle of heavily medullated fibers which is usually apparent to the naked eye as a strand on the dorso-lateral aspect of the spinal cord and which is separated from the more ventral masses of the funiculus lateralis by a fissure or groove. This, I shall term the fasciculus dorsolateralis (Figs. 1 to 6, *f. d. l.*). It includes the spinal residue of the spinal V and descending secondary VII tracts and ventrally of these a much larger number of long fibers, most of which pass cephalad from the spinal cord to end in the region of the funicular nuclei and farther forward into the medulla oblongata. It does not receive dorsal root fibers of the spinal nerves. These enter the funiculus dorsalis (Figs. 1 and 2). The impression given by my preparations is that the dorso-lateral fasciculus is composed wholly of ascending fibers, save for the descending trigeminus and secondary facialis tracts just mentioned. On the other hand, the remainder of the funiculus lateralis (marked *f. l.* on the figures) seem to be composed chiefly of descending fibers.[1] There is a broad band of unmedullated external arcuate fibers between the cephalic end of the funicular nucleus and the visceral commissural nucleus above and the ventral funiculi below. This connection is especially well developed in cyprinoids.

In the dorso-lateral fasciculus the following distinct elements may be recognized:

1. The greater portion terminates in the median funicular nucleus (ascending fibers, Figs. 3, 4, 9, 13 and 14).
2. Another division of ascending fibers ends in the lateral funicular nucleus (Figs. 4, 5 and 13).
3. Another part consists of the spinal V tract, descending fibers which terminate in the nucleus of the spinal V tract and farther caudad in the spinal cord (Figs. 3, 4, 7, 13 and 14).

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[1] It should be stated, however, that my preparations do not give positive proof that the latter fibers run in the direction indicated. I mention this here because it is my rule in these papers to make no unqualified statements regarding the direction taken by a fiber tract without observational evidence. That the dorso-lateral fibers are chiefly ascending I can assert positively from their mode of ending in the funicular nuclei as shown by Golgi preparations.

4. A fourth component is the descending secondary gustatory tract from the facial lobe, which ends in the median and lateral funicular nuclei and also passes far downward into the spinal cord.

5. A well defined bundle, marked *x* on Figs. 3 and 4, extends cephalad into the oblongata beyond the funicular nuclei closely accompanying the spinal V tract. This bundle can be distinguished in Ameiurus as far cephalad as the motor V and VII nuclei. In Prionotus a similar bundle can be followed with ease through the whole length of the oblongata to the cerebellum, which it enters dorsally of the ascending secondary gustatory tract and nucleus. Although I have not been able to follow this tract with certainty into the cerebellum in Ameiurus, I feel sure that its course is the same as that of the similar tract of Prionotus. My preparations do not enable me to say whether it is an ascending or a descending tract. I presume that it is ascending, and have accordingly provisionally designated it, tractus spino-cerebellaris. In Ameiurus a large proportion of its fibers seem to end in the facial region of the oblongata.

Internally of the fasciculus lateralis is a compact bundle of heavily medullated fibers which probably arise in the dorsal cornu and immediately cross in the ventral commissure as internal arcuate fibers. This tract, which I term the *tractus-spino-tectalis*, is joined by the similar fibers of the tractus bulbo-tectalis in the medulla oblongata and both terminate together in the colliculus of the mesencephalon. In its upper course this tract was termed the lateral longitudinal bundle by Stieda and Mayser and lemniscus in my former paper (Herrick, '05, p. 386). The tract as a whole is undoubtedly homologous in a general way with the lateral lemniscus of mammals. Unfortunately an entirely different tract, the tractus tecto-bulbaris et spinalis, has been called lemniscus by several of the leading students of fish brains.

Passing cephalad, as we approach the end of the spinal cord, in Ameiurus the cornu dorsalis rapidly expands and becomes clearly differentiated into two parts which are very distinct in Weigert preparations (Fig. 2). Meantime the formatio reticularis has also enlarged, especially dorso-laterally of the canalis centralis. The deeper one of the gray derivatives of the dorsal cornu is intimately connected by means of medullated and unmedullated fibers with this formatio reticularis. It is the nucleus funiculi, or to distinguish it from the lateral funicular nucleus to be described below, I shall designate it the *median funicular nucleus*. Dorso-laterally of the funicular nucleus and farther cephalad, forming a sort of cap upon it, is the nucleus of the spinal V tract. This nucleus is more closely related to the dorsal cornu of the spinal cord than is the funicular nucleus.

The funiculus dorsalis ends in both nuclei, as also does the spinal V tract (Figs. 3, 4, 7 and 13). The funicular nucleus, however, receives far larger numbers of fibers from the fasciculus dorsolateralis than from both the other tracts mentioned. The nucleus of the spinal V tract is distinguished from the funicular nucleus, as in the mammals, by its clearer texture in WEIGERT preparations and greater freedom from medullated fibers. The spinal V tract and funicular nuclei and their associated fiber tracts form a protuberance caudad of the vagal lobes which is very conspicuous in all siluroid brains. The two nuclei attain about equal proportions in this protuberance (Fig. 3).

The *spinal V nucleus* extends cephalad as far as the caudal end of the vagal lobe. Here it shrinks to very small proportions and is continued cephalad directly into the substantia gelatinosa Rolandi (Fig. 5), the spinal V tract assuming a crescentic form in cross-section with the substantia gelatinosa on the mesial side embraced within the horns of the crescent. From this substantia gelatinosa voluminous secondary tracts pass through the ventral commissure to the tractus bulbo-tectalis (Fig. 6) of the opposite side (internal arcuate fibers). Other connections are made with the formatio reticularis and the motor nuclei of the same side and with the interior of the facial lobe.

Figs. 9 to 12 illustrate various forms of neurones in the spinal V nucleus. Fig. 13 shows the mode of ending of the fibers of the spinal V tract in the nucleus, some of them passing through to terminate in the median funicular nucleus. Figs. 11 and 13 show that some fibers of the dorso-lateral fasciculus also end in this nucleus. The small intrinsic neurones of Figs. 11 and 12 have short branched neurites which end within the nucleus or in the adjacent formatio reticularis of the same and the opposite side. The large spinal V neurones of Figs. 9 and 10 do not show the full course of the neurites. They probably reach the tractus bulbo-tectalis or one of the other long secondary tracts. WEIGERT sections show heavily medullated internal arcuate fibers from the spinal V nucleus and substantia gelatinosa for their entire extent passing into the tractus bulbo-tectalis.

It is evident from the preceding description that the dorsal cornu, spinal V nucleus and substantia gelatinosa are parts of a single structure whose morphological relations are quite simple, the dorsal cornu being the point of departure for the differentiation of the other two. The termination of a part of the spinal V tract in the funicular nucleus shows, moreover, that the latter nucleus is also intimately related morphologically with the dorsal cornu.

The relations of the funicular nuclei, however, are not so easily mastered. They are without doubt primarily correlation centers for descending tactile fibers in the spinal root of the trigeminus nerve and for ascending secondary fibers (chiefly tactile in function) in the dorso-lateral fasciculus (Figs. 13 and 14). The latter tract increases notably in size as we pass cephalad and its larger part ends in the funicular nuclei, though a considerable portion extends farther cephalad into the oblongata. Associated with this latter portion are the ascending and descending secondary gustatory tracts, a spino-cerebellar tract and the spinal V tract. All of these except the last may properly be regarded morphologically as parts of the dorso-lateral funiculus, whose spinal portion is equivalent to the dorsal part of the funiculus proprius lateralis of mammals. Accordingly, the funicular nuclei are to be regarded as derivatives of the formatio reticularis, with which the median nucleus is in very close relations, as we saw above. The formatio reticularis in this region contains many small cells and also very large cells which are closely similar to those of the median funicular nucleus and the somatic commissural nucleus. These cells are practically equivalent in the three places (*cf.* Figs. 9, 11, 12, 13 and 14).

The relations of the median funicular nucleus at its caudal end where it begins to appear as a derivative of the underlying formatio reticularis grisea are seen in Fig. 2 (*n.fn.m.*). As we pass cephalad it rapidly enlarges parallel with the enlargement of the nucleus of the spinal V tract and receives on its lateral border large masses of fibers from the dorso-lateral fasciculus, including both ascending fibers from the spinal cord and descending secondary gustatory fibers from the facial lobe. On the mesial border it receives the greater part of the small dorsal funiculus and dorso-laterally it receives for its entire extent fascicles from the spinal V tract, which break through the intervening nucleus of the spinal V tract, as shown in Figs. 4 and 7. In the boundary between the nucleus of the spinal V tract and the median funicular nucleus there are scattered medullated fibers and some more compact fascicles. These are the efferent tracts of secondary and tertiary fibers from these nuclei. They accumulate at intervals and, accompanied by strong unmedullated bands, pass downward. Some enter the adjacent formatio reticularis, others cross to the opposite side through both the dorsal and the ventral commissures, while still others pass ventrad to make direct connections with the ventral cornu.

The lateral funicular nucleus is a crescentic area enveloping the dorso-lateral border of the medulla oblongata in the cephalic part of the funicular region, attaining its greatest dimensions laterally of the extreme caudal end of the vagal lobe (Fig. 5). Cells of this nucleus are shown in Figs. 13, 14 and 15. It is smaller in Ameiurus than in some of the other teleosts examined. It is continuous dorsally with the median nucleus and seems to be an outgrowth from the latter in the only direction in which enlargement was possible. That is, the funicular nucleus, having been prevented from further enlargement laterally by the spinal V tract and its nucleus, reached the dorsal surface of the medulla oblongata and then spread out laterally over the outer surface of the spinal V tract. It is improbable, however, that the peculiar relations of the lateral funicular nucleus are determined wholly by mechanical factors. By far the greater part of the descending secondary gustatory tract from the facial lobe ends in this nucleus and it might almost be termed an inferior secondary gustatory nucleus, as in fact I did in my paper on the gustatory paths ('05); for this connection is the most distinctive feature of the nucleus, and gives to it its character as the most important center of correlation between gustatory and tactile stimuli. But in view of the way in which the tactile fibers are distributed to the nuclei of this region and in particular the liberal distribution of the secondary gustatory fibers to the median funicular nuclei and probably also to the underlying formatio reticularis, it would appear that this whole somatic area is the field of discharge of the descending gustatory fibers from the facial lobe. No special part of this field can then be properly called the inferior secondary gustatory nucleus; and since the commissural nucleus of CAJAL may be in part a terminus of secondary gustatory fibers from the vagal lobe (though it is more probable that the secondary vagus tracts which reach this nucleus are general visceral, not gustatory), I have in this paper avoided the term inferior secondary gustatory nucleus altogether. This is further justified by the fact that in some other fishes the descending secondary gustatory tract from the facial lobe ends chiefly in the median nucleus.

The lateral funicular nucleus is much less compact than the median nucleus and is permeated throughout by medullated fibers in diffuse formation, many of which accumulate on its dorsal border and cross to the opposite side in the somatic portion of the commissura infima dorsally of the commissural fibers from the median nucleus (Fig. 4). Some fascicles of the dorso-lateral fasciculus appear to pass through the lateral nucleus to enter the commissure, where they cross to the opposite side, without being interrupted in the nucleus. This nucleus receives fibers from the dorso-lateral fasciculus of the spinal cord, as we saw above. These are doubtless ascending tracts bearing tactile impressions from the spinal cord. It also receives collaterals from the fibers of the spinal V tract and direct root fibers from the general cutaneous root of the vagus and fibers arising from cells of the substantia gelatinosa Rolandi of the oblongata. Long dendrites of its cells extend out into the substantia gelatinosa.

Under the caudal end of the vagal lobe both funicular nuclei disappear; but a considerable mass of medullated fibers extends farther cephalad from the median nucleus into the formatio reticularis. A considerable bundle of feebly medullated fibers extends cephalad from the lateral nucleus also (Fig. 6, *n.fn.l.*) and constitutes the chief efferent path from this nucleus. This tract rapidly diminishes cephalad and evidently contains large numbers of ascending fibers for the oblongata. It sends strong fascicles of internal arcuate fibers into the ventral commissure, as well as fibers to the formatio reticularis and motor nuclei of the same side. A small residue can be traced as far forward as the level of the facial lobe, where it is lost in the surrounding tracts.

We may summarize the efferent tracts from the cornu dorsalis, nucleus spinalis trigemini, substantia gelatinosa Rolandi and the median and lateral funicular nuclei together, as they are of common type. (The tuberculum acusticum might well be added to the list; but as its connections are somewhat more special and as these features bear no relation to our present problem, these tracts will not be considered in this paper.) The common efferent tracts from the somatic sensory centers of the lower oblongata are as follows:

1. Short paths, mostly unmedullated, to the formatio reticularis grisea of the same side and similar tracts, partly medullated, to the formatio reticularis of the opposite side through the dorsal commissure (somatic portion of the commissura infima Halleri in the oblongata). The number of these fibers in any region varies in proportion to the size of the somatic sensory centers.
2. Broad tracts (chiefly medullated) directly to the ventral cornu of the same side and opposite side (through the ventral commissure).
3. Long paths of medullated fibers to the formatio reticularis alba of the same and the opposite side (crossing in the ventral commissure). These are both ascending and descending.
4. The ventro-lateral funiculus contains large uncrossed descending tracts which must be regarded as more highly developed fascicles of the tracts last mentioned (fasciculus bulbo-spinalis).
5. Likewise derived from the formatio reticularis alba are the heavily medullated internal arcuate fibers which pass from the somatic sensory centers through the ventral commissure to the tractus spino- et bulbo-tectalis (lemniscus). These are chiefly or wholly ascending.
6. Accompanying the latter are internal arcuate fibers for the ventral funiculi of the opposite side. These are doubtless long descending tracts for spinal cord reflexes.
7. From the region of the funicular nuclei there is also an uncrossed tract to the cerebellum, tractus spino-cerebellaris.
8. Commissural fibers, both medullated and unmedullated, in the somatic portion of the commissura infima Halleri from the nuclei of one side to those of the opposite side.

It appears, then, that the chief tracts for efferent impulses from the somatic sensory centers to distant regions are the descending paths in the ventral funiculus (crossed) and the ventro-lateral funiculus (crossed and uncrossed) and the ascending path in the tractus spino-et bulbo-tectalis or lemniscus (wholly crossed) to terminate in the opposite optic lobe. The former is for direct reflex movements of the body as a whole (unspecialized somatic motor type); the latter is for correlation of cutaneous stimuli with visual and other cerebral nerves, especially for the coördination of movement of the eye-muscle nerves (specialized somatic motor type). Throughout the spinal cord there is in addition to the tracts just mentioned a large uncrossed ascending secondary tactile path in the dorso-lateral fasciculus, which arises in the dorsal cornu and terminates chiefly in the funicular nuclei but partly in the formatio reticularis of the oblongata farther cephalad.

The two funicular nuclei, then, and the spinal V nucleus together represent differentiations of the somatic sensory column of the spinal cord. They have little, if any, direct connection with the phylogenetically ancient visceral sensory centers represented in the commissural nucleus of CAJAL and the vagal lobes. They do, however, receive the secondary gustatory tract from the facial lobes, this being a connection recently acquired by these highly specialized fishes to effect a cerebral connection between the long established tactile organs of the skin and taste buds which have later appeared in these same cutaneous areas. The facial lobe is known to receive all of the peripheral nerves from these cutaneous taste buds and it is the only visceral center which is closely connected with the somatic sensory centers of the medulla oblongata. The gustatory fibers from within the mouth terminate in the vagal lobes and have no such intimate relations with the somatic sensory centers. The descending secondary gustatory tract from the facial lobe must, then, be regarded *functionally* as a somatic reflex path, even though morphologically it belongs to the visceral division of the nervous system; for it is excited only by gustatory stimuli arising in the outer skin and accompanied ordinarily by simultaneous tactile stimuli. Moreover, it terminates in the primitive tactile coördination center of the brain, which suffers but little modification in consequence, and the motor return paths for the tactile and the gustatory stimuli seem to be identical. The last point is correlated with the fact that experiment shows that identically the same somatic reactions follow from either tactile or gustatory excitation of a given area of skin, though the fish may be taught to react to one and not to the other by training (HERRICK, '04).

SUMMARY

The analysis of the lower region of the medulla oblongata and upper region of the spinal cord in Ameiurus shows that the visceral and somatic divisions are as clearly separable here as in other parts of the central nervous system. The visceral sensory zone is ill defined in the spinal cord, but in the oblongata is concentrated into three massive structures. The lowest, the commissural nucleus of

Cajal, receives the descending sensory root of the vagus and is chiefly concerned with unspecialized visceral impressions. The next is the vagal lobe, which includes both unspecialized and gustatory centers, the taste fibers coming from within the mouth. Finally, the facial lobe is a neomorph concerned exclusively with gustatory impressions from the outer skin.

In the somatic zone the dorsal cornu gives rise directly to the spinal nucleus of the trigeminus and farther cephalad to the substantia gelatinosa Rolandi, while the adjacent formatio reticularis grisea is enlarged to form the median and lateral funicular nuclei.

The commissura infima of Haller is a very complex structure. It has two main divisions; (1) a visceral part associated with the commissural nucleus of Cajal, and (2) a somatic part, which is chiefly a commissure of the funicular nuclei. Associated with the latter is a somatic commissural nucleus, not hitherto described.

The centers for unspecialized visceral sensation and for taste fibers arising within the mouth have no direct connection with the somatic sensory nuclei; but the facial lobe, which receives gustatory sensation from the outer skin, sends a strong tract downward to end in the two funicular nuclei and farther caudad into the spinal cord, for the purpose of effecting correlation between the two modalities of cutaneous sensation, taste and touch.

This descending secondary gustatory tract from the facial lobe is, of course, morphologically a derivative of the visceral sensory division of the medulla oblongata; but it has assumed all of the characteristics of a somatic tract, ending in the somatic sensory centers with the tactile pathways and exciting the same somatic motor nuclei to action in the response, as the latter. That is, a functional adaptation has crossed one of the most rigid morphological barriers in the central nervous system, the barrier between the visceral and somatic sensory systems.

Denison University.
October 13, 1906.

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FIG. 1. Transverse section through the spinal cord of an adult specimen of Ameiurus nebulosus about 20 cm. long, stained by the method of WEIGERT-PAL. Figs. 1 to 6 are drawn from the same series of sections, all to the same scale. The first section is taken at the level of the second spinal nerve. × 35.

c.d., cornu dorsalis; *com.d.*, commissura dorsalis; *f.d.l.*, fasciculus dorso-lateralis; *f.l.*, fasciculus lateralis; *f.l.m.*, fasciculus longitudinalis medialis; *f.n.d.*, funiculus dorsalis; *f.r.d.*, formatio reticularis dorsalis; *tr.sp.tec.*, tractus spino-tectalis (lemniscus); 2 *sp.d.*, dorsal root of second spinal nerve.

FIG. 2. Section through the spinal cord of Ameiurus at the level of the first spinal nerve. At this level the dorsal cornu has enlarged and separated into two nuclei, the median funicular nucleus and the nucleus of the spinal V tract. The funiculus dorsalis at this level contains both ascending fibers from the spinal cord for the funicular nuclei and descending fibers from the spinal V tract. The fasciculus dorso-lateralis contains chiefly ascending fibers from the spinal cord for the funicular nuclei, but also some descending secondary gustatory fibers from the facial lobe. × 35.

com.d., commissura dorsalis; *f.d.l.*, fasciculus dorso-lateralis; *f.l.*, fasciculus lateralis; *f.l.m.*, fasciculus longitudinalis medialis; *fn.d.*, funiculus dorsalis and spinal V tract; *f.r.*, formatio reticularis; *f.r.d.*, dorsal part of the formatio reticularis which is related to the funicular nucleus; *f.v.*, funiculus ventralis; *n.fn.m.*, median funicular nucleus; *n.sp. V.*, spinal V nucleus and dorsal cornu; *tr.sp.tect.*, tractus spino-tectalis (lemniscus); *v.c.*, ventral cornu; 1.*sp. d.*, dorsal root of first spinal nerve; 1.*sp.v.*, ventral root of first spinal nerve.

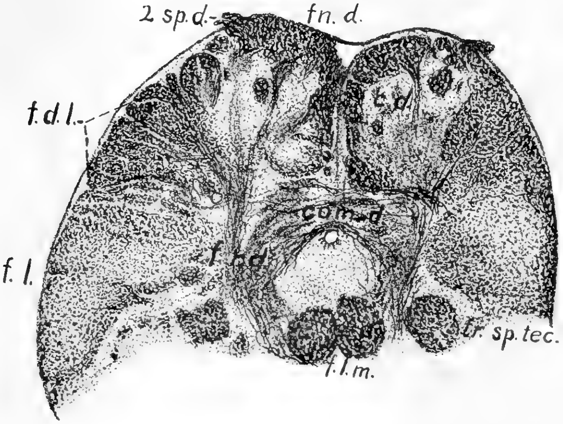
2 sp.d.
fn. d.
f.d.l.
com. d
f.l.
f.r.d.
tr. sp. tec.
f.l.m.

FIG. 1.

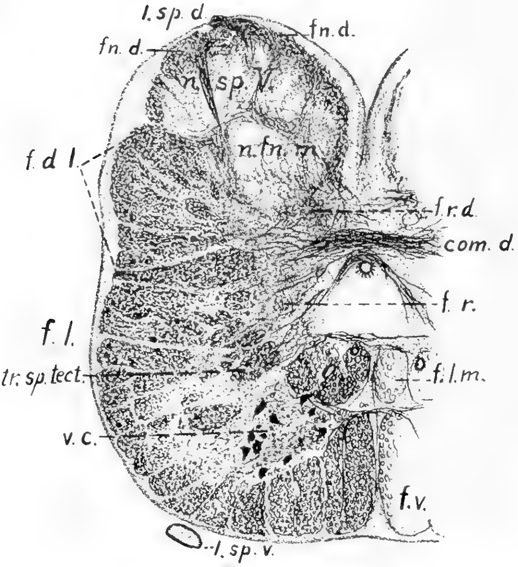
l. sp. d
fn.d.
fn. d.
n. sp. V.
f. d l.
n. fn. m
f.r.d.
com. d.
f. r.
f. l.
tr. sp. tect.
f. l. m.
v. c.
f. v.
l. sp. v.

FIG. 2.

FIG. 3. Section a little farther cephalad than the last. At this level the funiculus dorsalis has been almost entirely replaced by the spinal V tract and the fasciculus dorso-lateralis has begun to move upward along the outer side of the spinal V tract to reach the lateral funicular nucleus farther cephalad. Extensive tracts also pass from this fasciculus inward to reach the median funicular nucleus and formatio reticularis. Bundles of secondary fibers appear between the spinal V nucleus and the median funicular nucleus, which pass downward into the formatio reticularis. The dorsal commissure has considerably enlarged, its fibers passing chiefly between the formatio reticularis of the two sides. From this point cephalad this commissure is known as the commissura infima Halleri. In the dorso-lateral fasciculus there is a separate bundle, designated *x* in Figs. 3 and 4, which ascends into the oblongata beyond the level of the funicular nuclei, joining itself to the ventral part of the spinal V tract. I have designated it provisionally the tractus spino-cerebellaris. The most dorsal part of the fasciculus is designated *w* and termed tractus bulbo-spinalis. It arises in the lateral part of the formatio reticularis in the region of the funicular nuclei (Figs. 6 and 5), and appears to be a descending tract for the spinal cord. × 35.

com.inf., somatic part of commissura infima; *f.d.l.*, fasciculus dorso-lateralis; *f.l.*, fasciculus lateralis; *f.l.m.*, fasciculus longitudinalis medialis; *f.r.*, formatio reticularis; *f.v.*, fasciculus ventralis; *n.fn.m.*, median funicular nucleus; *n.sp.V.*, spinal V nucleus; *s.*, secondary tracts from spinal V nucleus and median funicular nucleus; *sp. V. tr.*, spinal V tract; *tr.sp. tect.*, tractus spino-tectalis (lemniscus); *w.*, tractus bulbo-spinalis; *x.*, tractus spino-cerebellaris *y.*, secondary tracts from lateral funicular nucleus (*cf.* Fig. 4).

FIG. 4. Section through the funicular nuclei at their widest part. The lateral funicular nucleus appears external to the spinal V tract and its nucleus, receiving many fibers from the fasciculus dorsolateralis and sending large tracts to the formatio reticularis and the commissura infima. This commissure receives also a large mass of fibers from the median funicular nucleus and probably also from the spinal V nucleus. This section shows the somatic portion of the commissura infima at its greatest extent. Fibers are seen passing from the spinal V tract into its nucleus, and some pass through this nucleus to end in the median funicular nucleus. × 35.

com.inf., somatic part of commissura infima; *f.d.l.*, fasciculus dorso-lateralis; *f.l.*, fasciculus lateralis; *f.l.m.*, fasciculus longitudinalis medialis; *f.r.*, formatio reticularis; *f.v.*, fasciculus ventralis; *n.amb.*, caudal end of nucleus ambiguus; *n.fn.l.*, lateral funicular nucleus; *n.fn.m.*, median funicular nucleus; *n.sp.V.*, spinal V nucleus; *s.*, secondary tracts from spinal V nucleus and median funicular nucleus; *sp.V.tr.*, spinal V tract; *tr.sp.b.tect.*, tractus spino- et bulbo-tectalis (lemniscus); *w.*, tractus bulbo-spinalis; *x.*, tractus spino-cerebellaris; *y.*, secondary tracts from lateral funicular nucleus.

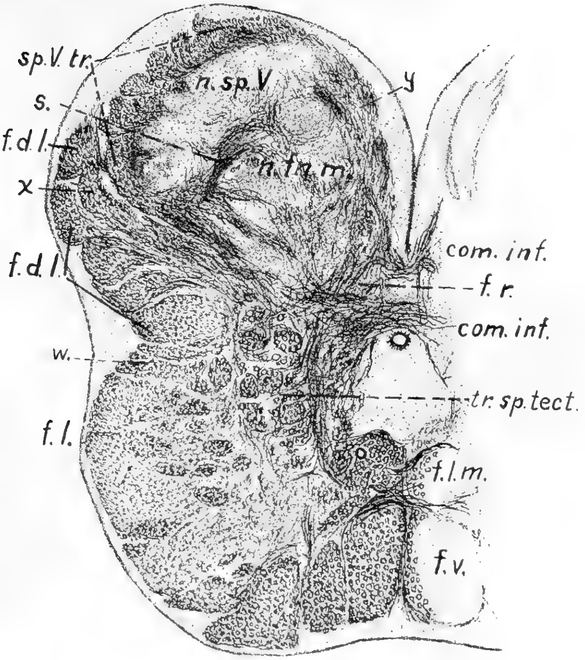
sp.V.tr.
n.sp.V
y
s.
f.d.l.
n.fn.m.
x
com. inf.
f.d.l.
f.r.
com. inf.
w.
tr. sp. tect.
f.l.
f.l.m.
f.v.

Fig. 3.

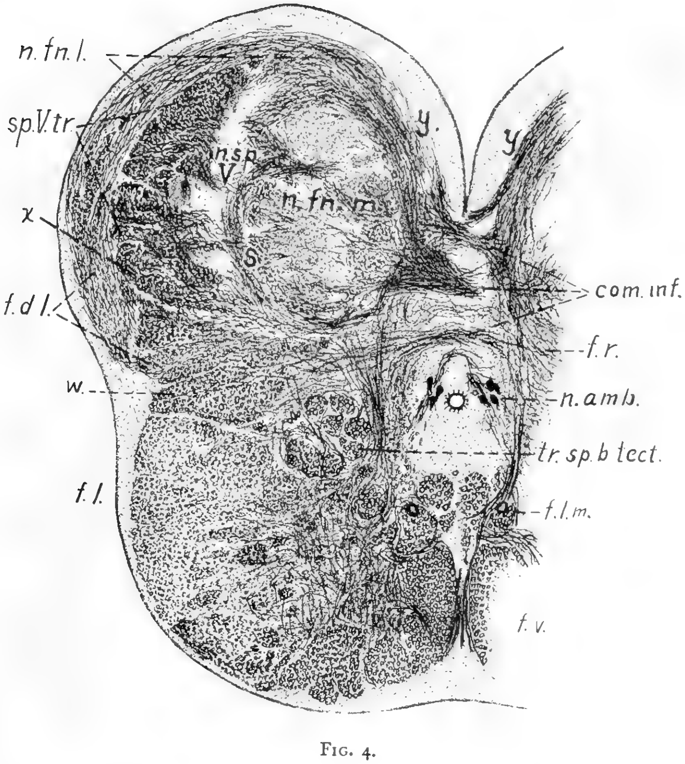
n.fn.l.
sp.V.tr.
y.
y
n.sp.
V
n.fn.m.
x
s
com. inf.
f.d.l.
f.r.
w.
n.amb.
tr. sp. b tect.
f.l.
f.l.m.
f.v.

Fig. 4.

FIG. 5. Section through the commissural nucleus of CAJAL, showing the visceral division of the commissura infima above and a vestige of the somatic division below. At this level the median and lateral funicular nuclei are extensive, but the spinal V nucleus has shrunken to a mere vestige, the substantia gelatinosa of Rolando. Extensive secondary tracts run from the latter nucleus and from both the lateral and the median funicular nuclei for the formatio reticularis of the same side and, by way of the ventral commissure, for the formatio reticularis and lemniscus of the other side. The ascending portion of the dorso-lateral fasciculus is reduced in size, having largely terminated in the formatio reticularis and funicular nuclei farther caudad. The tract designated *x* in Fig. 4 is present in the ventral part of the spinal V complex. The dorsal part of the dorso-lateral fasciculus is composed almost exclusively of descending secondary gustatory tracts from the facial lobe, which likewise terminate in both the median and lateral funicular nuclei, chiefly the latter. × 35.

com.inf., commissura infima, visceral part above and somatic part below; *com.nuc.v.*, visceral commissural nucleus (nucleus of CAJAL); *cut. X.*, general cutaneous root of the vagus nerve; *f.d.l.*, fasciculus dorso-lateralis; *f.l.*, fasciculus lateralis; *f.l.m.*, fasciculus longitudinalis medialis; *f.r.*, formatio reticularis; *f.v.*, fasciculus ventralis; *n.amb.*, nucleus ambiguus; *n.fn.l.*, lateral funicular nucleus; *n.fn.m.*, median funicular nucleus; *n.int.X.*, caudal end of nucleus intermedius vagi; *r.d.X.*, descending sensory root of the vagus; *s.gel.*, substantia gelatinosa Rolandi; *sp.V.tr.*, spinal V tract; *tr.sp.b.tect.*, tractus spino- et bulbo-tectalis; *w.*, tractus bulbo-spinalis; *y.*, secondary tracts from lateral funicular nucleus.

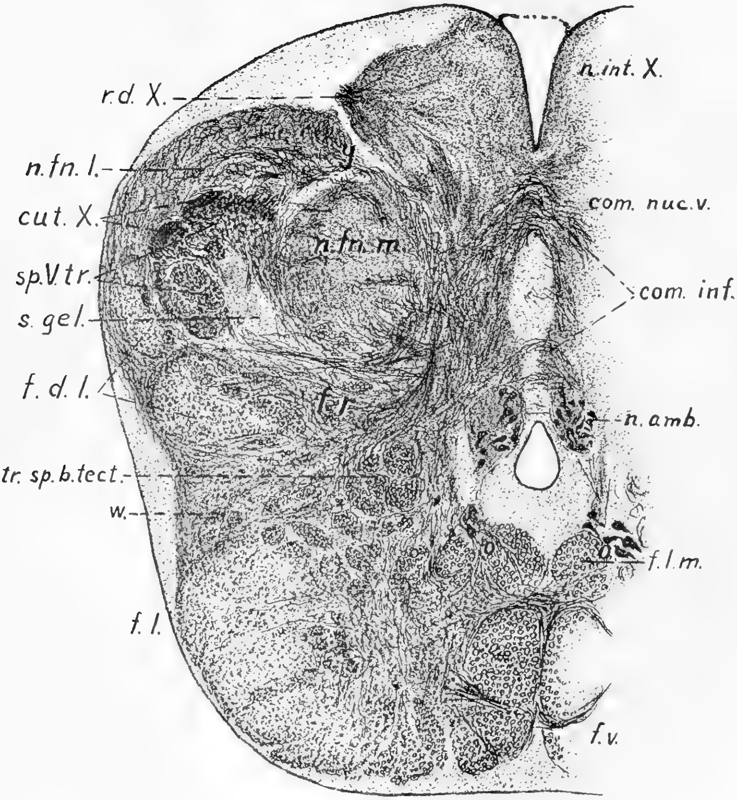
r.d. X.
n.int. X.
n.fn.l.
cut. X.
n.fn.m.
com. nuc.v.
sp.V tr.
com. inf.
s. gel.
f. d. l.
tr.
n. amb.
tr. sp. b. tect.
w.
f. l. m.
f. l.
f. v.

FIG. 5.

Fig. 6. Section through the caudal part of the vagal lobes of Ameiurus, including the cephalic tip of the commissural nucleus of Cajal at the point where it fuses with the nucleus intermedius vagi. Both funicular nuclei have disappeared. The area marked substantia gelatinosa Rolandi includes the indistinguishable vestiges of the spinal V nucleus and the median funicular nucleus. Above the spinal V tract a vestige of the lateral funicular nucleus is seen from which tracts of heavily medullated fibers run downward as internal arcuate fibers for the ventral commissure and lemniscus of the opposite side. These tracts are still larger in the sections immediately caudad of the one figured. The fasciculus dorso-lateralis at this level is composed chiefly of descending secondary gustatory tracts from the facial lobe. Some strands of these fibers (marked *v.*) pass up internal to the substantia gelatinosa to reach the nucleus intermedius of the vagal lobe where it passes over into the commissural nucleus of Cajal. The latter nucleus is broadly connected with the formatio reticularis by both medullated and unmedullated tracts.

asc.sec.X., ascending secondary gustatory tracts from the vagal lobe; *com.nuc.v.*, extreme cephalic end of the visceral commissural nucleus (nucleus of Cajal); *cut.X.*, general cutaneous root of the vagus; *f.d.l.*, fasciculus dorso-lateralis; *f.l.*, fasciculus lateralis; *f.l.m.*, fasciculus longitudinalis medialis; *f.r.*, formatio reticularis; *f.v.*, funiculus ventralis; *n.amb.* nucleus ambiguus; *n.fn.l.*, extreme cephalic end of lateral funicular nucleus; *n.int.X.*, nucleus intermedius vagi; *r.X.*, chief sensory root of the vagus; *s.gel.*, substantia gelatinosa Rolandi, with which is fused the extreme cephalic end of the median funicular nucleus; *sp.V.tr*, spinal V tract; *tr.b.tect.*, tractus bulbo-tectalis from lateral and median funicular nuclei; *tr.sp.b.tect.*, tractus spino- et bulbo-tectalis; *v.*, strands of the descending secondary gustatory tract from the facial lobe for the cephalic end of the commissural nucleus of Cajal.

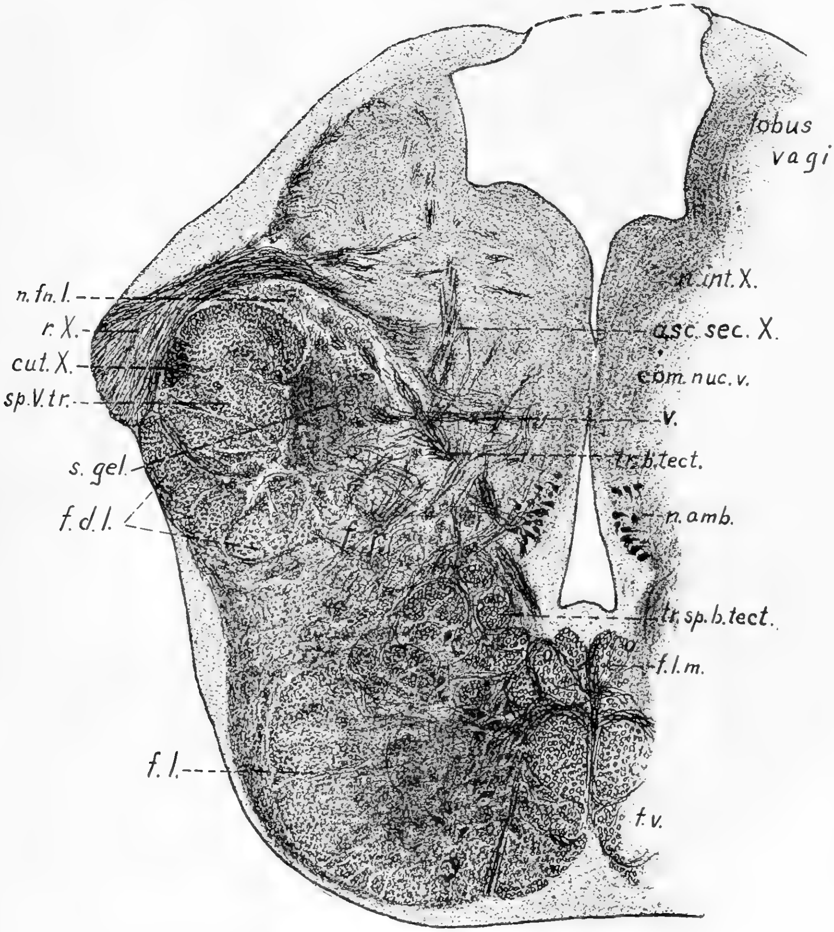
lobus vagi
n.fn.l.
n.int.X.
r.X.
asc.sec.X.
cut.X.
com.nuc.v.
sp.V.tr.
v.
tr.b.tect.
s.gel.
n.amb.
f.d.l.
f.r.
tr.sp.b.tect.
f.l.m.
f.l.
f.v.

FIG. 6.

FIG. 7. A horizontal longitudinal section through the medulla oblongata of an adult Ameiurus nebulosus about 20 cm. long, stained by the method of WEIGERT-PAL. ×23.

The section is somewhat oblique, the left side being further dorsad than the right side. On the right side the spinal V tract is seen terminating in its own nucleus and also sending strands into the median funicular nucleus. The lateral funicular nucleus lies farther dorsally, its apex being shown on the left side. On the right side the fibers of the dorso-lateral fasciculus for this nucleus are seen descending along the outer border of the spinal V tract at *f.d.l.* (*cf.* Fig. 5). The commissural nucleus of CAJAL is cut through its dorsal port. It receives afferent fibers from the most caudal vagus root and from the vagal lobes above—descending secondary visceral tracts. Its commissure at this level contains but few medullated fibers. The efferent tracts from the commissural nucleus do not appear so far dorsally as this section.

asc.sec.VII., ascending secondary gustatory tracts from the facial lobe; *asc.sec.X.*, ascending secondary gustatory tracts from the vagal lobe; *com.r.VII.*, communis root of the facial nerve; *com.s.gust.n.*, commissure of superior secondary gustatory nuclei; *desc.sec.VII.*, descending secondary gustatory tract from the facial lobe; *desc.sec.X.*, descending secondary tracts from the vagal lobe to the commissural nucleus of CAJAL; *f.d.l.*, fasciculus dorso-lateralis; *n.fn.l.*, lateral funicular nucleus; *nf.n.m.*, median funicular nucleus; *n.sp. V.*, spinal *V* nucleus; *r.d.X.*, descending sensory root of the vagus; *r.lat.VII.* lateral line root of the facial nerve; *r.lat.X.*, lateral line root of the vagus nerve: *r.V.*, root of the trigeminus nerve; *r.X.*, chief sensory root of the vagus nerve; *s.gel.*, substantia gelatinosa Rolandi; *s.gust.nuc.* superior secondary gustatory nucleus (n. lateralis cerebelli, n. visceralis cerebelli, JOHNSTON); *sp.V.tr.*, spinal V tract; *tub.ac.*, tuberculum acusticum; *visc.com.nuc.*, visceral commissural nucleus (nucleus of CAJAL).

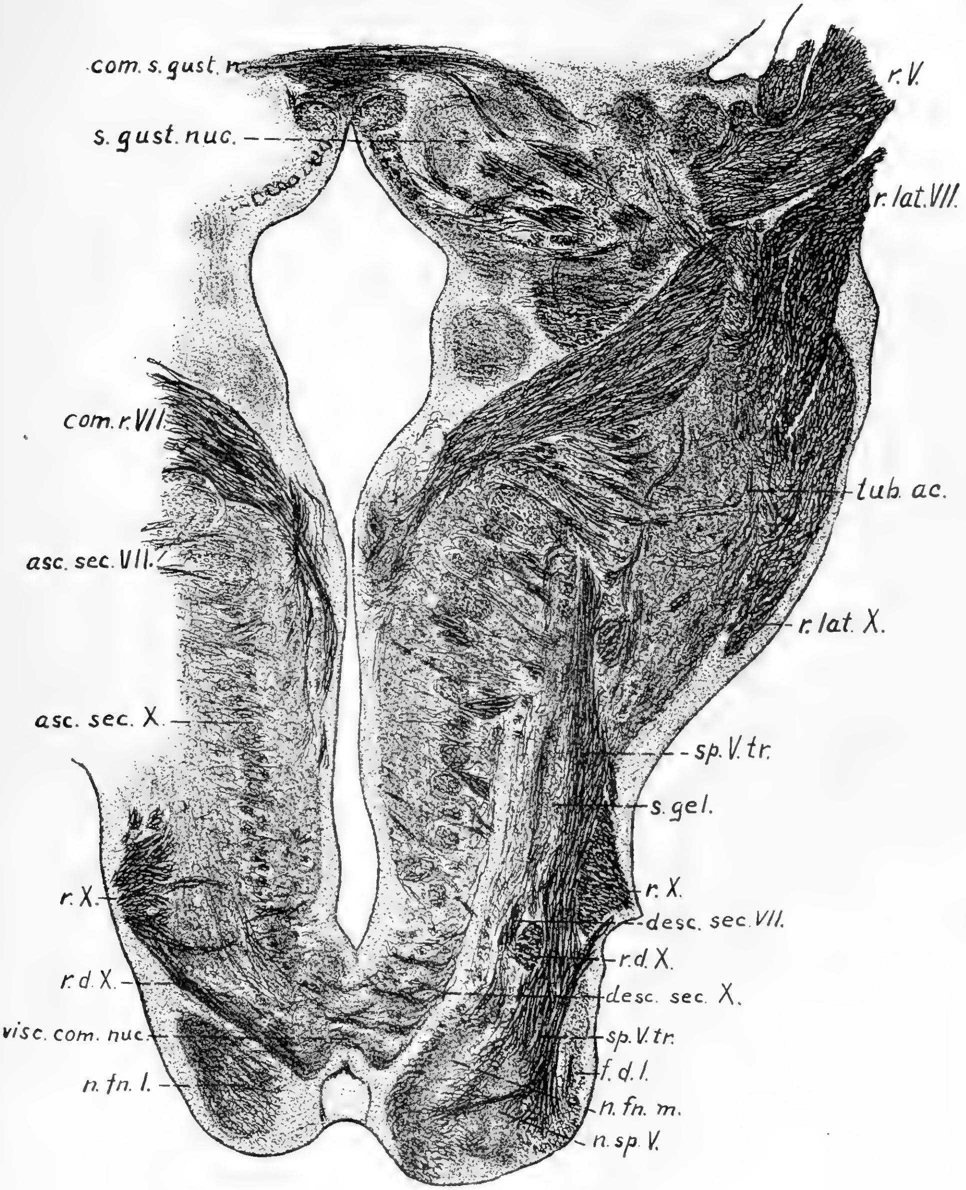
com. s. gust. n.
s. gust. nuc.
com. r. VII.
asc. sec. VII.
asc. sec. X.
r. X.
r. d. X.
visc. com. nuc.
n. fn. l.
r. V.
r. lat. VII.
tub. ac.
r. lat. X.
sp. V. tr.
s. gel.
r. X.
desc. sec. VII.
r. d. X.
desc. sec. X.
sp. V. tr.
f. d. l.
n. fn. m.
n. sp. V.

FIG. 7.

Fig. 8. Two neurones from the dorsal cornu of the spinal cord of fry of Ameiurus nebulosus, about 3 cm. long. The section is taken at about the level of the second spinal nerve (*cf.* Fig. 1). Golgi method. × 195.

The dotted line indicates the median plane (dorsal fissure). The neurite enters the formatio reticularis of the same side.

Fig. 9. A large neurone of the spinal V nucleus of Ameiurus nebulosus about 3 cm. long. Golgi method. × 75.

The section is taken at about the same plane as Fig. 3. Several small intrinsic neurones of the spinal V nucleus and one large neurone of the formatio reticularis are also impregnated. Termini of the spinal V tract and dorso-lateral fasciculus in the spinal V nucleus are shown.

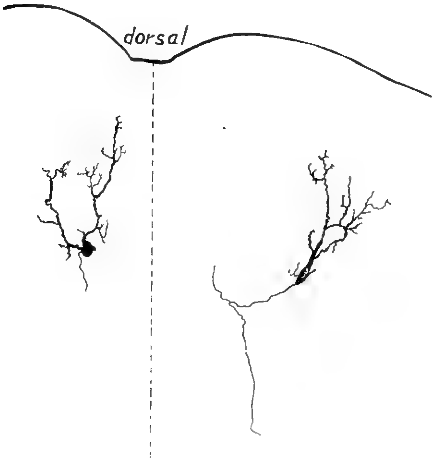
dorsal

FIG. 8.

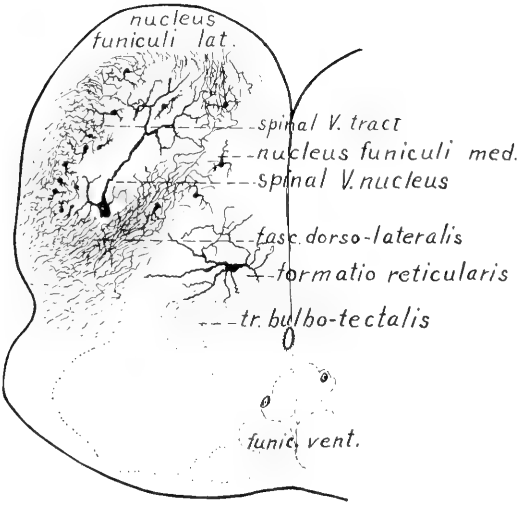
nucleus funiculi lat.
spinal V. tract
nucleus funiculi med.
spinal V. nucleus
fasc. dorso-lateralis
formatio reticularis
tr. bulbo-tectalis
funic. vent.

FIG. 9.

FIG. 10. A large neurone of the spinal V nucleus of Ameiurus from the same region as that of Fig. 9. GOLGI method. × 195.

A secondary tract (internal arcuate fibers) is impregnated as it leaves the spinal V nucleus. The neurite of the cell figured probably enters this tract.

FIG. 11. Transverse section through the funicular nuclei of Ameiruus fry. GOLGI method. × 75.

Several small intrinsic neurones of the spinal V nucleus are impregnated and one large neurone of the somatic commissural nucleus, whose neurite enters the funiculus ventro-lateralis. The section shows termini of the spinal V tract and dorso-lateral fasciculus in the spinal V nucleus and one terminal from the latter tract in the formatio reticularis.

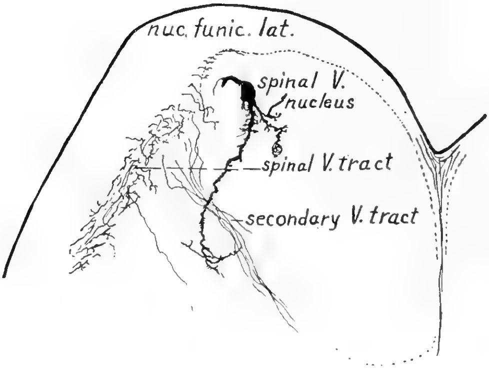
nuc. funic. lat.
spinal V. nucleus
spinal V. tract
secondary V. tract

FIG. 10.

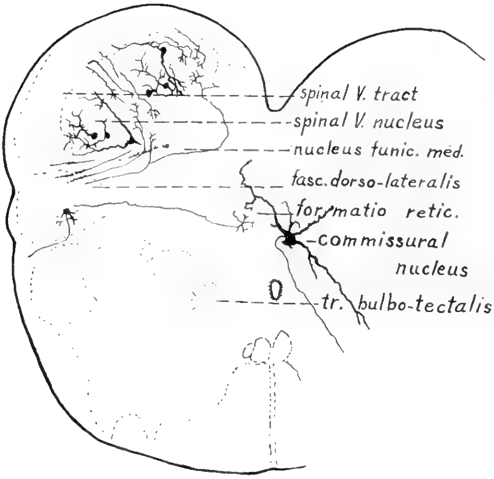
spinal V. tract
spinal V. nucleus
nucleus funic. med.
fasc. dorso-lateralis
formatio retic.
commissural nucleus
tr. bulbo-tectalis

FIG. 11.

Fig. 12. Transverse section through the funicular nuclei of Ameiurus farther cephalad than the plane of Figs. 9, 10 and 11. Golgi method. × 75.

On the left side are shown one chief neurone and two small intrinsic neurones of the spinal V nucleus and several intrinsic neurones of the median funicular nucleus. On the right side are three intrinsic neurones of the spinal V nucleus and several neurones of the median funicular nucleus and formatio reticularis.

Fig. 13. Transverse section through the funicular nuclei and visceral commissural nucleus of Cajal of Ameiurus. Golgi method. × 75.

The endings of the descending sensory vagus root in the commissural nucleus are shown and of the spinal V tract and dorso-lateral fasciculus in their nuclei. One big neurone of the somatic commissural nucleus is impregnated and a few neurones in the lateral funicular nuclei. The drawing is a composite of two adjacent sections, the right side drawn wholly from one and the left from the other.

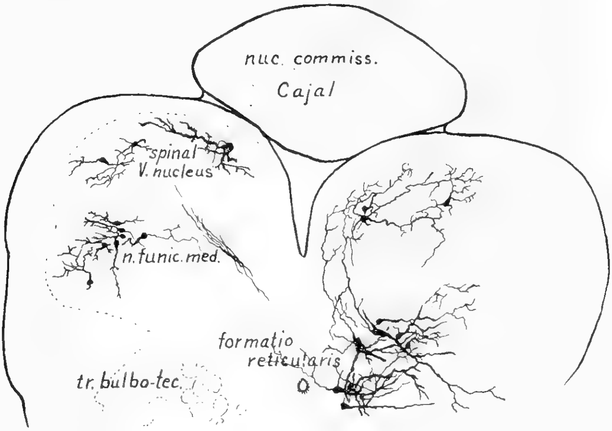
nuc. commiss.
Cajal
spinal
V. nucleus
n. funic. med.
formatio
reticularis
tr. bulbo-tec.

FIG. 12.

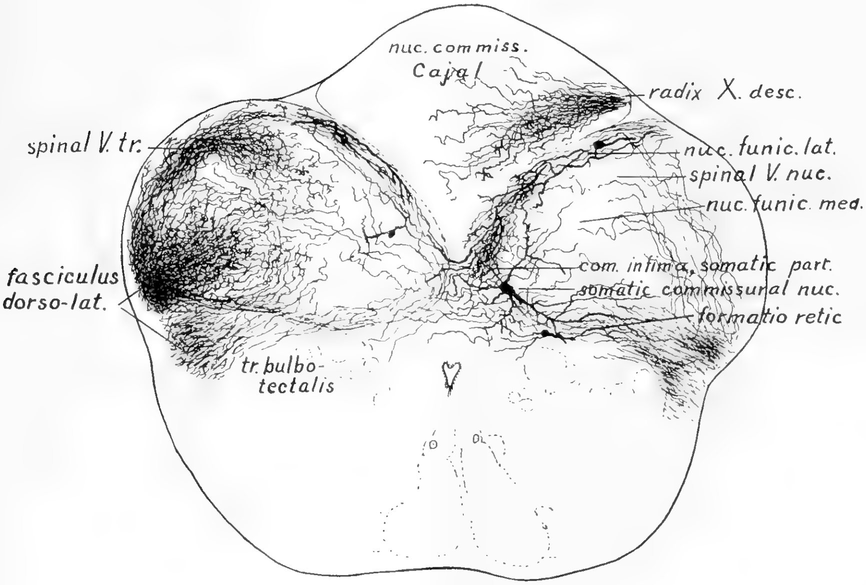
nuc. commiss.
Cajal
radix X. desc.
spinal V. tr.
nuc. funic. lat.
spinal V. nuc.
nuc. funic. med.
fasciculus
dorso-lat.
com. intima, somatic part.
somatic commissural nuc.
formatio retic
tr. bulbo-
tectalis

FIG. 13

FIG. 14. Transverse section a little farther cephalad than Fig. 13 (*cf.* Fig. 5). GOLGI method. × 75.

The section is slightly oblique (the right side being farther cephalad) and somewhat distorted in cutting. The dotted line indicates the sagittal plane. The drawing is a composite of two adjacent sections, and neurones *A* and *B* are drawn in from sections of the same series a little farther caudad. *A* is a neurone of the somatic commissural nucleus, and *B* of the adjacent formatio reticularis. In adjacent sections the dendrites of many neurones of the same type as *B* cross the median line in the somatic portion of the commissura infima. Termini of the spinal V tract and fasciculus dorso-lateralis are shown and neurites from cells of the median funicular nucleus which probably pass as internal arcuate fibers to the tractus bulbo-tectalis of the other side.

FIG. 15. Portion of a parasagittal section of the medulla oblongata of a specimen of Ameiurus nebulosus 5 cm. long. GOLGI method. × 75.

The section passes through the extreme lateral edge of the left lateral funicular nucleus, showing several neurones of that nucleus, with dendrites spreading out over its whole lateral face. The fascicle of neurites directed dorso-caudad from these cell bodies (*y*) probably springs from them. These fibers probably curve around to enter the tracts marked *y*, in Figs. 3 and 4. The commissural nucleus of CAJAL lies mesially of the point marked *C*.

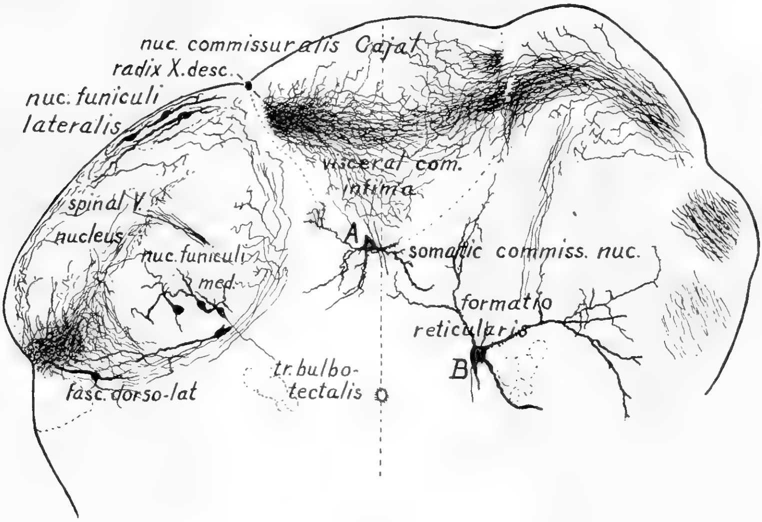
nuc. commissuralis Cajal
radix X. desc.
nuc. funiculi lateralis
spinal V. nucleus
nuc. funiculi med.
visceral com. intima
A
somatic commiss. nuc.
formatio reticularis
B
tr. bulbo-tectalis
fasc. dorso-lat

FIG. 14.

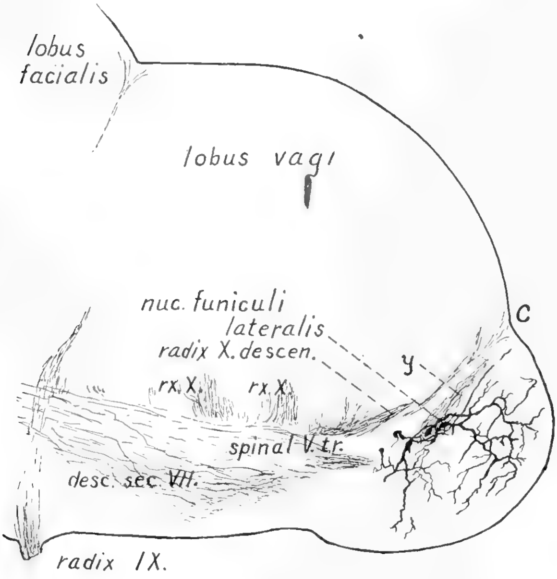
lobus facialis
lobus vagi
nuc. funiculi lateralis
C
radix X. descen.
y
rx. X.
rx. X.
spinal V. tr.
desc. sec. VII.
radix IX.

FIG. 15.

MODIFIABILITY OF BEHAVIOR IN HYDROIDES DIANTHUS V.

BY

ADA WATTERSON YERKES.

The sensitiveness of the tubicolous annelid Hydroides dianthus V., manifested by its prompt withdrawal into its tube when jarred or when a shadow falls upon it, suggested this worm as a good object for a study in modifiability of behavior. Such a study was carried on for a few weeks at the Marine Biological Laboratory at Woods Hole during the past summer. Unfortunately the time was too short for extensive experiments but the results obtained thus far seem to be of sufficient value to warrant presentation.

The reactions of Hydroides to light have been studied by Hargitt,[1] who found that "under varying degrees of light intensity * * * the results of all experiments involving increased intensity of light were uniformly negative. On the other hand, experiments involving a sudden decrease of light intensity gave results as uniformly positive" (p. 319). This confirms a statement made by Loeb[2] (p. 103) concerning H. uncinata to the effect that only a decrease in the intensity of light acts as a stimulus upon the animals. In the present experiments this stimulus was, therefore, one of those selected for use and the decrease in intensity of the light was obtained by bringing down rapidly a black cardboard screen between the window and the dish which contained the worms. After one or two seconds the screen was removed. For convenience this decrease in light intensity will be referred to as a shadow. Though the window faced south, the sunlight did not fall directly upon the worms during the experiments. The response to the stimulus was usually a quick contraction of the animal into its tube. Occasionally this contraction occurred

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[1] Hargitt, C. W. Experiments on the Behavior of Tubicolous Annelids. *Journal of Experimental Zoölogy,* Vol. 3, pp. 295–320, July. 1906.

[2] Loeb, J. Ueber künstliche Umwandlung positiv heliotropischer Thiere in negativ heliotropische und umgekehrt. *Pflüger's Archiv.* Vol. 54, pp. 81–108. 1893.

more slowly and the tips of the circle of branchiæ remained projecting a trifle from the mouth of the tube. The time during which the animals remained contracted was noted in each case and was found to vary in a way which will be described later.

A considerable number of tests were made to determine the sensitiveness to shadow alone. In most of these the shadows were given at unequal intervals; for instance, if the animal contracted in response to the first shadow, the second was given as soon as the worm was again fully expanded. The time thus varied between ten seconds and a minute or, in a few cases, two or three minutes. If the animal did not respond, the shadows were repeated at short intervals, from five to ten seconds. Ten such trials were given in succession. In the greater number of these tests (16 out of 27) with different specimens the animals responded only the first time, or possibly from one to three times, and then gave no further response throughout the ten trials. This fact seems to be comparable to the results obtained by JENNINGS[1] (p. 172) with attached infusoria which reacted the first time to a jet of water striking against the disk or to other faint stimuli, or a few times to a stronger stimulus, but did not respond to later repetitions of the stimulus. This behavior JENNINGS interprets as due, not to fatigue, since the number of reactions is few, but to a change in the organism itself (p. 173), a change which has distinctly a regulatory character in the behavior of the animal. HARGITT, on the contrary (p. 301), who observed that when shadows fell rhythmically on Hydroides and "the experiments were repeated with any considerable frequency, specimens sooner or later became somewhat irresponsive," is inclined to regard this as the result of fatigue. Evidence, however, from a later series of the present experiments, tends to show that fatigue is not the cause, since the animals are capable under stronger stimulation of contracting a large number of times in rapid succession without apparent fatigue.

In ten cases of the twenty-seven mentioned above, the worms did not respond the first time nor later during the ten trials. Whether this is due to individual variation in sensitiveness or whether the animals had responded previous to the experiments to the shadows which fell upon them by chance while still in the aqua-

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[1] JENNINGS, H. S. Behavior of the Lower Organisms. *New York, Macmillan.* Pp. 366, figs. 144. 1906.

rium, it is impossible to say. The former seems probable, since one animal was tested which responded every one of the ten times, although the conditions were apparently exactly similar to those of another worm which was tried simultaneously and reacted only four times out of ten.

After some experiments of a different kind, to be described later, had been given, some of the specimens used in them and a few new ones were tested again for the effect of shadow alone. The shadows this time were given at regular intervals of one or two minutes. The number of responses in these cases is larger than in the preceding, for out of twenty series of ten trials each, *i. e.*, a possible two hundred reactions, there were ninety-five responses to the shadow. The longer interval between shadows seems, therefore, to interfere with the process of getting accustomed to the stimulus which occurs when the intervals are only a few seconds in length. In Table I are shown the records of two series with one specimen. In the first series the intervals between shadows were fifteen seconds. In the second series, given four days later but without any intervening training, the intervals are two minutes.

TABLE I.

SERIES 1.			SERIES 2.		
No.	*Shadow.*	*Time.*	*No.*	*Shadow.*	*Time.*
1	o	—	1	“	18″
2	o	—	2	“	30″
3	o	—	3	“	15″
4	o	—	4	“	48″
5	o	—	5	“	4′
6	o	—	6	“	28″
7	o	—	7	“	30″
8	o	—	8	“	38″
9	o	—	9	“	33″
10	o	—	10	“	16″

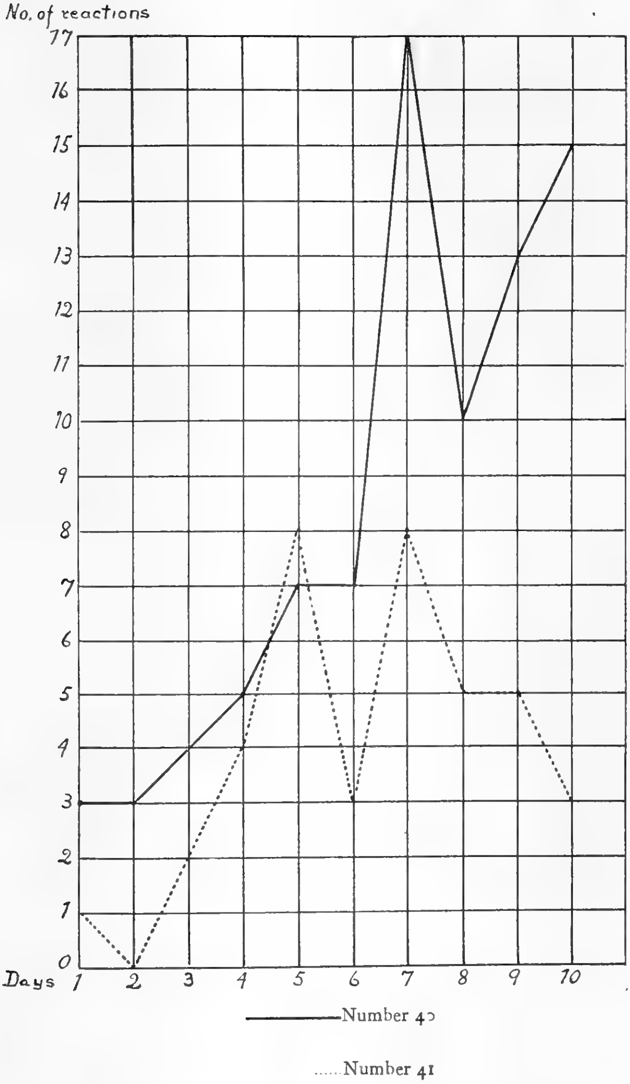
In all of the tables o means no reaction, and “ means reaction.

A series of experiments was now started in which two different stimuli were given in rapid succession. The response to light, it has been shown, is variable, since the animals sometimes respond and sometimes do not. The response to mechanical stimulation caused by jarring the animals or by touching the branchial filaments with a glass rod is much more regular. In fact, the worms respond immediately and invariably except in certain instances to be mentioned later.

In these experiments three or more individuals in the same dish, usually growing on the same piece of shell or stone, were used simultaneously. At the beginning all were given ten trials with shadow alone with the usual result. Then the shadow was given and if the animals did not respond to this the mechanical stimulation caused by touching the filaments gently with a glass rod followed immediately. The period of retraction was noted and when the animals were again expanded the experiment was repeated. The trials were recorded in groups of ten each and from one to six of these groups were given daily. A number of specimens were tested thus for several days each. Some of these, having been in the laboratory for some time, then became inactive and refused to come out of the tube after being placed in the experimenting dish. Two animals, however, Nos. 40 and 41, obtained from fresh material were tried for ten days and the records of these two, which show a number of interesting points, will be discussed in detail.

In the trial experiments in which shadow alone was given at intervals of 5 to 10 seconds No. 40 responded not at all and No. 41 only the first time. After a short interval the shadow and touch series was given. In this No. 40 reacted to shadow alone three times during the first ten trials, No. 41 only once and neither of them again throughout the forty trials given that morning. The fact that when responses to shadow alone occurred they almost always came within the first twenty trials soon became evident and the records will, therefore, be given for these twenty alone. The results for the ten days can best be represented by the following curves in which the number of responses to shadow alone for each of the successive days, as indicated on the base line, is marked on the ordinates.

In the case of No. 40 there is a marked increase in the number of responses to shadow from the first to the eighth day and those of the later days are much higher than at first. For No. 41 the increase is not so great, though the rise in the curve from the second to the fifth day is pronounced. Even at the beginning, the responses of this individual were not as numerous as for No. 40 and after the tenth day it became so inactive, sulking at the mouth of the tube or remaining retracted into it so long, that it became


No. of reactions
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
Days
1
2
3
4
5
6
7
8
9
10
Number 40
Number 41

impossible to use it further for the experiments. This seems to indicate a good deal of individual variation and unfortunately the specimens tried were not numerous enough to provide averages: After the tenth day No. 40 was used for the experiments where shadows alone were given at regular two minute intervals and these series render further work with combined stimuli incomparable.

TABLE II.

REACTIONS OF NO. 40.

No.	*Shadow.*	*Touch.*	*Time.*	*No.*	*Shadow.*	*Touch.*	*Time.*
1	“	—	34″	31	0	“	17″
2	“	—	19″	32	0	“	26″
3	“	—	29″	33	0	“	12″
4	0	“	235″	34	0	“ (2)	20″
5	“	—	50″	35	0	“ (3)	85″
6	0	“	93″	36	0	“	57″
7	“	—	34″	37	0	“	25″
8	0	“	59″	38	0	“ (4)	710″
9	“	—	27″	39	0	“	59″
10	0	“	41″	40	0	“	32″
11	0	“	52″	41	0	“	27″
12	0	“	43″	42	0	“	36″
13	0	“	27″	43	0	“	15″
14	0	“	26″	44	0	“ (5)	37″
15	0	“	18″	45	0	“ (2)	29″
16	0	“	25″	46	0	“ (2)	15″
17	0	“	18″	47	0	“ (5)	25″
18	0	“	236″	48	0	“ (2)	16″
19	“	—	35″	49	0	“ (3)	17″
20	0	“	37″	50	0	“ (3)	22″
21	0	“	24″	51	0	“ (2)	24″
22	“	—	35″	52	0	“ (7)	22″
23	0	“	25″	53	0	“ (9)	148″
24	0	“	21″	54	0	“ (10)	11″
25	0	“	18″	55	0	“ (152)	10″
26	0	“	20″	56	0	“ (12)	20″
27	0	“	21″	57	0	“ (3)	22″
28	0	“	16″	58	0	“ (30)	20″
29	0	“	16″	59	0	“ (76)	25″
30	0	“	17″	60	0	“ (29)	250″

In explanation of this increase in responsiveness to shadow alone it seems possible that the shadow and touch have become so associated that the occurrence of the one intimates the probability that the other will follow. The response to touch is fairly uniform and after a few such experiences, the shadow, cast before, as it were, by the coming event, more frequently produces a reaction. The repetition of both stimuli many times in succession causes this effect to wear away temporarily, since the touch is not sufficiently injurious to force reaction.

Two other interesting facts have appeared in the course of these experiments. One is shown clearly in the record of one day's experiments given in Table II. In this both stimuli were given; the responses to shadow are shown in the first column, those to touch in the second and the length of time during which the animal remained retracted into its tube in the third.

The period of retraction is short the first three times—19 to 34″—but the fourth time it is nearly four minutes. For the next thirteen times it ranges from eighteen to ninety-three seconds; then comes another period of nearly four minutes followed by nineteen contractions which last from twelve to eighty-five seconds each and then a contraction of nearly twelve minutes' duration. Thus after the fourth, eighteenth, thirty-eighth and sixtieth trials the animal remained contracted for a relatively long period, varying from four to twelve minutes, whereas the intervening contractions seldom lasted more than one and a half minutes and are usually less than thirty seconds. This rhythm is very marked in all the series which were carried on long enough each day to show it, and in the short series there is usually one period of retraction noticeably longer than any of the others.

The occurrence of unusually long periods of retraction in the case of another individual, No. 41, for the first five and the tenth days of the experimentation is shown in Table III. It is worthy of note that the frequency of the prolonged retraction periods is much greater on the tenth day than on the first.

These periodic "rests" might be attributed to fatigue, but they do not seem necessarily due to that. Being a tube-dwelling animal, Hydroides is narrowly limited in the kind of reactions possible to it. It responds to mechanical stimulation repeated at frequent intervals in the most apparent way, by a contraction into the tube. If the behavior of the animal were modifiable we might expect after a number of repetitions of this stimulus a change in reaction comparable to that of Stentor[1] when, after repeated faint

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[1] JENNINGS, H. S. *Loc. cit.*, pp. 173–175.

stimuli, it ceases to contract and begins to bend in different directions, or, when after increase in the stimulus it breaks loose and swims away. This prolonged contraction in Hydroides may be simply a difference in the response to stimulation as the result of past experience. This instance seems, in fact, an illustration of one of the conclusions stated by JENNINGS (p. 445)[1] in a recent paper on the modifiability in behavior of the earth-worm, to the effect that "the reaction to a given stimulus depends partly on previous stimuli received."

TABLE III.

PERIODIC OCCURRENCE OF PROLONGED RETRACTION IN NO. 41.

1st day.		*2d day.*		*3d day.*	
No. of Reaction.	*Time.*	*No. of Reaction.*	*Time.*	*No. of Reaction.*	*Time.*
4	142″	2	312″	8	185″
7	384″	6	267″	17	285″
20	160″	15	384″	23	150″
23	230″	28	160″	29	261″
29	505″	31	620″	40	273″
37	560″	38	447″		
4th day.		*5th day.*		*10th day.*	
No. of Reaction.	*Time.*	*No. of Reaction.*	*Time.*	*No. of Reaction.*	*Time.*
1	184″	7	282″	5	167″
3	185″	21	370″	7	210″
13	305″	35	382″	10	170″
33	504″	50	470″	12	292″
40	140″			15	200″
58	148″			16	240″
				18	223″

A second fact which may perhaps be explained by the same hypothesis is brought out in some of the longer series. In the record given above in Table II, for instance, after some thirty-three trials the animal did not respond to the shadow nor to the first touch from the glass rod. Two, three, or five strokes were required to bring about a reaction. The number of strokes needed each time is recorded in parenthesis. This tendency increased throughout the series until in the fifty-fifth trial the filaments were stroked 152 times in rapid succession before they were withdrawn. The touch at first was quick and slight, but producing no reaction it was made heavier until the filaments were stroked

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[1] Jennings, H. S. Modifiability in behavior. II. Factors determining direction and character of movement in the earth-worm. *Jour. of Exper. Zoöl.*, Vol. 3, pp. 435-55. 1906.

from base to summit and the reverse so forcibly as to turn the whole crown of filaments over to one side or the other in a horizontal position. The contraction after such treatment this particular time lasted only ten seconds. This change in behavior could certainly not be due to fatigue since the resting condition is surely that of withdrawal into the tube and in this case the animal not only endured the stimulus repeatedly but after a contraction which lasted a remarkably short time was ready for it again. This occurred many times with several specimens when series of twenty or more trials were given in succession. In many other cases there was only a partial retraction into the tube and the crown of branchiæ would remain half out of the tube until the next expansion took place.

SUMMARY

1. To a photic stimulus consisting of a decrease in the intensity of light, repeated at short and irregular intervals, Hydroides responds at first by contraction but later gives no reaction.

2. When the stimulus occurs at longer intervals the responses are more frequent.

3. To tactual stimulation the animal responds almost uniformly by a contraction into the tube.

4. When the photic stimulus is followed immediately by the tactual the worms gradually respond more frequently to the former alone than they did previous to this training; *i.e.*, they learn to react to the shadow.

5. The time of retraction after the tactual stimulus is usually short but in any long series a retraction of much longer duration occurs periodically as a possible variation in the method of response to repeated stimulation.

6. After many repetitions of shadow and tactual stimuli the animals no longer react normally to either but require frequently a large number of tactual stimulations to induce contraction.

7. The behavior of Hydroides is thus eminently modifiable since it varies with repetitions of a stimulus or when two stimuli of different reactive value are repeatedly given in succession.

Woods Hole, Mass.,
September, 1906.

NOTES ON THE BEHAVIOR OF GONIONEMUS.

BY

MAX MORSE.

Perkins ('03), Yerkes ('02, '03 and '04), and others have studied the behavior of Gonionemus murbachii (Ag.), the work of Yerkes being most comprehensive and complete. Aside from a general account of the habits, Perkins does not enter into the responses of the medusa to the various external stimuli, such as light, heat, etc. With respect to one conclusion reached by Perkins, experiments of the writer point to a different interpretation. When a number of jelly-fish are placed in an aquarium, they begin to swim directly upward to the surface. On reaching the surface, the apex of the bell is pushed through the surface film for perhaps three or four millimeters and immediately there occurs an inversion of the bell and complete cessation of pulsation. The medusa sinks passively downward with the oral portion upward while the tentacles are thrown far out into the surrounding medium. This process has been identified by Perkins as one of "fishing," as by this means the tentacles bearing the stinging cells come in contact with the prey and this is brought to the manubrium with readiness.

The observations of the writer are as follows: A number of the medusæ were placed in a small glass vessel, a decimeter in diameter and five centimeters in depth. Commercial olive oil was poured on the surface of the water so that is was covered save in one place, of about two centimeters diameter. The medusæ began swimming upward against the oil, but instead of inverting and sinking, as in the case of pure water, they continued swimming against it until in some cases they became exhausted and sank, apex upward, to the bottom of the vessel. Some of the medusæ, as they swam around the dish reached the portion of the surface left uncovered by the oil. The result was an instantaneous inversion of the bell followed by the cessation of all movements.

A glass plate was lowered, in another case, below the surface of the water and parallel to it. The medusæ swam against the plate exactly as in the case of the oil. The surface was then covered with kerosene, which forms a very delicate film. In this case the result was the same as in the case of pure water; the bells were inverted. In order to show that it is not a matter of lack of oxygen, a column of ammonium chlorid (NH_4Cl held in suspension in water vapor, formed by adding a few drops of HCl to a similar amount of ammonia), was superposed on the surface of the water with the result that the animals continued to invert the bells and passively sink.

YERKES has shown that most probably the margin of the bell which leaves the water receives a stimulus, by so doing, to contract, inasmuch as that portion of the bell must contract earlier than the other portions in order to cause the inversion. The writer has found that the mechanism of varying the direction of swimming is that of contracting one side of the bell more strongly or in advance of the opposite side. The result is a more or less complete rotation of the bell on a transverse diameter as an axis. Neither the tentacles nor the velum exert any influence on the direction of swimming, since when the tentacles are cut away from one-half of the bell, the medusa swims either in a straight line or curved one as before. Likewise, one-half of the velum was removed without appreciable result and even cutting away completely both tentacles and velum was without effect on the swimming movements as far as direction is concerned. By paralyzing one side with a crystal of silver nitrate which at the same time left a deposit of metallic silver as a point of reference, the medusa swam in a circle with the injured side on the inside of the circle. By cutting two windows in the bell, near the apex and on one side, the pressure of the water was removed from that side and the path in swimming was again circular with the intact portion peripheral.

YERKES would account for the inversion of the bell by the stimulus given to the exposed portion by light. It is difficult to see why light affects only the exposed portion of the bell and not the other parts. That it is not a matter of light striking one side of the bell more strongly than the other is made evident by the fact that if the light is admitted parallel to the surface of the water, the invariable result obtains that the portion of the bell first striking the water contracts first, although the opposite side may be toward the light. The cause for reaction is not evident. The writer has observed the process in collecting Gonionemus in the Eel Pond as they came to the surface on being disturbed. It is, therefore, a normal reaction.

Reactions to Light and to Heat.

JENNINGS ('06) after a résumé of the work on the reactions of Gonionemus states that "in the behavior of Gonionemus with respect to light, there are a number of paradoxical facts." These "paradoxical facts" refer to the reactions which have been described by previous workers, viz: The medusæ collect first in the illuminated portion of the jar and later are to be found in the shaded portion. The swimming movements cease as the medusa swims from a region of greater to one of less intensity of illumination and also when it swims in the opposite direction. The reaction to sunlight is a direct response whereby the medusa turns directly toward the shadow and swims into it. Finally, the reactions of a swimming organism are different from those of one at rest.

The writer has examined these several reactions and finds his results somewhat at variance with those previously described. Thus, about forty medusæ were put into a Chester jar, 33 cm. high, and 21 cm. in diameter which was placed in a box lined with black paper so that no light could fall upon the jar except upon one side. The medusæ began swimming directly to the surface of the water, inverting and sinking in their usual way. At no time could it be said that the medusæ had collected on the illuminated side of the jar. YERKES obtained the reaction by stirring the water and this was done in the present case, but the result was the same. Sunlight was thrown horizontally through the jar by means of a large mirror and later, sunlight was thrown vertically downward and then vertically upward through the jar, the box being discarded for a cylinder of black paper. In no case was there a collection of medusæ in the illuminated portion of the vessel.

Attention was then turned to the matter of cessation of movements. A glass vessel, 15.5 cm. long, 14 cm. high and 4 cm. deep was covered on three sides with black paper. The fourth side was left uncovered in order to observe the reactions of the medusæ, this being done from under a black cover. By removing strips of various widths from the black paper, the light was allowed to enter the vessel in any direction or with any size of beam. It may be said at once that the same results were reached regardless as to whether the light was sent parallel to the surface of the water, at right angles to it, or obliquely. In each case, when the medusa moved from the shaded region to the light portion, it immediately ceased pulsating and sank to the bottom of the jar, or to some intermediate depth. This is entirely in agreement with ROMANES' ('93) statement for Sarsia and YERKES' ('03) statement for Gonionemus. This inhibitory action of light is as striking as the stimulating effect of that factor as both ROMANES and YERKES have shown. If, for instance, light is suddenly thrown upon a medusa resting in the dark it will respond by pulsations of the bell. The character of the pulsations vary from a few ineffectual contractions to a swimming bout more or less prolonged. As a rule, strong sunlight simply causes a series of ineffectual pulsations.

With respect to the passage of the medusa from a region of illumination to one of darkness, the case is different, judging from the experiments of the present writer. The jar just mentioned was used as follows: One-half of the top of the jar was covered so that the sun, reflected by means of a large mirror perpendicularly downward, illuminated one-half of the vessel, the boundary between the light and the dark zones being vertical. In this case, a medusa swimming from the light area to the dark would, on reaching the transition line, exhibit no reaction whatever and very frequently it would swim for a dozen pulsations within the dark area. However, the pulsations became less vigorous and less frequent until they ceased altogether. The same result was obtained when the border from light to darkness was horizontal, and also when it was oblique. YERKES' experiment of the white porcelain dish was repeated and the results just mentioned were again obtained.

It seems quite evident, then, that we have no inhibition of movements in passing from light to darkness. In the dark the stimulating effect of light is absent and hence the movements ultimately cease. Obviously the case is materially different from the movement from darkness into sunlight.

YERKES ('03) has observed that if a number of medusæ are placed in a vessel, one-half of which is darkened and the other half is exposed to the direct sunlight, the medusæ in the sunlight begin to swim toward the shadow, enter it and come to rest, as we have just described. The response is definite and direct, according to YERKES, the medusæ seldom swimming in a direction away from the shadow. With these observations the work of the present writer does not agree. He has failed to find that, in the case of the porcelain dish experiment, the vessel being illuminated by sunlight falling directly perpendicularly, the medusæ swim oftener toward the shadow than in any other direction. The medusæ begin to swim in all directions, many of them upward, some following the walls of the vessel directly away from the shadow. Being thus in motion almost incessantly, and swimming in all directions, it is obvious that sooner or later they will enter the dark area. Once having entered this area, the stimulating effect of sunlight being cut off, they remain as in a trap.

The application of the theory of trial and error which JENNINGS ('06) has used so effectually for Protozoa and Rotifera, MAST ('03) for Hydra, and HARGITT ('06) for tubicolous annelids, to the present case is quite evident and requires no comment. YERKES has accounted for the reaction in the light of the theory of tropisms of VERWORN, J. LOEB, HOLT and LEE, and others. He believes that the sunlight striking one side the bell more directly, stimulated this one side to contract in advance of the other, or more strongly, the result being to turn the animal back into the shadow. On this explanation it is difficult to see how, when the medusæ are swimming, a beam of sunlight, falling perpendicularly, would cause the medusæ to swim into dark, as they do, as will be seen from the accompanying table:

TABLE SHOWING THE MOVEMENT OF GONIONEMUS FROM THE SUNLIGHT INTO THE SHADOW.

Time	*No. in Light*
9:45	33
9:50	29
9:55	28
10:00	27
10:05	27
10:10	27
10:15	24
10:20	24
10:25	20
10:30	18
10:40	15
10:50	16
11:00	14

On YERKES' explanation the direction of movement must ever be directly away from the sun. In the present case it is obvious that this would cause them to swim downward rather than into the shadow.

The trial and error method of response is nowhere better exemplified than in the reactions of the medusæ to heat. The observations of the writer will be briefly recounted. A glass trough, 7.8 cm. in width, 26.8 cm. in length and 4 cm. deep, was so placed that one end rested on a triangular copper bath while the opposite end was surrounded by a freezing mixture. The extremes were 36° C. and 2° C. Several medusæ were put into the vessel, where they began to swim in all directions. Four proceeded at once to the heated end where they came to rest in a temperature of about 35°. Four others swam to the opposite end and came to rest in a temperature of about 5°. Obviously these were strong swimmers and swam into a temperature which was too far beyond their normal to recover. The great majority of the medusæ were to be found after a while in a temperature of from 20° to 30°. Apparently this is an optimum. The medusæ would be seen to swim for some distance toward the heated end, turn, swim into the cold end again, turn again and repeat the operation with the general result that they finally settled in the zone of optimum temperature.

The writer is indebted to Dr. T. H. MORGAN for suggesting the work and for much kindly aid in the course of its preparation. The writer wishes also so express his thanks to Dr. R. M. YERKES for much kindness shown him in this and other instances. The work was done at the Woods Hole Station, U. S. Bureau of Fisheries.

The College of the City of New York,
September, 1906.

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CONCERNING THE BEHAVIOR OF GONIONEMUS.

BY

ROBERT M. YERKES.

(From the Marine Biological Laboratory, Woods Hole, Mass.)

The courtesy of Mr. Morse in calling my attention to the results of his study of the reactions of Gonionemus and in discussing them with me before their publication has made possible the following prompt explanation, on my part, of the apparent differences in our results.

Since Mr. Morse told me of the results of his study of the reactions of Gonionemus to light I have repeated certain of my earlier experiments and made such additional observations concerning the influence of light as the scarcity of material at the time permitted. I wish now to present the results of my recent experiments, in connection with my reply to the criticisms of my work.

As appears from Mr. Morse's paper,[1] we disagree concerning the following five points:

1. That light is an important factor in the determination of the inversion of the bell when the medusa reaches the surface of the water.

2. That there is at times a temporary gathering in the brighter region when the medusæ are exposed to intense light in a vessel of which one portion is shaded.

3. That sudden decrease in the intensity of illumination temporarily inhibits the movement of an active individual.

4. That intense light may determine the direction of movement.

5. That the influence of light on active individuals is different from its influence on resting individuals.

Mr. Morse has contradicted all of the above statements of my papers.

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[1] Morse. Notes on the Behavior of Gonionemus. *Jour. Comp. Neurol. Psychol.*, Vol. 16, No. 6. 1906.

First, as to the cause of the surface reaction of Gonionemus, Mr. MORSE states, incorrectly, that I believe the reaction to be due to light. As a matter of fact, I have said, and have attempted to show that, although light seems to be one of the important conditions for this reaction, it may occur in the absence of light. My view concerning the reaction, together with one of my chief grounds for holding the view, are expressed in the following quotation from one of my papers: "In sunlight the medusæ at first come so forcibly to the surface that half the bell may appear above the water. Usually a bell thus forced out of the water inclines slightly to one side, and thus tends to turn the animal over, so that the observer can never be quite sure whether the turning is due altogether to the action of gravity, or whether it is in part due to some peculiarity in the final contraction of the bell. After having been in sunlight for a few minutes, the animals come to the surface with noticeably less impetus, and soon they fail to reach the surface at all. But even in the latter case they turn over, just as they do in ordinary light after reaching the surface. Under these conditions the turning due to stimulation by light evidently is accomplished by bell contractions."[1] And I further add, in an attempt to account for the inhibitory influence of light, "Light having been one of the most important stimuli for the initiating of the surface reaction; *i.e.*, turning, inhibition of activity, expansion of organs, may finally have come to be the cause of a very similar reaction in the presence of other conditions, so that increase in light intensity now uniformly causes an active Gonionemus to expand fully for a few seconds and permit itself to sink passively."[2]

As Mr. MORSE, without contradicting any of my statements of fact and without offering further facts or suggesting an explanation of the surface reaction of Gonionemus, simply questions the correctness of the partial account of the phenomenon which I have given, I can not do otherwise than hold to my earlier view of the matter.

On p. 3 of Mr. MORSE's paper attention is called to certain "paradoxical facts" in my work which demand further investigation. These facts, or better statements, are numbers 2 to 5 of the above list of points in which Mr. MORSE disagrees with me. The

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[1] *Amer. Jour. Physiol.*, Vol. 9, p. 285. 1903.

[2] *Amer. Jour. Physiol.*, Vol. 9, p. 288.

first of these apparently paradoxical statements made by me is that, the medusæ under certain conditions at first gather in a region of bright illumination and later come to rest in a shaded region. In his experiments, Mr. MORSE did not observe "a collection of the medusæ in the illuminated portion of the vessel."[1] As I was utterly unable to account for the disagreement in our results I at once repeated my former experiments. Eleven medusæ were placed in a white earthenware dish such as AYER and I used in our experiments with Gonionemus. The dish was illuminated by direct sunlight from a southeast window. All of the animals at once began to swim about actively, mostly, however, keeping close to the bottom of the dish as if seeking to move away from the light. After a few seconds one-half of the dish was covered with a piece of black cardboard. Within a minute, ten of the eleven medusæ were in the sunlit portion of the dish, and there they remained for about two and a half minutes, swimming about actively but without moving far in any direction. Then, as quickly as they had gathered in the sunlit portion, they moved to the shaded portion, and in less than a minute all but two were in the shade of the cardboard.

There is no doubt in my mind that the behavior just described is due to a complex of stimuli and internal states of which light, temperature and the condition of the organism are of prime importance. I have always suspected that the temporary gathering of the medusæ in bright light which I have repeatedly observed is due rather to the strong stimulating power of the light than to any definite directive influence. The matter deserves further attention, for AYER and I have done little more than call attention to the fact.

The second paradox appears in my statement that "when an individual, in swimming about, chances to cross from the sunlit region into the shadow, it very quickly ceases swimming and sinks to the bottom. If, later, in swimming about it chances to cross from the shaded region into the sunlight, it in most cases immediately ceases swimming, turns over, and sinks passively to the bottom."[2]

Perhaps the contrast between "very quickly" and "immediately" in the above description was not sharp enough. At any

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[1] *Journ. Comp. Neurol. Psychol.*, Vol. 16, p. 452. 1906.

[2] *Amer. Jour. Physiol.*, Vol. 9, p. 282. 1903.

rate, Mr. MORSE noted no definite reaction as the medusa passed from light to shadow, but instead merely a gradual cessation of activity due, as he believes, to the absence of stimulation.

I am compelled to disagree with the view that decrease in the intensity of light means absence of stimulation. I have already shown that a rather sudden increase in the intensity of light inhibits the movement of an active Gonionemus, in most cases, whereas a considerable decrease causes a more gradual cessation of activity, and I have abundant evidence that change in the intensity of light stimulates the medusa. Whether this change be increase or decrease in intensity, it may either augment or inhibit the activity of a moving individual and it may or it may not bring a resting individual into movement.

According to Mr. MORSE, the third paradoxical statement in my papers is that "the reaction to sunlight is a direct response whereby the medusa turns directly toward the shadow and swims into it."[1] I have never made any such statement, I believe, and I agree with Mr. MORSE that it is false. What I have said is, not that the medusa swims toward the shadow, but instead that, "when it chances to cross from the shaded region into the sunlight, it in most cases immediately ceases swimming, turns over and sinks passively to the bottom. But in this case when it again becomes active, it does not move indifferently in any direction as it does when in the shadow; instead it usually turns in such a way as to move back into the shaded region."[2] This is precisely what I said and what I meant; I repeat the statement in the light of further observations made during September, 1906.

Mr. MORSE's criticisms have served the good purpose of revealing to me an important omission in the description of the conditions under which Mr. AYER and I observed the behavior described below. We omitted to state that the direct sunlight by which the earthenware dish was illuminated came from a southeast window and was not exactly perpendicular to the surface of the water and the bottom of the dish. From our description, one is led to infer that the line between light and shadow was perpendicular to the bottom of the dish, whereas it inclined slightly toward the shaded region. In the figure given in our paper[3] to

[1] *Jour. Comp. Neurol. Psychol.*, Vol. 16, p. 452. 1906.

[2] *Amer. Jour. Physiol.*, Vol. 9, p. 282. 1903.

[3] *Ibid.*

represent the reaction of the medusa at the transition line between light and shadow the dotted line should incline slightly toward the shaded end of the dish, for the black card which covered the right end of the dish permitted the sunlight to illuminate a larger area at the surface of the water than at the bottom. As a consequence of this condition a Gonionemus when it reacted to the sunlight, as it passed into it, by ceasing to swim, turning over and sinking passively, usually came to rest on the bottom of the dish, unless it resumed its swimming before reaching the bottom, partly in the sunlight and partly in the shaded region. In this position it was unequally stimulated on opposite sides, and as a result the bell contracted in such a manner as to turn the animal toward the shaded region.

In my repetition of this experiment the importance of this marked inequality of illumination has been demonstrated for I found that when the animals swam so far into the sunlit region before turning over that they were entirely in the sunlight when they came to rest on the bottom of the dish, they moved away from the region of shadow about as often as toward it. When they came to rest with a part of the body in the shadow they turned back toward the shaded region in about 70 per cent of the cases. With one group of animals there were forty-four movements toward the shade to twenty away.

The effect of suddenly increasing the illumination of a portion of the bell by allowing sunlight to fall upon it was noted. The result apparently depends upon the intensity of light to which the organism happens to be adapted at the moment of the experiment. If it has been in weak light, the brilliant illumination of one side of the bell in more than two cases out of three, according to my recent observations, brings about movement toward the region of lower illumination. Lack of material compelled me to leave this work uncompleted, but in reply to Mr. MORSE I may say that my experiments indicate that Gonionemus turns from the region of strong stimulation in as definite a manner as the structure of the organism and method of locomotion permit in the cases of all stimuli which are injurious. Light is not an exception to this rule, nor have I discovered any, although I do not doubt that some such exist.

While repeating my experiments I noticed for the first time another form of local reaction to light. A medusa partly in sunlight and partly in shadow was drawn from the light into the shadow by the contraction of the tentacles on the portion of the organism which was in the shadow. The effect was a sort of crawling movement. This reaction I saw only three times.

The reasons for certain of the apparent disagreements in the results of Mr. MORSE's experiments and my own are my failure to state that the sunlight was not perpendicular to the bottom of the dish, and his failure to take note of the exact form of my statement of results. With the light perpendicular to the bottom of the vessel I obtained the same results as Mr. MORSE. There was no evidence of the directive influence of light. There is a flat contradiction in our statements, however, so far as the reaction to oblique light is concerned. Possibly this would disappear if the meaning of the term were more fully explained in Mr. MORSE's paper.

Of the fourth paradoxical fact to which attention is called at the beginning of Mr. MORSE's paper—namely, that the reactions of active medusæ when stimulated by light are different from those of resting individuals under the same conditions of stimulation—I find no further mention. Possibly it was his intention to dispute the statement on the basis of the other facts to which he had called attention. I am unable to see anything paradoxical in the statement that the effect of light depends upon the physiological condition of the organism. It would be strange indeed if the active and the quiescent medusa reacted to light in the same manner.

Finally, Mr. MORSE concludes from the results of his study of Gonionemus that the behavior of this organism conforms to the theory of trial and error rather than to the theory of the tropisms proposed by VERWORN and LOEB. While partially agreeing with him in this, I still hold that several of the reactions which I have described are in part determined as to the direction of movement by the quality, intensity and location of the stimulus and therefore conform to the theory of the tropisms formulated by LOEB. There is more or less trial in all the reactions of Gonionemus, but I fail to see why trial and error and local action should be mutually exclusive. It seems to me that VERWORN and LOEB, in connection with the tropism explanation of certain reactions, have laid emphasis upon the definiteness and uniformity of reactions, while JENNINGS, HOLMES and others have laid all stress upon the variableness, complexity and modifiability of the same reactions. Both points of view are important, but they supplement rather than destroy one another. When Gonionemus in swimming from a low intensity of light into a high intensity responds to the sudden increase of light by turning over and sinking to the bottom, its reactions conform to the local action tropism theory in that stronger stimulation of the bell on one side than on the other, causes that side to contract in such a manner as to turn the bell away from the strongly stimulated side. If the organism happens to make a complete circle because of the force of contraction of the stimulated side of the bell, and this often occurs, it is brought into the strong light again and the same reaction may be repeated, with some variation perhaps. Unless this directive influence of the unequal contraction soon brings the medusa into the weak light, other forms of reaction inevitably appear, for the relation of the animal to the stimulus has changed because of the continued action of the light. Is this a series of trial and error reactions or is it merely an instance of the complex relations of local action and the various forms of reaction exhibited by Gonionemus ? I should say that it is trial and error only from a superficial view, for analysis of the conditions of reaction indicates that local action determines the direction of the medusa's movement in a pronounced way when certain rather unusual conditions exist. Change the conditions—even the repetition of a given photic stimulus may meet with a form of reaction markedly different from the directed movement due to the local action effect of the original stimulus because of the changes in the physiological condition of the organism—and a new form of reaction appears.

At the earliest possible date I shall undertake a thorough study of the light reactions of Gonionemus in their relations to other external conditions, as well as to the physiological states of the organism.

Woods Hole, Mass.
September 20, 1906.

EDITORIAL.

HUMAN AND COMPARATIVE NEUROLOGY.

It has long been held and assiduously taught that the comparative method offers the only means of approach which is adequate to prepare the student for the study of the human brain. But when the beginner takes up the study of comparative neurology, either by the aid of the existing manuals and memoirs or by a direct appeal to the specimens themselves, so far from finding his path easy, he is quite likely to find himself completely submerged in a mass of detail largely uncoördinated and with only very indirect application to the anatomical and physiological problems of human neurology. Accordingly, comparative neurology continues to be regarded as a specialty too intricate and technical for practical use, even pedagogically.

Now, it is unquestionably true that the comparative method is more fruitful (one may say more absolutely indispensable) in neurology than in any other department of morphology; but it must be admitted that, up to the present time, this has been more patent to the investigator than to the elementary student. What is wrong? Certainly something rather fundamental, for the beginner should be the first to profit by a genetic mode of approach.

We have had for many years an enormous literature on comparative neurology, a mass of material which is increasing progressively more rapidly each year. And yet as a whole it is inchoate and indigestible. The periodic critical reviews of this literature (the term digest is inappropriate to most of these amorphous and distasteful compends) serve chiefly to impress the reader with its bulk and inaccessibility. As a rule they leave on the mind no clear impress of definite progress. There have evidently been no coördinating principles running through this series of researches, and mere descriptive detail has accumulated as an inert mass until it threatens to block the wheels of progress of investigation.

Dr. BARKER's text-book, "The Nervous System and its Constituent Neurones," met the difficulty in the only practicable way. The nervous system was analyzed into its functional systems and these were taken as the units—not the neurone, not the segment or neuromere or any artificially bounded region, but the aggregate of nervous centers and tracts which act together for the performance of some definite function. The result was the most accessible compend of data and literary references regarding the structure of the human brain which has ever been published.

But some years before the appearance of Dr. BARKER's book a movement was inaugurated in the field of comparative neurology which was designed to define these functional units much more accurately and by comparative studies to outline their phylogeny. This movement began naturally and properly with the analysis of the peripheral nerves and their primary centers, and hence was termed the doctrine of nerve components. The simplicity of organization thus revealed in the peripheral nervous system gave the key to a similar functional analysis of the central nervous system with still more gratifying results.

In brief, the functional analysis of the nervous system, in the form in which it has grown up within the past decade, has furnished us with the unifying principle necessary to organize comparative neurology into a truly scientific discipline and at the same time make it really effective as the hand-maid of human neurology.

This movement was born in America and has been largely cultivated here. It is still too young to permit a final adjudication of its merits; but that was a significant remark made by a careful and patient observer, Dr. KAPPERS, in our issue for last January. He admits that he began his studies on the brains of fishes prejudiced against the ideas of what he terms the "American school;" but when his research was completed he states that he found no facts inconsistent with these views and he is in fact cordially appreciative of this work.

In view of the importance of the rôle played by American students in the elaboration of the newer phases of this functional analysis, it is fitting that the first comprehensive text-book of comparative neurology written from this point of view should appear in this country. In Professor JOHNSTON'S "Nervous System of Vertebrates," a more extended notice of which appears in our review columns, we have the most consistent and satisfactory application of the genetic method in comparative neurology which has yet been made. Each functional system is first taken separately and given a searching analysis in representative types and then the centers of correlation are similarly treated genetically. The study of the vertebrate nervous system is not easy and no primer of neurology can be expected which will make it so; but the comprehension of the human brain should be greatly facilitated by the careful study of JOHNSTON's exposition of the vertebrate type form for each functional system and its evolutionary history. The mastery of this manual by a student well grounded in general vertebrate anatomy and embryology, followed by a text-book of human neurology written from the standpoint of the functional pathways, should provide an excellent foundation for research in neurology, comparative psychology and the related fields.

LITERARY NOTICES.

Johnston, J. B. The Nervous System of Vertebrates. *Philadelphia, P. Blakiston's Son & Co.* 1906. Pp. xx + 370, 180 Figs. $3.00.

Progress in the investigation of animal behavior has, undoubtedly, been retarded by the imperfections of our knowledge of the nervous systems of the animals under investigation, and especially by the fact that the published data, which are by no means inconsiderable, are technical anatomical descriptions usually imperfectly correlated among themselves and always written in a scientific vernacular which is unintelligible except to the initiated. And conversely, morphological research has often signally failed to make the most of its own material because of lack of attention to the functional relations of the parts under investigation. The time for more perfect correlation of structure and function has come, and that not merely by the arm-chair neurologist and psychologist, but by all investigators as a matter of routine method.

Professor JOHNSTON's book is most timely. It gives a brief yet comprehensive summary of the present status of the functional analysis of the vertebrate nervous system in form comprehensible to any one with a rudimentary foundation of vertebrate morphology and a willingness to apply himself seriously to the mastery of considerable rather intricate detail. The style is direct and clear and the text is illustrated by numerous excellent diagrammatic figures; the book should present few serious difficulties to the properly prepared student who will read the earlier chapters faithfully and get the author's point of view. And this is a matter which should be emphasized for the benefit of those who have had occasion to go to the technical literature on the brains of lower vertebrates for either general or special information.

The first chapter is brief, devoted to a statement of the point of view and an exposition of the more important neurological methods. The orienting of the student is fairly well accomplished within the compass of about ten pages. I distinctly do not concur in the author's suggestion that this chapter may well be omitted by the elementary student. No student can read intelligently the subsequent anatomical descriptions without some knowledge of the procedures involved in their preparation. Indeed I would go even further and recommend that in the description of all figures of actual sections the method of preparation be stated. The advanced student as a rule does not require this; but the beginner will often be helped by it. The second chapter, devoted to general morphology of the nervous system, is also brief. It might well be expanded a little and a few additional figures introduced to illustrate the external form of some of the leading types of brains to which constant reference is made in the following chapters. The third chapter, on the development of the nervous system, is devoted chiefly to histogenesis and the general morphology of the head. Readers of this journal are already familiar with JOHNSTON's studies in the latter field. In the fourth chapter, nerve elements and their functions, attention is directed chiefly to the external forms of neurones and their modes of inter-relation. A conservative position is taken with reference to the neurone theory and the modifications necessitated by the recent studies on neuro-fibrillæ. No mention is made of the cytological characteristics of the cell body or of functional changes in the neurone.

Next follow 123 pages (Chapters 5 to 13) devoted to the functional divisions of the nervous system. First, the functional divisions are defined and tabulated. Then they are taken up *seriatim*, described in detail and the phylogenetic history of each is sketched. These chapters are of great value. The treatment is unique and gives the character to the whole work. Among other useful illustrations, there is a series of diagrams of the peripheral nerve components, taken from the literature, and a similar series of original diagrams of the central conduction pathways of each functional system of components. The mastery of these simple diagrams gives the student the principal landmarks for all of his subsequent study of the vertebrate brain.

The conflicting accounts and chaotic nomenclature of these connections in the lower vertebrates are harmonized and brought into relation with the conditions in the human brain as far as possible. Our knowledge of the structure of the lower brains is still so imperfect that much of this correlation is necessarily theoretical, and it is too much to hope that all of JOHNSTON'S homologies will stand the test of time. It can fairly be claimed that the evidence for them is good as far as it goes, though it must be kept in mind that the demonstration is not equally convincing in all cases. For instance, in the somatic sensory system, the demonstration of the genetic relations of the dorsal cornu, funicular nuclei, substantia gelatinosa Rolandi, tuberculum acusticum and cerebellum may be regarded as proved. The homologies of the somatic sensory column in front of the cerebellum are by no means so well established. The probability that the tectum opticum belongs here is strong; but the evidence for the addition of the retina, nervus terminalis and neopallium to this list of somatic sensory structures is still very defective. The visceral sensory column has suffered less modification of the primitive relations in the upper regions of the brain and the homologies of these centers may be regarded as established in a broad way, about as JOHNSTON describes them, from the olfactory bulb to the intermediate zone of the spinal cord, though here, also, the pre-cerebellar connections are by no means so clearly defined as the post-cerebellar.

Chapter 13 is devoted to the sympathetic nervous system, and the remainder of the book (pp. 218 to 360) to the centers of correlation. The brief introductory chapter (14) contains some of the most important generalizations in the book. The substantia reticularis (a derivative of the central gray) is recognized as the starting point for all of these centers, which make up by far the greater part of the brains of all higher animals. "In the lowest vertebrates, cyclostomes, a large part of the substantia reticularis of the brain remains in its primitive indifferent condition; few special nuclei are developed and the activities of the animal are correspondingly simple." The following chapters illustrate the author's views of the way in which this indifferent material has been shaped in response to the varying functional needs of the successive types of vertebrates. Special attention is called to the value of the teleostean fishes in elaborating type schemata of the vertebrate plan of the several functional units.

In the sketch of the phylogenetic history of the cerebellum, which is quite completely elaborated, there are several new features, notably in the history of the cerebellar hemispheres, whose antiquity is established. The chapter on the mesencephalon also contains several important new contributions. Of these, the most important is the sharp analysis which separates the centers of various other types of somatic sensation from those for vision. In cyclostomes the tectum mesencephali receives the lemniscus and, apparently, direct general cutaneous root fibers, besides termini of the optic tracts. As we pass up the vertebrate series, the optic centers become specialized away from the other somatic centers, the latter in higher fishes appearing as a swelling in the lateral wall of the mesencephalon, the colliculus, and in mammals as the colliculus inferior behind the tectum opticum.

The final chapters on the evolution of the cerebral hemispheres are full of stimulating suggestion. The series of diagrams of homologous centers and fiber tracts in all the types of fishes is impressive; still more so is the identification of the same structures in substantially the same relations save as modified by neomorphs in the brains of the higher animals, including man.

It is only in the discussion of the neo-pallium that we find much which might be termed distinctively human neurology. In general, whatever is well done in the other text-books has been omitted by JOHNSTON, so that this work will not supplant any others, but rather serve as an introduction to their study. The great merit of the book is its independence of tradition and authority. The brief bibliographies at the ends of the chapters contain few titles save those connected with the newest results of the functional school of neurologists. In fact, it is possible that the monotonous repetition of the titles of a few American monographs throughout the book will excite the derision of some critics. Still it must be remembered that there are other general neurological bibliographies (one of the best of which we owe to JOHNSTON) and there was no need here for the citation of other originals than those from which the motive of the work has been drawn. This independence, coupled with the dogmatic form of statement fitting in a text-book, is responsible not only for the greatest merit of the book, but also for its greatest defect. The delicate balancing of probabilities on debatable points is of course out of place in an elementary text-book; but the definite affirmation of well established fact and rather precarious hypothesis in equally dogmatic form is at the best unfortunate and is usually unnecessary. The somatic sensory character of the nervus terminalis, the theory of the paleostoma, the homology of the direct cerebellar tract with the secondary vagus bundle (in some places dogmatically asserted, though qualified in others) and the termination of sensory trigeminus root fibers in the mesencepalon of mammals may be cited as instances of over-zealous dogmatism which in my opinion mar the value of the book. To some well-informed neurologists it may appear that a similar criticism should be applied to the book as a whole. The author cuts his furrow across well cultivated fields in so original a fashion that some may fear to follow him. To these it may be replied in advance: First master the very recent literature of nerve components and functional divisions of the brain in lower vertebrates; no just criticism of JOHNSTON's course is possible until the data which form his premises are thoroughly assimilated. His method and chief conclusions will stand this test.

There are a few unfortunate typographical errors. The most serious is the transposition of Fig. 175 with Fig. 177 and Fig. 176 with Fig. 178. If these cuts are transposed as indicated, their descriptions will read correctly. On p. 158 the reference line for the *N. ophthal. prof.* ends upon the *R. ophth. super. VII.* It should be extended to reach the nerve immediately ventrad. On page 211 there is a lapse which probably also belongs in the list of misprints. The sentence at the end of the first paragraph should be amended by the addition of the words enclosed in brackets, as follows: "This is the portion of the gray matter which has previously been called the visceral efferent column. As already stated, the fibers from this column in lower vertebrates pass out through [both] the dorsal [and ventral] roots, but in mammals which have been most used for the study of the sympathetic, they pass out by way of the ventral roots [only]." But such lapses are not common and most of the cases where the reader may question the words of the author are fairly debatable matters of fact or interpretation. The directions for laboratory work impress one as being the part of the book which received the least care. They are not intended to serve as a manual for a coördinated laboratory course; but they do contain many valuable suggestions which we should like to see elaborated into such a manual.

It is refreshing to see so many new figures, especially the diagrams and schemata, whose pedagogic value is enormous. Some of the diagrams serve very effectively as summaries of long descriptive passages. All are very clear and most have the legend written directly upon them so that a minimum of time is required for their consultation.

All students of comparative anatomy and comparative psychology, and not merely the professional neurologists, will find much of value in this book, which is sure to exert a profound influence upon the future course of research in comparative neurology.

C. J. H.

Hrdlicka, A. Brains and Brain Preservatives. *Proceed. U. S. Nat. Mus.*, Vol. 30, pp. 245-320. 1906.

The weight and form of the brain have come to be features of such scientific importance that the value of many brain collections depends more and more upon the success with which these features are preserved. With the view of ascertaining the best method for accomplishing this, HRDLICKA has made a systematic study of some of the more promising brain preservatives. Of these the most satisfactory was formaline, but when this is used alone, it produces ordinarily an initial increase in weight which after about a week is followed by a gradual loss. The addition of salt or alum to the formaline did not remedy this defect. Excellent results were obtained by adding alcohol to the formaline; this mixture when rightly proportioned gave rise to very little initial change and to almost no subsequent loss of weight. The mixture should be made up in different proportions for brains of different sizes, and HRDLICKA gives an excellent table of the best proportions for brains weighing from 50 grams or less to those above 900 grams.

G. H. P.

Hugo Münsterberg. The Harvard Psychological Studies. Vol. II. *Houghton, Mifflin & Co., Boston and New York.* 1906. Pp. 644. Price $4.00.

The second volume of the Harvard Psychological Studies, although published under the auspices of Houghton, Mifflin & Co., is uniform in appearance with the first volume, which was published as a monograph by the *Psychological Review.* The present volume is a fit companion to the previous one, and is well qualified to serve as a memorial to the opening of Emerson Hall.

The book under review contains the results of several investigations made upon a variety of psychological subjects. A section each is devoted to optical studies;

feeling; association, apperception, attention; motor impulses; and animal psychology. "Emerson Hall," by Professor MÜNSTERBERG, serves to introduce us both to the book and to Harvard's new psychological laboratory.

The number and scope of the investigations are too large to admit of comprehensive treatment in a single review. We shall attempt to deal here merely with the studies on animal psychology, and the review of even this limited portion of the book must be, of necessity, of a summary character.

Four investigations are reported under the general heading of animal psychology: First, "The Mutual Relations of Stimuli in the Frog, Rana clamata Daudin;" second, "The Temporal Relations of Neural Processes;" third, "The Mental Life of the Domestic Pigeon;" fourth, "Reactions of the Crayfish." The first two are reported by ROBERT M. YERKES, the third and fourth by JOHN E. ROUSE and J. CARLETON BELL, respectively.

The first paper of YERKES, as is shown by the title, treats of the mutual relations of stimuli in the frog. In part, the results from these experiments have already been reported upon. It is a distinct gain to the research public, however, to have so interesting a series of facts brought into the compass of a single paper. YERKES treats here, primarily in a physiological way, of the important phenomena of reinforcement and inhibition in the reactions of the frog to an electric stimulus, when photic and auditory stimuli are given either simultaneously with the electrical stimulus, or at definite intervals before it. Whether reinforcement or inhibition of the reaction to the electrical stimulus occurs under these circumstances depends upon the temporal relation of the other stimuli to the electric. At the end of the paper, he correlates his own work with that of others and attempts a partial explanation.

YERKES' second paper, on the temporal relations of neural processes, is, in our opinion, distinctly inferior to his first. He attempts to answer the following questions: First, "Do reaction-times, in any given animal, range with equal frequency of occurrence from short to long, or are there certain modes (most frequented classes) which indicate definite types of reaction, such, for example, as the reflex, the instinctive, etc.? Second, "If there is distribution of the reaction-times about one or more modes, what are the types of reaction indicated thereby?" Third, "Finally, is reaction-time of service as a sign or measure of consciousness?" By recording the reaction-times (HIPP chronoscope) of several hundred reactions of the frog to electrical stimuli of different intensities, and finding the modes of the series for any given intensity of stimulus, YERKES obtains evidence for the existence of certain types of reaction, and he suggests that this distribution of the reactions around given modes indicates their reflex, instinctive and voluntary character.

YERKES goes further and answers his third question in the affirmative: "Hesitation in reaction is commonly accepted as an important sign of volitional consciousness in man, consequently, delayed reactions in lower animals are supposed to be indicative of psychic processes." And again: "Reaction time with respect to its two aspects of duration and variability may be used as a sign or criterion of consciousness, for in accordance with the nature of these two sets of facts, we classify acts as reflex, instinctive or voluntary." While YERKES does not say specifically that he means the above statements to apply to the reactions of the frog, this interpretation is forced upon the reader in view of the following sentence taken from his introduction to the paper: "Voluntary reaction-time may be as short as 150 σ or as long as life, in an animal capable of profiting by experience as does the frog. It is preëminently of the delayed type of reaction-time" (p. 575).

That the author can take the position he evidently does in this paper is somewhat surprising, since his own admirable study of the associations formed by this animal is chiefly responsible for our judgments concerning the extremely low order of its intelligence. In our own opinion, variability and length of reaction time of animals as they are ordinarily recorded are, in any immediate sense, precarious indices of intelligence, even when taken in conjunction with other "signs."

ROUSE's paper on the mental life of the domestic pigeon is pioneer work upon that animal. It is divided into two parts—one treating of its emotional life, the other, of the variety and complexity of its associations. We cannot at present agree with the author in all of his conclusions, especially with the one which asserts that a correspondence exists between "agreeable feelings and increased breathing activity." The paper, as a whole, is of value, undoubtedly, in that it gives us new data upon the behavior of the pigeon in specific and controlled situations. A more accurate comparison can now be made of the behavior of this animal with that of other animals which have been studied in a similar manner.

J. CARLETON BELL's paper on the reactions of the crayfish requires an extended review to do it justice. It treats of the reactions of this type of crustacean to (1) white light; (2) colored light, and (3) to "objects." It discusses also the lack of reaction in this form to "vibratory stimuli which to the human ear produce a sound." He finds that the crayfish is positively geotactic, negatively barotactic, and, to a high degree, positively thigmotactic.

These papers thus summarily treated here are deserving of, and will undoubtedly receive, separate and individual notice.

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