BEHAVIOR MONOGRAPHS

Edited by
JOHN B. WATSON
The Johns Hopkins University

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The Development of Certain Instincts and Habits in Chicks

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CONTENTS

PART I. INSTINCTIVE REACTIONS

I. Introduction and Statement of the Problem

The experimental work reported in this monograph was carried on during the years 1907, 1908, and 1909 in the Harvard Psychological Laboratory. The variety of chick used in all the work was the Barred Plymouth Rock. It is usually considered by poultry breeders a hardy chick, and for this reason more than any other was selected for these tests. The program of research began with a cursory study of the first activities of the animals, preliminary to a more detailed study of certain instinctive modes of response such as drinking, pecking, and "imitating." In the case of drinking, interest centered in the nature of the stimulus; in the case of pecking, in the accuracy of the reaction; as for imitation, the question was asked, In how far is social influence a means to improvement in the accuracy of pecking? After some knowledge of the natural tendencies of the chicks had been gained, an attempt was made to trace the course of development of certain habits of response to optical stimuli, as well as to study the interrelation and persistence of these habits. Quantitative methods were devised and applied wherever they suggested themselves to the experimenter.

The investigation was pursued under the immediate direction of Professor Robert M. Yerkes. What I owe to his searching criticism and fertile suggestions, a mere word of acknowledgment will not suffice to say. I shall be only too glad if my immature effort reveal some trace of his admirable scientific spirit. I am also much indebted to my colleague, Professor Charles Scott Berry, for a critical reading of the manuscript, and to Dr. William F. Hauhart, Instructor in German, University of Michigan, for valuable assistance in reading the proof.

II. Previous Experimental Work on Chicks

Attention is limited in this résumé to the conclusions of investigators in regard to the accuracy of the pecking response. The results of some previous studies of the drinking reaction will be discussed in connection with the results of a study of the reaction reported later in the paper.

Spalding's [1] observations on the pecking reaction have been quoted widely. Concerning the pecking of his chicks he says: "They did not attempt to seize things beyond their reach, as babies are said to grasp at the moon; and they may be said to have *invariably hit the objects at which they struck*—they never missed by more than a hair's breadth, and that too, when the specks at which they aimed were no bigger, and less visible, than the smallest dot of an *i*. To seize between the points of the mandibles at the very instant of striking seemed a more difficult operation. I have seen a chicken seize and swallow an insect at the first attempt; most frequently, however, they struck five or six times, lifting once or twice before they succeeded in swallowing their first food." (*Italics mine.*)

On the question of the accuracy of the pecking of chicks, Preyer [2] disagrees with Spalding. "I cannot admit," he says, "the supposed infallibility to within a hair's breadth. They miss in pecking by as much as two millimeters, though seldom. On the other hand, the attempts at swallowing frequently fail. Here it should be considered that even grown fowls are not sure in their pecking, seizing, and swallowing, as any one that observes closely may easily perceive. *The accuracy is, however, marvelous at the very beginning.*" (*Italics mine.*)

Romanes,[3] though reporting no experimental work of his own, deserves notice on account of his wide influence. He quotes Spalding extensively and with approval. For Romanes, perfection as applied to instinct means perfect adaptation independent of individual experience. He illustrates such perfection "by considering *the wonderful accuracy of many among the highly refined and complex adjustments* which are manifested by the newly-born young of the higher animals," (italics mine), citing first in his list of examples of perfection the pecking reaction of chicks as reported by Spalding.

Eimer [4] experimented on chicks during two different years. The impression he got of the accuracy of pecking appears in the

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[1] Spalding, D. A.: Instinct. With original observations on young animals. *Macmillan's Mag.*, 1873, vol. 27, p. 284.

[2] Preyer, W.: The senses and the will. (1881.) Tr., New York, 1890, p. 67.

[3] Romanes, G. J.: Mental evolution in animals. New York, 1884, p. 161.

[4] Eimer, G. H. T.: Organic evolution. Tr., London, 1890, p. 246.

following report of the reactions of one of his animals: "At the first attempt it touched a grain with as much certainty as if it had pecked at millet for ever so long. But it did not succeed in taking up the grain in its beak. A second attempt immediately afterwards likewise failed, but at the third, which succeeded without a pause, the grain was grasped and swallowed, and now the little creature *went on feeding as though it had done so for years!*" (Italics mine.)

Mills [1] thinks that some of Spalding's statements exaggerate. "Instinct is not the hard and fast thing it is sometimes supposed to be." On the basis of his own experiments he concludes: "*Thus one* (chick) *may strike a crumb accurately every time it pecks*, and pick it up on the first attempt; another misses, or shows great difficulty in getting it into the mouth." (Italics mine.)

Morgan [2] concludes that the complicated process of striking, seizing, and swallowing "is performed so soon, and with so few trials—often at the third or fourth attempt—that *one must regard the whole as essentially congenital in its definiteness*, and look upon the few preparatory efforts as merely the steadying of the inherited organic apparatus to its work." (Italics mine.) By congenital response is meant one that is not the result of acquired skill.

Writing earlier on the same topic, Morgan [3] had said the chicks "required a little intelligence, acting by and through experience, to perfect their (instinctive) activities. The instincts were very nearly, but not quite, perfect."

Thorndike [4] criticises Morgan's conclusions on the improvement in accuracy of the pecking reaction. "Lloyd Morgan, for instance, has chosen a dubious example of perfecting through habit in the seizing of bits of food by chicks. They often do fail to seize in their first experiences, as he observed, *but they often, perhaps just as often, fail even after long experience.*" (Italics mine.)

Finally, a further matter, aside from the question of the

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[1] Mills, W.: The psychic development of young animals and its physical correlation. Trans. R. S. Can., Sec. IV, 1895; or, The nature and development of animal intelligence, New York, 1898, p. 262.

[2] Morgan, C. L.: Habit and instinct. London and New York, 1896, p. 37.

[3] Morgan, C. L.: Introduction to comparative psychology. London, 1894, p. 207.

[4] Thorndike, E. L.: The instinctive reaction of young chicks. *Psych. Rev.*, VI, 1899, p. 282. Also, Instinct. *Biol. Lectures*, Woods Hole, 1899, p. 61.

accuracy of pecking. Katz and Révész[1] support Hess[2] in the view that the hungry chick does not peck at food which it does not see. The former assert, for example, that a chicken in the dark-room, even if placed directly in the food, will not peck at it. The point happens to be vital to their method in some important work.

It has seemed best to report the essential conclusions of the writers mentioned, so far as possible, in their own words. It may not be amiss, however, to note two general impressions one gets from these studies of the pecking instinct: (1) that the reaction has a high degree of congenital accuracy, and (2) that it has less of this than was formerly supposed.

III. General Apparatus

The room used for these experiments had a western exposure. It was equipped with an incubator[3] and a brooder[4] so that chicks for the experiments might be hatched at any time during the year in the laboratory. Such an arrangement also provided a good opportunity for complete knowledge of the history of the animals. For the sake of safety, economy, and convenience, both brooder and incubator were heated with gas. In addition to the regular thermostat on the incubator, a gas regulator[5] was attached to insure a more constant temperature. No trouble was experienced at any time in securing eggs of the special kind desired. The incubator and brooder were easily operated after a careful study of the directions that came with the machines. The percentage of fertile eggs hatched during the first year was 65.6. At times two settings were run simultaneously in the same incubator.

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[1] Katz, D. und Révész, G.: Experimentell-psychologische Untersuchungen mit Hühnern. *Zeitschrift f. Psych. u. Physiol. d. Sinnesorgane*, 1909, Bd. 50, S. 93.

[2] Hess, C.: Ueber Dunkeladaptation und Sehpurpur bei Hühnern und Tauben. *Archiv f. Augenheilkunde*, 1907, Bd. 57, S. 298–316.

————: Untersuchungen über Lichtsinn und Farbensinn der Tagvögel. *Ibid.*, 1907, Bd. 57, S. 317–327.

————: Untersuchungen über die Ausdehnung des pupillomotorisch wirksamen Bezirkes der Netzhaut und über die pupillomotorischen Aufnahmeorgane. *Ibid.*, 1908, Bd. 58, S. 182.

————: Untersuchungen über das Sehen und über die Pupillenreaktion von Tag-und von Nachtvögeln. *Ibid.*, 1908, Bd. 59, S. 143–167.

[3] Junior No. 2, sold by the Prairie State Incubator Co., Homer City, Pa.

[4] Indoor Brooder, No. 5, sold by the same firm.

[5] Single Float Standard Automatic Gas Regulator, secured from the Gas Consumers' Association, 18 Boylston St., Boston, Mass.

Greater freedom of movement was provided for the birds by the use of two cages that were connected with the brooder. For litter, white sand and shredded alfalfa were found satisfactory. Sand is more suitable than ordinary earth where it is desirable to avoid dust. A chick food [1] that is regularly on the market served our purposes very well. With the above simple equipment the chicks for the experiments were hatched and kept in the animal wing of the laboratory.

IV. Observations and Experiments

A. First Activities

If one would have the ontogenetic history of a chick, he must begin his study of the development of activity while the chick is still within the egg. A movement of the egg tray was sometimes found to be the occasion of a chirp within the egg hours before the shell was chipped. Or, chirping at times occurred so loud that it could be heard distinctly in the room in which the incubator was situated, when the incubator was tightly closed and no external stimuli, such as noises and jars, were noticed. Before the shell was broken at any point, a continuous tapping sound could often be heard within the egg, somewhat as if the chick were pecking against the inside of the shell. The movements of chicks just after the shell was chipped were observed through the glass door of the incubator and also seen to good advantage when the eggs were removed from the incubator and put in an appropriate receptacle under an electric light. Upon these latter occasions the ragged edges of the egg shell near the beak of the chicken were removed to give a better view of the animal's movements. Upon the observations following the transfer of a chipped egg to a nest warmed by an electric light, I find the following note: "I broke away much of the shell. After bill of chick was entirely out of reach of the shell, the chick continued to make a sound somewhat like pecking, and that, too, without opening and closing the bill. The 'clicking' sounds seemed to accompany the rhythmical heaving of the animal, which I took to be breathing. . . . Eyes were open, apparently, as soon as chick had unfolded itself." At the next hatch another chick was observed under an electric

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[1] Cyphers Chick Food, sold by the Cyphers Incubator Co., Boston, Mass.

light in the same way. I follow my notes: "Made at times a regular clicking noise with breathing. Frequently clapped mandibles together. . . . Repeatedly raised bill with a lifting motion of the head. This reaction might bring tip of bill, and hence the bill scale, in contact with the shell. Opened mouth and lifted bill. Eyes closed while in egg. Sometimes pushed bill forward, following this movement with a clapping together of the mandibles."

While the chicks were still in the egg the legs were folded well up on the breast and the head was turned down toward the breast. After the egg was chipped so that the behavior of the animal could be observed, the lifting movement of head and beak above referred to was more frequent than any other. One much less often saw anything like a forward thrust of the bill.

The chicks came out of the eggs wet and, in a temperature of 103° F., remained several hours before drying off. Spells of vigorous activity alternated with periods of passivity during the chicks' struggles just prior to hatching, as well as for some hours after hatching. The post-embryonic life of the chick in its early hours seemingly prolonged without interruption the life in the embryo. Chicks appeared to break the shell in two by a lifting, struggling movement of the head accompanied by a stretching, straightening movement of the legs. At least I have observed this combination of movements at the moment of hatching. Now if one watch carefully the behavior of a chick for some time after exclusion, he finds that there are these similarities between the later life within the shell and the earlier life outside the shell. The positions of the head and legs within the shell correspond to the positions assumed by these members during the passive states shortly after hatching. In both cases activity and passivity alternate, the periodicity of which alternation seems to be largely determined by intra-organic stimuli. If it be true that the legs participate in the action that finally breaks the shell, as I think they do, the lifting of the head and the pushing with the legs would be represented in the early post-embryonic life by those pulses of activity in which the chick lifts its head, rises to its feet, staggers a few steps, or struggles a few moments, and lapses again into the passive state. And just as the chick in the shell often claps its mandibles together without marked activity in other regions of the organism, so the chick during the first few hours after exclusion may be seen to work its mandibles in a similar way without disturbing its sitting posture. The pulses of activity, embryonic and post-embryonic alike, are often accompanied by loud chirping.

One might expect to find more unmistakable evidence of a pecking reaction while the chick is yet within the egg. There is an impression abroad that the chick pecks its way out of the shell. When the position of the head in the embryo is taken into consideration, one can see two reasons why most of the movements of the head are lifting movements, and not pecking reactions: (1) the lifting movement tends to free the head and neck from their folded position, and (2) pecking would seem to be a difficult matter with the head folded down on the breast in this wise. Besides, the lifting reaction does actually break shell and tear confining membranes, and so is effective in releasing the chick. It may be found that the chick does not peck its way out of the shell. However, the matter will need more careful study. For hours I have watched chicks laboring in the egg to discover a clear case of the pecking reaction. At times, before the egg has been broken in two, one does see short, quick, forward thrusts of the bill followed by working of the mandibles. And chicks only a few hours out of the egg may be observed repeatedly executing what might be called a pecking reaction "into the air," followed by clapping together of the mandibles. The following note describes the reaction more adequately: "Chicks after exclusion, on becoming aroused from a dormant period, often open bill with a chewing motion and sometimes thrust the bill forward sharply into the air even without fully opening the eyes, no object, apparently, being pecked at. Noticed a number of times."

The following activities, generally recognized as instinctive, were observed within the incubator on the first day, before the chicks were completely dry: Preening the down of the neck, wings, and breast; flapping of wings; chirping; walking; pecking; lying on side and stretching out legs (in the rays of a 16 c.p. electric lamp); following a moving object with a motion of the head; and chirring. Scratching, twittering, and wiping of the bill have been noticed on the second day when the chicks were taken out of the incubator for the first time and placed on a black cardboard for their pecking tests. Our knowledge of the time of appearance of the various instincts should not be left to depend entirely upon chance stimuli. Who shall say that a given reaction might not have occurred much earlier if the appropriate stimulus had been provided?

The chicks, while still in the incubator, are known to be positively phototropic. The incubator trays that have near the glass door a trap through which the chicks fall to a screen below, depend for their effectiveness on the fact that the chicks crowd toward the light.

B. Drinking

a. Problem.—In the study of instincts from the objective point of view, interest naturally centers first in function, second in structure. The activities which are known as instinctive must be analyzed into component units of behavior, of which they are nearly always complexes. Furthermore, no account of instinct will be satisfactory, no explanation complete, until we understand the structure of the machinery involved in each action. But so much accomplished, this is not all. These structures are not of such a nature that they in some way get themselves into action. So far as we know, they have no inherent principle of spontaneity. Intra- or extra-organic stimuli are necessary to touch them off. Environment in the form of energies external to the structures and additional to the functions seems to be a *sine qua nōn.* Hence a complete understanding of instinctive actions will include a detailed knowledge of the "objects" in conjunction with which the particular activities manifest themselves. In the following bit of work on the instinct of drinking, consideration of the problems of function and structure is made secondary to an inquiry into the nature of the extra-organic stimulus.

b. Method and Tests.—Chicks no. 69 to no. 81, inclusive, were hatched during the afternoon and evening of Dec. 2 and the morning of Dec. 3, 1908. Beginning with Dec. 3, their pecking had been tested in the regular manner each day. As the animals finished the first pecking tests they were marked, numbered, and transferred from the incubator to the brooder. Although given food and freedom to run about in the litter, they were allowed nothing at all to drink until tested as described below, neither were they permitted to see other chicks drink. A possible chance of coming in contact with something like water was afforded through deposits of waterish excrement. Even if this as a stimulus were able to elicit the drinking reaction, the fact that the chicks in the incubator rested on an elevated wire screen lessened the probability of the occurrence of such a stimulus. In the brooder the floor was constantly covered with the regular litter from one to two inches deep. On Dec. 5, from 3 to 5:30 p. m., when the chicks varied from 2.5 to 3 days of age, they were brought one at a time to the experiment table, just as if they were to be given a pecking test, and were returned to the brooder each as its drinking test was completed. In front of each animal was set a clean watch glass containing fresh water devoid at the start of bubbles or sediment. The watch glass rested on a square piece of smooth, white, plain note paper. As the observations on each chick were completed, the soiled paper was replaced by a clean piece, the dish was washed, the water renewed, and bits of food or drops of water carefully brushed from the table. The report of the observations follows in the order in which the chicks were tested.

While no. 70 was eating on the table, the watch glass, in the manner set forth above, was presented. The chick pecked grains which had been scattered over the white paper and then ran its bill in a forward direction along the paper in the drinking reaction. This it did repeatedly. Later I helped it to find the water in the dish. It seems unnecessary to state that precaution was taken to see that the paper was dry.

No. 72 was tried next. It pecked the plain, clean, white paper. Before the water was found by no. 72, no. 70 was brought out and allowed to drink in the presence of no. 72. No. 72 followed no. 70 about, performing the drinking reaction along the edge of the dish. One of the chicks stepped into the dish and carried some water to the paper surrounding it. No. 72 got its bill into this and forthwith responded with the drinking reaction. Then it wandered about the table and ran its bill along the black leather of my watch fob, 30 cm. distant from the dish, giving the drinking reaction. This does not mean that it touched the fob with its bill and then lifted its head in the manner so well known. The reaction to the fob was just what one sees when he watches a chick gathering water into its bill and throat while the bill is inserted in the liquid. This reaction is not easily confused with pecking. It was repeated on the silver charm of the fob.

No. 71 learned to drink by pecking at a bit of excrement that chanced to get into the water. Time after time it pecked about the edge of the dish. It was not observed to dip its bill into clear water. It secured water first by pecking and persisted in getting it this way throughout these first trials.

No. 74, when set on the table, pecked the edge of the white paper. First contact of the bill with water came from pecking a drop of water deposited on the paper. I put its bill into the water in the dish, whereupon it reacted to the situation by pecking the edge of the dish.

No. 77. By catching the paper on which the dish rested, the water was caused to wave slightly in the presence of the chick. Its head went down hard in a pecking reaction and hit the bottom of the dish, following which the head was lifted in the manner characteristic of drinking. On the second trial the head approached the water not in the manner of pecking but of drinking. The pecking approach to an object is decidedly different from the drinking approach. In contrast to the sharp descent upon the object in the former, the low gentle reaching movement in drinking, accompanied by a straightening of the neck, opening of the mouth, and a peculiar motion of the throat, is most marked.

No. 69. The surface of the water was agitated as for no. 77. No. 69 pecked directly into the water. Shortly afterward it pecked the water without my shaking it and at a point where I could discern no special stimulus like a bubble or particle of food. The positions of chick and dish were such that light reflected from the water might have been a factor.

No. 75. Pecked edge of the white paper. Pecked about the edge of the dish and its bill slipped into the water. The chick then pecked the edge of the dish twelve times, the bill getting into the water during some of these reactions. Pecked twice into the dish and got a little water. Of the next twenty reactions all were pecks and all but two were directed toward the side and edge of the dish.

No. 80. I thought I observed the chick performing the drinking reaction on a piece of glazed kymograph record paper about 3 cm. square that I vibrated between two fingers in front of the chick. But the reaction came out unmistakably a moment later on the side of the glass dish. The water was still, the glass was dry, and the chick ran its bill along the edge of the glass exhibiting plainly the drinking movements without touching the water. It later found the water and began to drink without assistance.

No. 81. On the first attempt it dipped its bill into the still water and drank from a point at which I could distinguish no special object in the water. While crouching by the dish drinking, as its bill was coming down slowly at the termination of a drinking reaction, it turned its head to the left, touched its bill gently to a bit of dry chick food lying within reach, and performed the drinking reaction upon it. It did not eat the grain.

No. 79. Pecked side of dish. Ran beak along edge of dish. Its beak (accidentally) slipped into the water. After this the chick began to drink. Frequently ran beak down the outside of the dish.

No. 73. Did not peck at dish nor find water. No. 74 was placed on the table with no. 73. No. 74 pecked five times at the edge of the dish, not touching the water, when no. 73 began to peck near the same place. The latter's bill slipped into the water and it began to drink energetically.

No. 76. I shook the water in its presence and it pecked into it. It began to drink and twitter. Pecked the edge of the dish. Ran its bill along the outside and inner edge of it.

c. *Discussion of results.*—Spalding,[1] commenting on the drinking of chicks, remarks: "It also appeared that, though thirsty, they did not recognize water by sight, ... and they had to some extent to learn to drink." Discussing the same instinct, Morgan [2] says: "The statement of fact (so far as my observations go) that I made was this: That the sight of still water evoked no instinctive response; but that the touch of water in the bill at once evoked the characteristic instinctive behavior." Mills [3] expresses his opinion thus: "It is not primarily so much the sight, but rather the touch of water . . . that in the very first instance leads to drinking."

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[1] Spalding, D. A.: *Loc. cit.*, p. 288.

[2] Morgan, C. L.: The habit of drinking in young birds. *Science*, N. S., 1896, vol. 3, p. 900.

[3] Mills, W.: The nature and development of animal intelligence. New York, 1898, p. 281.

On the basis of these and similar observations, it has been asserted that a chick swallows water instinctively, but must learn to drink by imitation or accident; that is to say, the drinking instinct requires supplementation. A passage from Baldwin [1] will illustrate: "In the case of the fowl's drinking, it is not the mere fact that drinking and eating may differ in the degree to which the performance is congenital; the reports seem to show that this varies in different fowl; but that instincts (in this case drinking) may be only half congenital, and may have to be supplemented by imitation, accident, intelligence, instruction, etc., in order to act, even when the actions are so necessary to life that the creature would certainly die if the function were not performed. That is the interesting point."

For the sake of clearness in the discussion of drinking, the parts of the drinking complex must be more sharply distinguished. There is (1) the approach to the object, elicited evidently by optical stimulation, (2) a sort of rhythmic movement of mandibles and throat, which brings the object within the mouth, and (3) the swallowing activity, which is evoked by stimuli resulting from the contact of water with the mouth, and which is marked by an elevating movement of the head and neck. We find an exactly parallel series upon analysis of the pecking reaction: (1) striking, (2) seizing, and (3) swallowing. Any full account of the drinking instinct must include the approach to the object as well as the subsequent manipulation.

No one, I think, will deny that the touch of water in the bill evokes reaction 3 of the above series. And we know that chicks may get this appropriate contact-stimulus indirectly by pecking. Furthermore, the drinking of one chick in the presence of another often stimulates this other to become active about the water and thereby leads to its drinking. That is, drinking usually does begin as the result of a contact stimulation mediated by the prior activity of the pecking and imitating instincts. But this at once suggests the further question, Are imitating and feeding necessary precursors to reaction 1 of the series, the movement of approach? The results of the foregoing experiments seem to show clearly that the drinking instinct is self-dependent in so far as its relation to these other instincts is

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[1] Baldwin, J. M.: Instinct. *Science*, N. S., 1896, vol. 3, p. 669.

concerned. When chicks, without having previously drunk, respond with the drinking reaction to the surface of smooth white note paper, the edge of white glazed kymograph paper, or the edge of a glass dish, all these objects must be supposed to have some quality or qualities, undoubtedly visual, which evoke the drinking reaction. Here are stimuli that call forth a first drinking reaction independently of other instincts. If further evidence were needed to substantiate the conclusion that the instinct is self-dependent, it is found in certain other observations. After the first actual drinking, the drinking response was made to a grain of food, a piece of black leather, a silver ornament, and, in the case of chicks other than those studied in the special experiment, to a line in some dust on a smooth surface, a white spot on the experiment table, the clean surface of black cardboard, and the polished surface of a table.

Thus the feeding and drinking instincts are more similar than writers have hitherto supposed. In the case of feeding, the fact seems to be that newly hatched chicks respond to a great variety of objects indifferently, and only later come to select those which are food from the rest; in the case of drinking, the observations show that, if the need be sufficiently urgent, a large variety of objects in like manner elicit the action, and apparently with a like result. The indiscriminate use of reaction 1 of the drinking instinct may bring the appropriate stimulus for reaction 3, without the co-operation of the pecking and imitative activities. The drinking instinct, therefore, does not "have to be supplemented by imitation, accident, intelligence, instruction, etc., in order to act."

Finally, is still water a sufficient stimulus for the act of drinking? I am by no means ready to say it is not. I regret that my experiments are not so complete on this point as they might have been. There is general agreement at present that chicks do not begin to drink in response to this optical stimulus. But deprive them of water for a sufficient length of time after hatching and perhaps the "sight of still water" will evoke this instinctive reaction. It is not improbable that the effective element or elements in the objects which have been observed to draw forth the reaction are common also to water.

C. Pecking

a. *Apparatus and method.*—A detailed and prolonged study of the pecking reaction was now attempted. The literature on this topic reveals the fact that the interest in the accuracy of this instinctive activity has been the central one. As suggested before, the accuracy of the reaction became the central interest also in the investigation that is reported in the following pages.

The apparatus used in these experiments was very simple. A table with a hard polished surface was set near a window where there was good light. To this table the chicks were each morning brought, one at a time, and permitted to eat in a natural way from the surface of a piece of black cardboard about 20 cm. wide and 25 cm. long. Carried daily to and from the experiment table, the chicks became so habituated to the transfer that the fear response did not enter in to mar the value of the results. From the first the chicks ate from my hand, and soon many of them energetically followed the hand from point to point, gathering up the bits of food as they were dropped. A little later many even gave the "food twitter" while in my hand on the way from the brooder to the table. But it may not be said with accuracy that the chicks became "habituated" to the operation, if at any age without previous trials they submitted, without signs of being disturbed, to the conditions of the experiment. As a fact, they did not thus submit. Animals that had not been used in the pecking tests nor been handled previously in any other experiment were brought to the table for a control test. They usually struggled when picked up and seemed so disturbed by the situation, when set on the table, that they would not eat at all. This was especially true if they had been allowed to live in the brooder unmolested for two or three weeks.

For the first tests, which were conducted on the second day, because of the physical weakness of the chicks and their indisposition to eat on the first day, slightly moistened bread was used, of such a consistency that it could be rolled between the fingers into food particles of suitable size. After the second day Cyphers Chick Food, slightly moist, replaced the bread pellets in the tests. This, which was the regular food of the chicks, is a mixture of whole wheat, Kaffir corn, cracked corn, millet, etc.

The food dish was kept out of the chicks' field of view and the bits of food to be pecked at were dropped by hand upon the cardboard in such a way that a particle would not be in motion when a chick pecked at it. From one to three grains only were dropped at a time. This proved advisable because the number of reactions elicited by more than three grains, considering also the possible variety and rapidity of the reactions, made it difficult at times to secure an accurate record.

In a letter published by Mills,[1] Bumpus[2] has suggested that the different aspects of the pecking reaction be distinguished. For these separate parts he proposed the terms seizure, mouthing or mulling, and deglutition. The terms used by Morgan[3] seem much more appropriate—striking, seizing, and swallowing. It is interesting to note that Spalding[4] distinguished these phases of the reaction and employed the same terms. These we have adopted, using in addition the term missing for failure to hit the object. As they appear in our records, these terms have the following definite meanings: (1) *Missing* denotes all cases of the pecking reaction in which the bill fails to hit the particular object supplied by the experimenter; (2) *striking*, those cases in which the bill hits the object without seizing it; (3) *seizing*, cases in which the object is grasped momentarily in the bill and then dropped; and (4) *swallowing* denotes what may be termed the perfect or complete reaction, the object being struck, seized, and swallowed in an errorless series or chain of movements. To facilitate the taking of records, the numerals 1, 2, 3, and 4 were used to represent *missed*, *struck*, *seized*, and *swallowed*, respectively. Note was taken, of course, of the reactions independently of the number of food particles pecked at, for a single grain might call forth a half dozen reactions in succession. For example, suppose one millet seed brought the result 1–2–3–4. In this case the chick first missed the grain, on the second reaction it struck it but did not get hold of it between its mandibles, on the third attempt it caught it in its bill but dropped it, and on the fourth, it struck, seized, and swallowed the grain without error.

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[1] Mills, W.: The nature and development of animal intelligence. New York, 1898, p. 296.

[2] Bumpus, H. C.: Instinct and education in birds. *Science*, N. S., 1896, vol. 4, p. 213.

[3] Morgan, C. L.: Habit and instinct. London and New York, 1896, p. 37

[4] Spalding, D. A.: *Loc. cit.*

For this, as well as for all other work, the chicks were marked by colored yarns tied on their legs. Each animal thus identified was assigned a number by which it was afterwards known and referred to.

b. Pecking artificially deferred.—The experiments of Spalding,[1] in which chicks on leaving the shell were blindfolded with little hoods or kept in a flannel bag, have attracted much attention from students of instinct. Spalding sought to ascertain the facts in regard to instinct. In his time the skeptical were holding "that all the supposed examples of instinct may be—for anything that has yet been observed to the contrary—nothing more than cases of rapid learning, imitation, or instruction." The hooding device was intended to permit the chicks to acquire "enough control over their muscles to enable them to give evidence as to their instinctive power." In other words, the aim was to test the activity of pecking when the factor of acquisition was eliminated. The conclusions of Spalding as to the accuracy of pecking, previously referred to, are based on the results of these tests.

In the similar tests that are reported below, the purpose was to measure the accuracy of the pecking response under circumstances like the above. Not much success was achieved by hooding the chicks. Other means of excluding the light were relied upon. After being tested the chicks were placed in the brooder with the rest of the flock.

On Dec. 10, 1907, chick no. 8, immediately upon hatching at 1:30 a. m., was blindfolded and transferred to the brooder where it was kept until 10 a. m., Dec. 12, under the curtained hover in a black-lined box at a temperature of 103° F. This box, open at the top, was enclosed in a green flannel bag. At 10 a. m., Dec. 12, the chick was brought carefully to the experiment table for a pecking test. Almost immediately it twice pecked the board upon which it stood. The particular stimulus to the reaction was not apparent. Then followed, in a series, seven reactions, in all of which the chick missed the pellet of bread (rolled as previously described) which elicited them. Seven more pecks at the same crumb followed without hitting it. Then the board on which it stood drew forth two more reactions, when the pecking was interrupted by an awk-

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[1] Spalding, D. A.: *Loc. cit.*, p. 282.

ward attempt to bite its wing. After a spell of violent chirping, it missed twice, and hit as often, a spot on the board upon which it stood, following which it lifted a foot to scratch its head and lost its balance. Then four pecks at a crumb missed, but a fifth was successful and the crumb was swallowed—the first perfect reaction. Thereupon came a series of 79 pecking reactions in no one of which a particle of food was hit, seized, and swallowed in a chain reflex. In many of these reactions the head wobbled from side to side as the bill moved slowly toward the object pecked at. On the twentieth reaction in this series of 79, the object was seized in the bill and apparently rejected by the chick. Prior to this, excluding the one perfect reaction, bits of food had been seized on two occasions but dropped through seeming lack of skill. Just preceding an interval occupied in preening the feathers of its wings, an interval which marked the end of the 79-reactions series, there occurred a group of five reactions, in three of which the object was struck and in the other two seized. It is but fair to state that many of the pecking reactions were not in the direction of food particles, there being something about the bare surface upon which the chick stood that drew the reactions forth. In the summary of the chick's record these reactions have been classified with the 1's. At this point it was incidentally noticed that the chick followed with both head and eyes a movement of the experimenter's hand. After the above mentioned preening diversion, twelve more pecking reactions ensued: seven 1's, one 2, and four 3's. Then the animal hesitated long enough to scratch its bill with its foot. The next nine reactions, of which three were 1's, five 2's, and one a 3, came out in straggling order, interrupted by gaping, pecking of toes, scratching the bill, and preening the feathers of the breast.

When tested by a moving object, a moist bit of bread swinging by a black silk thread, the chick's first impulse was manifestly toward it, but later it acted as if afraid. During these tests the chick appeared in no danger, except by accident, of stepping off the edge of the piece of cardboard upon which it was placed, when the cardboard was so arranged that the outer edge of it coincided with an edge of the experiment table. The animal could easily be pushed away from the edge but, when near the edge, *resisted strongly* if pushed toward it. This same behavior was noticed in other chicks. For example, no. 14, the day after it was hatched, when on the experiment table for the first time, was pushed toward the edge. It resisted by bracing its legs in front of itself and hurried back from the edge as soon as it was released.

The summarized record of no. 8 is as follows:—

1–1–1–1–1–1–1–1–1–1–1–1–1–1–1–1–1–1–1–1–2–2–1–1–1–1–4–1–1
2–1–1–1–1–1–1–1–1–2–2–3–1–2–1–1–3–3–1–1–1–1–1–1–1–1–1–1–
1–1–1–1–1–1–1–1–1–1–1–1–1–1–1–1–1–2–2–1–1–1–1–1–1–1–1–1–
1–1–1–1–1–1–1–1–1–1–2–1–1–1–2–2–2–3–2–2–3–1–1–3–1–1–1–1–1
–2–3–3–3–1–2–2–2–1–2–2–1–3.

Attention has been called to the fact that the chick pecked the cardboard at a place where no particular spot or grain was discerned by the experimenter. Not only that, but, like a child repeating da-da, it sometimes continued with a rapid succession of reactions at or near the same place. Twenty-five of the long series of 1's, immediately following the third 3 in the record above, represent such pecks at the bare card. They came out in three groups, first 2, then 18, and after an interval the other 5. To see a chick hammering in this way 18 times in rapid succession, and hard, too, at apparently "nothing," reminds one of the mere exercise of a function, and suggests what Baldwin has termed the circular reaction.

A comparison, in regard to accuracy, of no. 8's record, with the numerous records which will be presented later, will show that this chick was below the average efficiency in its first test. It is not unusual to find normally kept chicks that do not make a single swallowing reaction in the first twenty trials on their second day, and chicks sometimes fail at this age to seize a single grain in the same number of trials, but I have found only one in the regular tests that failed to strike at least one grain in the first twenty reactions. There were instances in these first tests in which the side of the chick's bill touched the side of the object as the bill slowly passed and hit the cardboard. These were recorded as 1's, here and elsewhere.

Naturally, after being kept 56.5 hours prior to the tests under the conditions previously described, the chick's down was ruffled and it lacked the general sleek appearance of its unconfined mates. Whether it was deficient in anything else but the results of practice, I cannot say. The confinement did not do it any permanent injury, it seems, for it continued in the pecking tests, lived to make a perfect record after an average number of trials in later black-blue color selection tests, and survived after that till it was killed and dissected for sex determination on March 14, 1908. Its record in the later pecking tests is submitted in table 1. This table shows the accuracy of its pecking during the nine days after Dec. 12, on the basis of twenty reactions a day.

TABLE 1

CHICK NO. 8. DEC. 13–21, 1907. PECKING

Date	13	14	16	17	18	19	20	21
Missed	2	1			2			
Struck	3	4	7		2	2	2	1
Seized	1	1		3	1			1
Swallowed	14	14	13	17	15	18	18	18

The record of this chick in its first test is not presented as typical, but is submitted to show how a chick may act under conditions like those set forth above.

Two other chicks, no. 7 and no. 14, of the same brood as no. 8, were enclosed at the same time in the dark-box with no. 8. These chicks were helped out of their shells just as they were hatching and transferred at once to the dark-box. They were not hooded, but even if they had been securely blindfolded, little would have been gained, for the light that reached the interior of the black-lined box was negligible in amount.

No. 7 was brought to the light for its tests at 11:05 a. m., Dec. 11, after 33 hours, 35 min. in the dark-box. My notes on its behavior are as follows: "Followed moving object (hand) with head. Pecked wood over edge of black cardboard. Wiped bill on board. Pecked three times at a pellet of bread moistened with milk. Missed it each time. Chick pushed bill slowly toward bread crumb on the black surface—a slow peck. Missed crumb, weak peck. Bit toes. Touched small white speck with bill. (The experimenter did not point at objects.) Rested under hand with its eyes closed. Missed a crumb twice. Missed another. Moved bill toward it slowly. Chick able to stand. Pecked at feet and lost balance. Bit wing twice. Pecked black cardboard. . . . Chick seemed cold and was returned to the brooder." The record of no. 7's pecking at food particles and spots on the card runs thus in its first test, as detailed above: 1–1–1–1–2–1–1–1. Table 2 shows the accuracy of its pecking from Dec. 13 to Dec. 26.

TABLE 2

CHICK NO. 7. DEC. 13–26, 1907. PECKING

Date	13	14	16	17	18	19	20	21	24	26
Missed					1					
Struck		7	5	2	3	1	7	1		2
Seized	3		3	1	2			1	1	1
Swallowed	17	13	12	17	14	19	13	18	19	17

Chick no. 14, as just stated, had been placed in the same enclosure with no. 7 at the same hour on the same date, and was kept there till 4:25 p. m., Dec. 11. After 38 hours and 55 min. thus enclosed, it was tested in the same way as no. 7. On the first pecking attempt it pushed its bill, mandibles closed, into a bread crumb. Then followed six pecks that missed. Attempted to scratch its head and lost its balance. Seemed weaker than the other chicks. Pecked toes and bare black cardboard; scratched bill. A second time it pushed its bill slowly into a bread crumb. Then followed a reaction in which it missed, etc. The summarized record for this test appears thus: 2–1–1–1–1–1–1–2–1–2–2–1–2–2–2–2–1–3–2–2–2–2–3–2–2–2. The accuracy of its later pecking, Dec. 13 to Dec. 26, is shown in the following table:

TABLE 3

CHICK NO. 14. DEC. 13–26, 1907. PECKING

Date	13	14	16	17	18	19	20	21	24	26
Missed					1					1
Struck	9	6	12	6	5			3	4	1
Seized	2	1		1			1	1	2	
Swallowed	9	13	8	13	14	20	19	16	14	18

A comparison of the records of these three chicks for Dec. 13 with the corresponding records of five others of the same age which were not subjected to confinement in darkness shows that there was no noteworthy difference in the development at this time. The averages of the three chicks on the above date were .7, 4, 2, and 13.3 for reactions 1, 2, 3, and 4, respectively, while the other five chicks averaged .8, 1.4, 4, and 13.8 for the same reactions, in a total of twenty reactions. On the other hand, the development of no. 8 on Dec. 12 was far behind that of any chick in the above group of five on the same date.

It looks very much as if (1) the development of the instinct was retarded by disuse, and (2) the retardation was quickly overcome with use. Several attempts to repeat these dark-box tests with other chicks failed. On these later occasions the plan was conceived of placing the dark-box inside the incubator just before the expiration of the period of incubation, depositing therein a few of the eggs, and allowing the prospective chicks to hatch and remain in the dark enclosure till needed. For some unforeseen reason the chicks did not appear.

We turn now to a more thorough investigation of the "congenital definiteness" of the pecking reaction, with a view to a quantitative determination of its course of development.

c. The natural development of the pecking reaction, with a collateral study of the effects of social influence. 1. Sources of error.—In addition to what has already been said of the method of taking records, the important sources of error might be mentioned. Investigators have noted the fact that the chick, if it misses the grain at all, usually comes within a hair's breadth of it. Hence, when the animal is working rapidly, it is sometimes difficult to determine whether the bill hits the grain or not. In the work herewith reported, a chick was credited with reaction 2 if there was any doubt between 1 and 2. In other words a 1 was recorded only when the miss was positively observed. The fact that more missing reactions seem to be recorded among the later results may be due rather to modification of the experimenter than to variation in the groups of chicks. I feel quite confident that I became a more efficient observer of the missing reactions as the work progressed.

Again, there are times when reactions 2 and 3 may be easily confounded. A grain seized simultaneously with the strike may almost immediately fly from the bill—like a cherry pit squeezed between the fingers. This reaction, properly 3, may be confused with the reaction where the grain is driven from its position by the mere impact of the bill. Still, as one becomes familiar with such cases, the difficulty of distinguishing them almost wholly vanishes.

Occasionally fewer than the regular number of reactions in the daily series are reported for a given date. In such cases the cause was usually the refusal of the chick to eat. This difficulty was soon obviated by carefully controlling the amount of food allowed the chicks, and compelling them to scratch for it in the litter. The objection also was thereby forestalled that many chicks under an improperly regulated food supply might react the required number of times but below their highest efficiency.

Not only did these difficulties threaten to affect the reliability of the results, but an additional reaction came in to complicate the record. When the food supply was improperly controlled, the chicks would quite often *reject* grains, that is, lift them from the ground with the bill and then either drop them or throw them some distance without attempt to recover. Forcible rejection is distinctly a reaction in addition to reaction 3. It involves control of the grain by the mandibles—sufficient, one should suppose, for manipulation without error prior to swallowing. If this be true, it is manifestly unfair to charge the chick with a degree of imperfection by recording reaction 2. Yet, one is not at liberty to credit it with reaction 4. A clear instance of rejection should simply not figure in the records. But this disturbing feature was practically eliminated when the chicks were confined in the brooder at night and were given the proper amount of food only after the morning tests. I say practically eliminated, because, even after taking the precaution mentioned, some chicks in time came to eat one kind of grain and not another. For example, I have found an occasional chick that discriminated in this fashion between millet seeds with the shell on and those without the shell, to say nothing of preferences for wheat as against corn, millet as against wheat, and the like. In such cases the chick was fed what it readily ate.

Another variation, which we may term switching of the bill, occasionally appeared. It is similar in character to the forcible-rejecting movement, and was observed in some very young chicks. It is executed while the food particle is held firmly between the mandibles. It is mentioned here rather as an additional type of reaction than as a source of error, for it did not noticeably affect the records.

I have so many times observed chicks, especially very young ones, peck where I could see nothing but bare wood or cardboard, that I am compelled to believe that the stimulus to the pecking reaction need not be some object of a size convenient for eating. In line with this consideration is the further fact that the bill of the chick is not only a feeding but a *testing* organ. If anywhere, the "oral sense" has its organ here. The chick often digs in the litter with its bill when the reaction is distinctly not the pecking reaction. While trying to escape from the reaction box of a discrimination apparatus in a dark-room, chicks often approached a sheet of clean, smooth, lighted opal glass and pecked it. In the same box they pecked the black walls and especially the black cardboard closing the exit, when they happened to enter the wrong side and found their egress barred. But, except where specially noted, no missing reactions were recorded when no object to be pecked was supplied.

Besides the occasional variation in the missing reaction in which the animal pecked the bare cardboard when no other stimulus seemed to be present, there were two other reactions that were easily distinguishable from each other and from the regular missing reaction, but which were, nevertheless, put down in the records as reaction 1. These variations in the missing reaction were altogether so few in number, compared with the many hundreds of reactions recorded, that the averages are not materially affected by the classification of them with reaction 1. I refer here (1) to cases in which the chick pecked in the direction of the grain but did not reach it, and (2) to cases in which the bill struck the cardboard almost exactly midway between two grains. Of the first of these I have records of thirteen instances; of the second, thirty-six instances. Case one needs no special comment. The bill each time was going in the right direction, but the innervation seemed to be insufficient. Case two is, if anything, more interesting. When the typical instance of it occurred, the grains were usually about 1 cm. apart, of about equal size, and the line connecting the two ran about normal to the direction in which the chick was oriented, the chick standing directly before them. One could say with little certainty that this was an instance of pure missing. We have already agreed with other observers that the chick from the first rarely missed by more than a hair's breadth an object pecked at. But here was a case where a chick from one to four weeks old missed a grain by 4 to 6 mm. Not only that, but I have five records where in a situation like that described above the chicks pecked twice in succession between the two grains, and one record in which there were four such successive pecks. There are two other observations that help to explain this reaction. On Dec. 23, no. 70 and on Dec. 29, no. 87, were working rapidly in their regular pecking tests. The pecking activity was interrupted momentarily while the bill poised in air above and about midway between two grains approximately 1 cm. apart. On Dec. 24, no. 76 was on the experiment table going through its pecking test. In the presence of two grains lying as those in the preceding cases, its pecking reaction started in the direction of one of the grains and was completed by a perfect reaction upon the other. I concluded, therefore, that case two was not an ordinary instance of missing, but that the reaction in response to one of the stimuli exerted an inhibitory effect on a reaction in response to the other. The poising of the bill in air, the zigzagging first toward one grain and then toward the other during a continuous forward movement of the bill, and the striking of the cardboard fairly between the grains, have at bottom, I believe, the above common principle of explanation.

In view of the recent important work of Hess and that of Katz and Révész, I feel impelled to report some activities of the chicks in the dark-room. The assumption that hungry chicks do eat when they can see the food is ordinarily true, but the second assumption, that chicks do not eat when they cannot see it, surely is not borne out by observations of the behavior of chicks in the dark-room. During some studies of individually acquired reactions, the chicks were placed in a dark-basket in the dark-room for ten minutes prior to the regular daily tests. The basket which was used for this adaptation work was a willow waste-paper basket lined with black cloth and covered with the same material. Food was placed in the bottom of the basket before the basket and chicks were taken into the dark-room. The animals were thus allowed to eat in the basket a short time before the period of darkness adaptation began. Again and again, after the basket was taken into the dark-room, the door closed, all lights turned off, and the basket covered, the animals continued to eat the chick food in the bottom of the basket. I have also gone out of the dark-room and returned at the end of the ten minute period to find the chicks eating. The darkness was so nearly absolute in the room that I could not see the dark basket while sitting in a chair nearby. The pecking sounds, as the bills of the chicks struck the bottom of the basket, could be distinctly heard. The usual mouthing noise made by the mandibles could be heard also when one held his ear near the side of the basket. And when I put my hand into the basket, I could feel the heads of the chicks rising and falling in the pecking reaction.

Before formulating a conclusion let me describe the behavior of no. 71. This chick, in the pecking reaction tests, made the following record from its second to its eleventh day, and then ceased to peck at the grains when brought to the experiment table:

TABLE 4

CHICK NO. 71. DEC. 3–12, 1908. PECKING

Date.........	3	4	5	6	7	8	9	10	11	12
Missed........	13	2	3	2	2			2		
Struck........	6	25	32	26	22	8	17	6	12	43
Seized........		9	5	3	2	3	3	3	1	1
Swallowed....	1	14	10	19	24	39	30	39	37	6

On Dec. 13 it staggered about in a peculiar way, but did not eat. It would walk directly off the table if not prevented. When tested with water in a watch glass, it drank when the water was held to its bill, but after the dish was moved three or four centimeters away, it dipped its bill about where the dish had been. Such indications as these convinced me that the animal was blind. For a day or two it was fed by having grain introduced into its bill. Then it was placed in a large dish partly filled with chick food, and on Dec. 16 it began to scratch and eat. For many days thereafter it was regularly placed in the food dish at the feeding hour and procured its meal without assistance. When I entered the room and the rest of the flock ran toward the wires of the cage, no. 71 was often seen approaching, running into obstacles in its path, bobbing up and down in a peculiar variation of the pecking movement, and taking time intermittently to scratch in the litter. In this fashion it lived until it was found dead one morning in the drinking vessel. The behavior of the chicks in the dark basket, as well as that of this supposedly blind chick, furnish quite clear evidence in refutation of the assumption that chicks do not peck at or eat food when they cannot see it.

But happily the reaction in which we are most interested, reaction 4, can be distinguished from all the others with practically no liability of error. Even supposing a few 1's, 2's and 3's were to become interchanged, the use of reaction 4 as a quantitative index of development would not be invalidated. The main interest is to discover the ratio of the number of perfect reactions to the whole number of legitimate pecking reactions in the daily series, and to plot the variation of this ratio. The necessary data for this can be gathered with precision.

2. Data and their significance. The first animals tested were numbers 1 to 6, inclusive, which will be referred to as Group A. They were hatched on Dec. 2, 1907. Their pecking records cover the period from Dec. 3 to 30, inclusive. Curve IV-A, fig. 1, shows the development of reaction 4 for the group. For the calculations only those totals were used in which every chick had a complete series of twenty reactions. Hence a very interesting part of this curve, namely, the detail for the third, fourth, and fifth days, is lacking. The blanks are due to the failure of some of the chicks on each of these days to respond to the food. Improper regulation of the food supply was the cause. Nevertheless, the results were such as to encourage a continuance of the experiment. Barring the vital omissions at

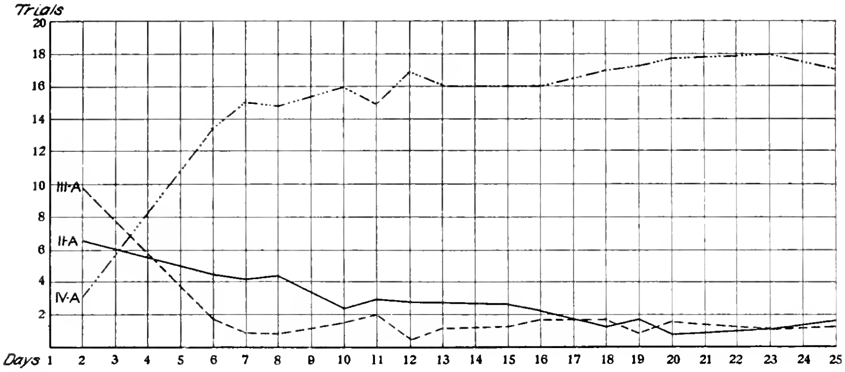

FIGURE 1—The development of the pecking instinct in the chicks of Group A, numbers 1 to 6, inclusive. Distances along axis of abscissae represent days after hatching; distances along axis of ordinates, the number of a given kind of reaction in a series of twenty pecking reactions. Curve II-A shows the rate of decrease in the daily number of reaction 2; Curve III-A, the same for reaction 3; Curve IV-A shows the improvement in accuracy of reaction 4 for the group.

the most critical stage of development, the curve on the whole not only indicates that the co-ordination of movements that constitute reaction 4 has a certain period of development, but it roughly marks out that course. The rate of improvement is not uniform from day to day, but is very much more rapid during the first few days than later.

Before discussing reactions 1, 2, and 3 of this group, let us be clear as to the meaning of these three reactions and their relation to 4. In the first place, it should be noticed that the records under 1, 2, and 3 may be regarded as error records. That is, under 1 are listed the errors of striking, under 2 the errors of seizing, and under 3 the errors of swallowing, if swallowing here may designate the manipulation of the object after it is seized. Although for convenience the term swallowing has been applied to reaction 4, it is clear that reaction 4 is really striking-plus-seizing-plus-swallowing in an errorless train.

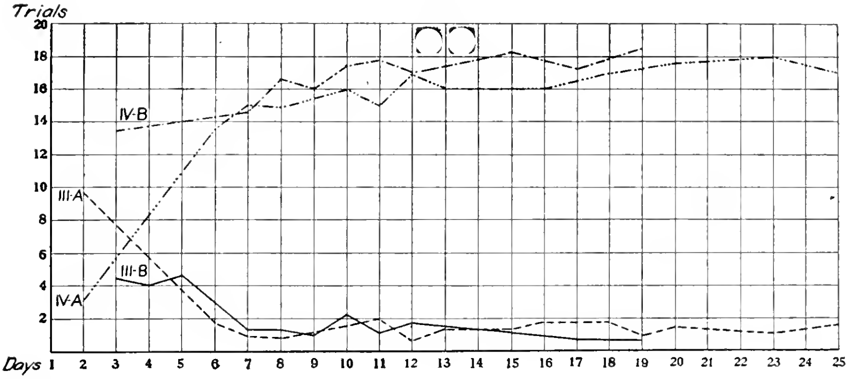

FIGURE 2—A comparison of curves of development of the pecking instinct to show the possible effect of social influence. Distances along axis of abscissae represent days of age; distances along axis of ordinates, the number of a given kind of reaction in a daily series of twenty pecking reactions. Curve IV-A shows the improvement in accuracy of reaction 4, Group A; Curve IV-B, the improvement in accuracy of the same reaction for Group B. Curve III-A shows the course of reaction 3, Group A; Curve III-B, the course of reaction 3, Group B.

There are always three regular chances of error, then, at the beginning of any pecking reaction. I shall aim to show the rate of decrease of each kind of error separately, and, correlatively, the improvement in the co-ordination of the three reactions.

Curve II-A, fig. 1, shows the course of reaction 2, and Curve III-A of reaction 3, for the chicks of Group A. The errors of swallowing tend to vanish more rapidly and more completely than those of seizing. The data on reaction 1 are too meager to justify consideration here.

Curve IV-B, fig. 2, is the curve of development of reaction 4 in Group B, chicks nos. 9 to 13, inclusive. These chicks were hatched just eight days after those of Group A. The two groups were segregated until chicks nos. 9 to 13 were beginning their seventh day, and then were allowed to mingle. The pecking tests were made throughout in the regular way, both groups being treated as nearly alike as possible. Curves IV-A and IV-B, fig. 2, are matched for corresponding days in the lives of the chicks—that is, for corresponding ages, and not for the dates on which the records were made. Although it was not part of the plan, when the experiment was conceived, to study social influence, the higher curve for Group B indicates that possibly association with the older chicks had the effect of facilitating improvement in the younger ones, and suggests a method of measuring this influence. A glance at Curve IV-A, fig. 2, shows that the efficiency of the chicks of Group A on their fifteenth day, when those of Group B joined them, was numerically 16 on a scale of 20, and that the efficiency of Group B at the same time, the seventh day for the latter, was 14.6. But the difference in the curves may be due to unsuspected irregularities in method, or to variability in the chicks. It seemed hazardous, therefore, to rest such an important conclusion on one test, and a repetition of the experiment was planned and executed.

Curves IV-A and IV-B indicate, then, that there is a very rapid improvement in the integration of the components of the complete reaction within the first three days, followed by a slower but fairly steady improvement after that for some time. It is interesting to note just how nearly the development approximates perfection,—18.4 on a scale of 20 representing the degree of approximation at the highest point.

Curves III-A and III-B, fig. 2, trace the course of reaction 3 for Groups A and B respectively.

The study of the pecking reaction was resumed almost a year later with chicks nos. 57 to 65, inclusive, which we shall style Group C. These chicks were hatched Oct. 25, 1908. With a desire to continue the study of the effect of association of younger with older chicks, eggs were set with the intention of having another brood eight days after Group C, so that the difference between the ages should correspond exactly with the difference in age between the chicks of Groups A and B. But the plan was frustrated to this extent, that the chicks of Group C came out of the eggs one day before the date on which they were scheduled to arrive, and a sudden change of temperature so chilled the second setting that only two healthy chicks arrived to constitute Group D. It was decided to make the most of the opportunity, however, and records were taken of the pecking of the nine chicks in one group and the two in the other. When the members of Group D were beginning their eighth day, the cages of the two groups were thrown together and the chicks allowed to mingle. For three days, beginning with this day, 100 pecking reactions per day were recorded for each chick in both groups; and, continuing for a week after this, 50 reactions a day were taken. It was thought that by this means the influence, if any, of one group upon the other might be more easily and accurately detected. The results are plotted in fig. 3, and the curves matched for corresponding ages as before. The chicks of Group C had a pecking efficiency of 17.1 at the beginning of their seventeenth day when those of Group D joined

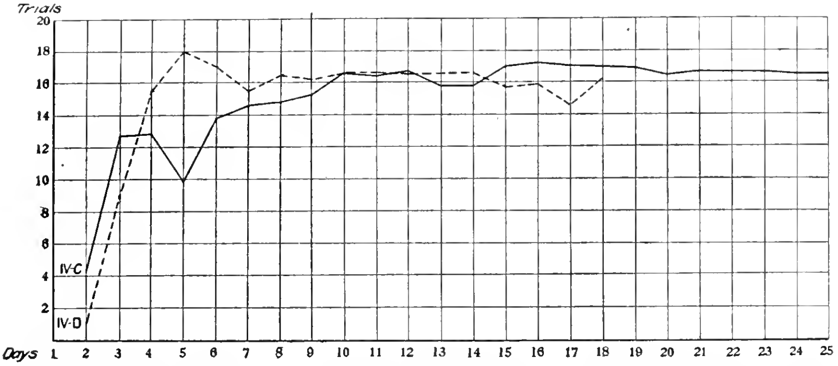

FIGURE 3—A comparison of curves of development of the pecking instinct to show the possible effect of social influence. Distances along axis of abscissae represent days of age; distances along axis of ordinates, the number of "perfect" reactions in a daily series of twenty pecking reactions. Curve IV-C shows the improvement in accuracy of pecking in Group C; Curve IV-D, the improvement in Group D.

them. On this same date, when the individuals of Group D were eight days old, they had an efficiency of 16.5. Very little change occurred in the accuracy of pecking of Group D after the commingling, nor indeed could a heightening of their curve after the eighth day be well expected, for they had by that time practically attained the maximum.

Nothing very conclusive having accrued here, it was deemed desirable to arrange a test so that younger chicks could be enclosed with older ones immediately after hatching. Thus, it was thought, the influence might be measured, if the effect of social influence be such as to affect the rate of improvement of the pecking reaction. The most active opponents of inferential, ideational, or voluntary imitation seem agreed that the presence of one animal, under the proper conditions, may have the effect of stimulating another of its kind to greater activity. There is no difficulty whatever in establishing this fact. My observations have proved it to my satisfaction many times. It may be that the change in the mode of functioning of the organism due to the presence of others is in the direction of increasing the intensity and rapidity of the reactions, without increasing their rate of improvement in accuracy. Such a variation would have selective value, inasmuch as the animal would get more food in a given time, even though the pecking were no more accurate. But such a speculation does no more for us than open up wider vistas of experimental research in which exact quantitative studies can no doubt be made.

Mention has previously been made of the rapidity with which reaction 4 improves. The curves all show very rapid improvement on the second day. To make a special measurement of the rate of this change, the pecking of six chicks in Group C was tested twice on the second day. The first record was taken from 10–12 a. m. and the second from 2–4 p. m. In the interim the chicks were committed to the brooder and allowed the freedom of the litter of the cage for the first time. From forenoon to afternoon, within the limits just stated, the improvement was 82%, assuming, as we have, that the development of reaction 4 is an index of the improvement of the chicks' pecking efficiency.

The sudden drop in Curve IV-C, fig. 3, on the fifth day is due mostly to the unusually poor records of no. 57 and no. 58

on that date. Twelve of no. 58's striking reactions were at one particle. It followed this up, hitting it time after time until the grain was knocked off the table.

The final test of social influence in its relation to pecking was made on two comparable groups of six chicks each, which will be referred to as Group E and Group F. The chicks of Group E were hatched on Dec. 2, 1908; those of Group F on Dec. 12, 1908. The members of Group F, thus ten days younger, were transferred from the incubator to the cages and brooder occupied by Group E. Records were taken as before. Still greater precaution was observed as to food supply. The food was not unnecessarily stinted, however. The chicks chirped loudly when I came into the room in the morning and crowded toward me when I approached the side of the brooder. In the tests they picked up the grains very energetically.

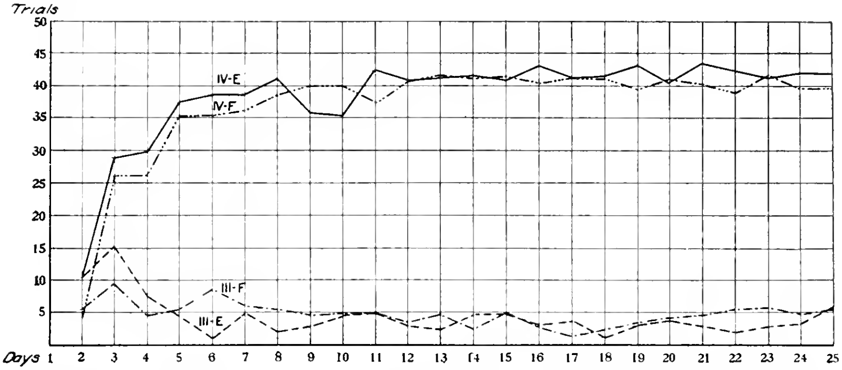

FIGURE 4—A comparison of curves of development of the pecking instinct to show the possible effect of social influence. Distances along axis of abscissae represent days of age; distances along axis of ordinates, the number of a given type of reaction in a daily series of fifty pecking reactions. Curves III-E and III-F show respectively the rate of decrease in the number of reaction 3 for Groups E and F; Curves IV-E and IV-F show the improvement in accuracy of reaction 4 for the same groups.

The records for Group E are given in full in table 5, the summary for Group F in table 6. The curves for reactions 3 and 4 of both groups are plotted in fig. 4; for reactions 1 and 2 in fig. 5. The efficiency of the pecking of the older group is represented numerically by 42.2 on a scale of 50 on their eleventh day, when the chicks of Group F entered the cage. The twelve chicks were confined in the brooder each evening together, were

TABLE 5

Pecking of Chicks nos. 69, 70, 72, 73, 76, and 79, Group E. Dec. 3–26, 1908

Chicks	Date	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
No. 69	Missed...	8		1	2		1				1	3	4				1			2	2		3		
	Struck...	7	5	8	6	7	4	2	8	3	5	7	7	4	5	5	6	9	2	5	2	4	5	5	4
	Seized....	1	4	5	1	4	1	3	4	4	2	2	1	3	5	2	4	1	2	3	3		1	3	6
	Swallowed	4	41	36	41	39	44	45	38	43	42	38	38	43	40	43	39	40	46	40	43	46	41	42	40
No. 70	Missed...	2											1	1	1		1	4		1	2	1			
	Struck...	10	4	7	7	5	5	4	4	8	2	6	6	5	3	4	3	8	7	3	3	5	9	4	1
	Seized....	8	32	14	4	3	6	2	3	5	6	7	3	8	6	5	8		3	4	4	4	1	3	7
	Swallowed		14	29	39	42	39	44	43	37	42	37	40	36	40	41	38	38	40	42	41	40	40	43	42
No. 72	Missed...	1										1													
	Struck...	4	3	9	1	4	1		2			2	3	2	2	1	3	2	4	2	1	2	1	1	2
	Seized....	2	10	3	1		7		4	4	3	4	2	5	2	5		2	2	5			2		3
	Swallowed	13	37	38	48	46	42	50	44	46	47	43	45	43	46	44	47	46	44	43	49	48	47	49	45
No. 73	Missed...	7	1	2			2			1				1		3	1	1			1	1			
	Struck...	7	7	31	18	14	10	17	8	15	8	8	7	1	8	3	4	8	3	13	8	6	6	5	2
	Seized....	6	17	6	5		4	1	2	5	8	2	3	6	9	3	4	3	5	3	3	3	6	8	11
	Swallowed		25	11	27	36	34	32	40	29	34	40	40	42	33	41	41	38	42	34	38	40	38	37	37
No. 76	Missed...	4	4			1																			
	Struck...	3	12	12	8	11	3	4	5	4	1	7	7	6	3	2	3	3	5	4	3	5	4	10	1
	Seized....	5	21	14	10	1	7	1	3	7	3	1		4	3	4	4	2	3	5	4	3	4	4	6
	Swallowed	8	13	24	32	37	40	45	42	39	46	42	43	39	44	44	43	45	42	41	43	42	42	36	43
No. 79	Missed..	4				1	5		6									1							
	Struck...	13	3	7	10	16	11	12	31	31	2	3	1	2	6	3	7	4	3	5	1	10	7	4	4
	Seized....	3	7	4	3	3	3	6	4		6	1	6		2	1	2	1	3	3	3	2	2	1	3
	Swallowed		40	39	37	30	31	32	9	19	42	46	43	48	42	46	41	44	44	42	46	38	41	45	43
	Age	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25

Totals 1......	(65)	5	3	2	2	8		6	1	1	4	5	2	1	3	3	6		3	5	2	3		
2......	(110)	34	74	50	57	34	39	58	61	18	33	31	20	27	18	26	34	24	32	18	32	32	29	14
3......	(62)	91	46	24	11	28	13	20	25	28	17	15	26	27	20	22	9	18	23	17	12	16	19	36
4......	(62)	170	177	224	230	230	248	216	213	253	246	249	251	245	259	249	251	258	242	260	254	249	252	250
Averages 1...	10.8	.8	.5	.3	.3	1.3		1.	.2	.2	.7	.8	.3	.2	.5	.5	1.		.5	.8	.3	.5		
2...	18.3	5.7	12.3	8.3	9.5	5.7	6.5	9.7	10.2	3.	5.5	5.2	3.3	4.5	3.	4.3	5.7	4.	5.3	3.	5.3	5.3	4.8	2.3
3...	10.3	15.2	7.7	4.	1.8	4.7	2.2	3.3	4.2	4.7	2.8	2.5	4.3	4.5	3.3	3.7	1.5	3.	3.8	2.8	2.	2.7	3.2	6.
4...	10.3	28.3	29.5	37.3	38.3	38.3	41.3	36.	35.5	42.2	41.	41.5	41.8	40.8	43.2	41.5	41.8	43.	40.3	43.3	42.3	41.5	42.	41.7

TABLE 6

Average Daily Number of Each Kind of Pecking Reaction for the Six Chicks of Group F

Age	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Missed...........	20.	1.5	.3	.2	.2	.2	.7	.3	0.	1.	.2	.5	.7	.3	.2	0.	1.	.2	.7	0.	.5	.5	.3	.3
Struck...........	20.3	12.7	18.3	9.2	6.7	7.3	5.8	5.2	5.2	7.	5.5	3.7	5.5	3.5	6.2	7.3	5.3	7.	4.5	5.	5.8	2.3	5.7	5.2
Seized...........	5.3	9.	4.5	5.2	8.	6.3	5.2	4.5	4.8	4.7	3.5	4.2	2.7	4.7	3.2	1.2	2.2	3.2	4.	4.5	5.2	5.3	4.8	5.2
Swallowed........	4.2	26.7	26.8	35.5	35.2	36.3	38.2	40.	40.	37.3	40.8	41.7	41.2	41.5	40.5	41.5	41.3	39.7	40.8	40.5	38.5	41.9	39.2	39.3

given their tests at the same period in the morning, and of course were fed together in the same litter, both groups being compelled to scratch for their food. Yet the similarity of the curves for the first eight days, when modification progresses most rapidly, is conspicuous, the curve for the younger brood running slightly lower. These young chicks, in spite of the examples of more accurate pecking furnished them by the behavior of the chicks of Group E, began less accurately than their elders, remained behind them by about the same margin during the critical period of development, and hardly equalled them while the experiment continued.

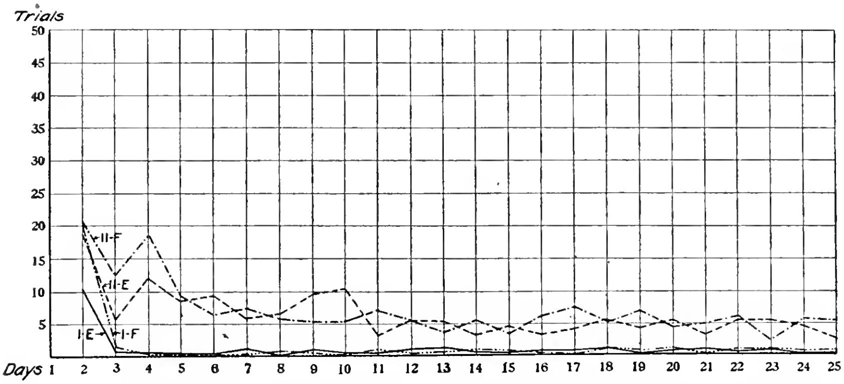

FIGURE 5—A comparison of the curves of development of the pecking instinct to show the possible effect of social influence. Distances along axis of abscissae represent days of age; distances along axis of ordinates, the number of a given type of reaction in a daily series of fifty reactions. Curves I-E and I-F show the rate of decrease in the number of reaction 1 for Groups E and F, respectively; Curves II-E and II-F, the rate of decrease in the number of reaction 2 for the same groups.

A feature worthy of notice is the fact that development of reaction 4 in both groups seemed to halt on the third day, with very rapid improvement preceding and following. A search for the cause of this retardation of development in the chain of actions is interesting. A detailed examination of the relations of Curves I, II, III, and IV for both groups brings out the following points:

1st day, the course of development is unknown;

2nd day, striking and seizing improve rapidly, while swallowing (in the restricted sense) declines considerably in effectiveness;

3rd day, swallowing improves rapidly, striking improves slightly, and seizing suffers a reversal of form.

In other words, from the beginning of the second day the accuracy of striking improves uninterruptedly, the accuracy of swallowing declines temporarily on the second day, and that of seizing temporarily on the third day. It is evident that the rate of improvement of reaction 4 depends upon the rate of decrease of the total number of errors in these reaction types. In neither Group E nor Group F was improvement in all three types of reaction uninterrupted. The retardation of reaction 4 on the third day is due specifically to a decline in the accuracy of seizing on that day.

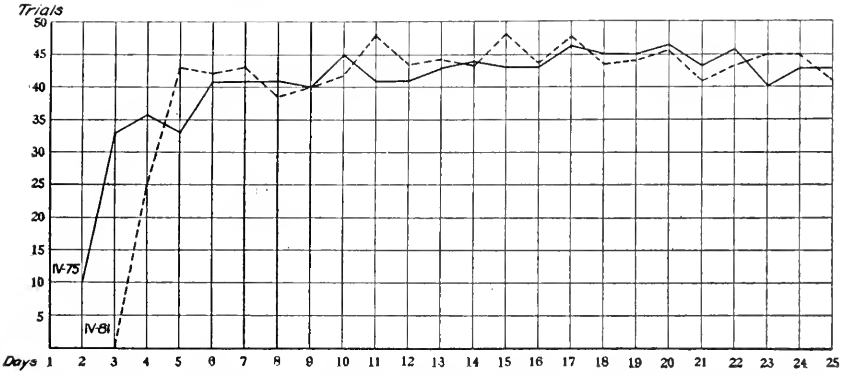

FIGURE 6—Curves showing the rate of improvement in pecking accuracy of two chicks kept in isolation. Distances along axis of abscissae represent days; distances along axis of ordinates, the number of perfect reactions in the daily series of pecking reactions.

In regard to the tests for social influence, the objection can be made that social influence, if it affect the accuracy of reaction at all, may work as well between members of the same group as between members of different groups. The objection has force. As a control test, chicks nos. 75, 80, and 81 were kept in individual apartments and tested. The results are exhibited in fig. 6. The record of no. 80 is omitted because valueless. This chick soon became physically unfit. No. 75, although it did not thrive under the conditions, made a good pecking record. No. 81 not only pecked with unusual accuracy but was lively and vigorous after the first few days. The curves do not furnish convincing evidence in support of the view that social influence accelerates improvement in the accuracy of the reaction studied.

The curve for no. 81 clearly suggests retardation of development—a very interesting fact, if due to the isolation. At first this animal seemed quite indifferent to food. Besides, its toes were bent under in such a way that it looked crippled. In a few days, however, neither of these failings was observable. They may indicate that the chick was slow in the process of unfoldment in more respects than in pecking. It would hardly be fair, for example, to attribute the slow expansion of the toes to the isolation. No. 81 turned out to be a fine animal. The rapidity with which the components of reaction 4 became integrated, once the process set in, is instructive. The maximum of accuracy attained, as well as the high average maintained, mark the nicety of adjustment in no. 81's pecking mechanism.

If chicks that are isolated peck with a normal degree of accuracy within the natural time limit, and chicks stimulated by the presence of others much more efficient than themselves fail to show a supernormal rate of improvement, one has good grounds for believing that the social influence, whatever else its effect, does not appreciably modify the natural course of development of the pecking concatenation.

In fig. 7 are presented the curves of development of the pecking reaction, based on the averages obtained from the records of the twenty-one chicks in Groups C, E, and F during their first twenty-four days. The data for these curves are given in table 7. Curves I, II, and III, standing for reaction 1, 2, and 3, respectively, represent, as explained before, the distribution of errors. Curve IV represents reaction 4. The sum of the heights of the error curves above the base line on any given day will equal the distance of Curve IV below its limit for the same day.

"In nearly all cases, as one might expect," says Morgan,[1] "the simple process of striking is more accurate than the more complicated process of striking and seizing; and this, again, than the yet more elaborate process of striking, seizing, and swallowing." From the data in table 7 it is an easy matter not only to substantiate this assertion, but to show the quanti-

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[1] Morgan, C. L.: Habit and instinct. London and New York, 1896, p. 37.

TABLE 7

PECKING AVERAGES FOR 21 CHICKS FROM THE DAILY TOTALS FOR REACTIONS 1, 2, 3, AND 4 OF GROUPS C, E, AND F

Age	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
REACTION 1																								
Group C.....	160	37	22		2				7	7	12	2	7	12		1	1	2	2	3		2	5	1
" E.....	65	5	3	2	2	8		6	1	1	4	5	2	1	3	3	6		3	5	2	3		
" F.....	120	9	2	1	1	1	4	2		6	1	3	4	2	1		6	1	4		3	3	2	2
Totals...	345	51	27	3	5	9	4	8	8	14	17	10	13	15	4	4	13	3	9	8	5	8	7	3
Averages.	16.43	2.43	1.28	.14	.24	.43	.19	.38	.38	.67	.81	.48	.62	.71	.19	.19	.62	.14	.43	.38	.42	.38	.33	.14
REACTION 2																								
Group C.....	115	25	35	162	95	110	115	92	65	60	40	67	82	27	47	46	58	61	68	51		67	69	70
" E.....	110	34	74	50	57	34	39	58	61	18	33	31	20	27	18	26	34	24	32	18	32	32	29	14
" F.....	122	76	110	55	40	44	35	31	31	42	33	22	33	21	37	44	32	42	27	30	35	14	34	31
Totals...	347	135	219	267	192	188	189	181	157	120	106	120	135	75	102	116	124	127	127	99	67	113	132	115
Averages.	16.52	6.43	10.43	12.71	9.14	8.95	9.	8.62	7.48	5.71	5.05	5.71	6.43	3.57	4.86	5.52	5.90	6.05	6.05	4.71	5.58	5.38	6.29	5.48
REACTION 3																								
Group C.....	80	102	105	65	40	17	10	15	7	17	22	25	5	25	10	17	8	9	11	14		5	9	11
" E.....	62	91	46	24	11	28	13	20	25	28	17	15	26	27	20	22	9	18	23	17	12	16	19	36
" F.....	32	54	27	31	48	37	31	27	29	28	21	25	16	28	19	7	13	19	24	27	31	32	29	31
Totals...	174	247	178	120	99	82	54	62	61	73	60	65	47	80	49	46	30	46	58	58	43	53	57	78
Averages.	8.29	11.76	8.48	5.71	4.71	3.90	2.57	2.95	2.90	3.48	2.86	3.10	2.24	3.81	2.33	2.19	1.48	2.19	2.76	2.76	3.58	2.52	2.71	3.71
REACTION 4																								
Group C.....	95	285	287	222	312	322	325	342	370	365	375	355	355	385	392	385	381	377	369	382		376	367	368
" E.....	62	170	177	224	230	230	248	216	213	253	246	249	251	245	259	249	251	258	242	260	254	249	252	250
" F.....	25	160	161	213	211	218	229	240	240	224	245	250	247	249	243	249	248	238	245	243	231	251	235	236
Totals...	182	615	625	659	753	770	802	798	823	842	866	854	853	879	894	883	880	873	856	885	485	876	854	854
Averages.	8.67	29.29	29.76	31.38	35.86	36.67	38.19	38.00	39.19	40.10	41.24	40.67	40.62	41.86	42.57	42.05	41.90	41.57	40.76	42.14	40.42	41.71	40.67	40.67

tative relations involved. E.g., on the second day, out of fifty trials the object was struck, on an average, 33.48 times on the first attempt. Of this number only 16.96 included seizing; and of the latter only 8.67 were reactions in which the object was struck, seized, and swallowed. As the chicks advanced in age, each of these sets of figures approximated the same limit, but naturally they preserved the original order as to size, for with each additional reaction in the series there was an added source of error.

Reverting to the earlier consideration that Curves I, II, and III may be regarded as error curves, an examination of these curves shows that the improvement of pecking accuracy is retarded more by failures in seizing than by failures in swallowing; and more by failures in swallowing than by failures in striking. After the third day, the difficulty of seizure remains greater than that of the other two reactions combined. The striking reaction improves in accuracy rapidly and without relapse, closely approximating perfection by the fifth day—a degree of accuracy that might easily inspire belief in the perfection of instinct, for, indeed, this is the reaction which has no doubt been central in the earlier discussions when accuracy has come into question.

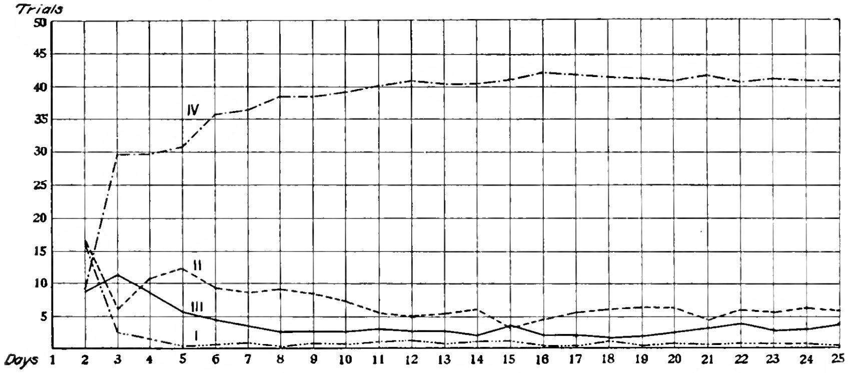

FIGURE 7—Curves of development of the pecking instinct, based on the averages obtained from the records of twenty-one chicks. Data in table 7. Distances along axis of abscissae represent days of age; distances along axis of ordinates, the number of occurrences of a given type of reaction in a daily series of fifty pecking reactions. Curves I, II, and III trace the course of reactions 1, 2, and 3, respectively. Curve IV shows the average improvement in accuracy of reaction 4.

Of course these averages hide the unusual performances of individuals. Chick no. 72, for instance, missed only once out of fifty reactions on its second day, on the fifth day it struck, seized, and swallowed forty-eight grains in fifty trials, and on the eighth day devoured every one of the fifty without a slip. The complete record of this animal is given in table 5. A comparison of its record with that of no. 70 brings out nicely the point of individual differences in accuracy. No. 72 developed more rapidly than no. 70, and also attained a much higher average degree of efficiency. The records of both chicks are consistent throughout. They bespeak a more finely adjusted mechanism in the one case than in the other. If we were seeking points of difference instead of identity in this investigation, we should dwell more at length on variations in other respects. Chicks, as one might expect, differ definitely and consistently from day to day in the accuracy of their reactions, in the rapidity of their movements, in their food preferences, and the like, much as men do.

To return to fig. 7. The curve representing the course of development of the complete co-ordination, Curve IV, reaches its highest elevation during the twenty-four days at 42.5 on a scale of 50. Each of these curves is intended to represent an aspect of the pecking of the chicks under the conditions described. Whether or not the reactions in the litter were more accurate than those on the harder cardboard, I cannot say, not having made any measurements. To be sure, the long periods of practice were spent in pecking under conditions quite different from those that obtained in the tests.

It has been the aim of this investigation to discover the meaning that should attach to such expressions as the accuracy, the perfection, or the congenital definiteness of the instinctive action that has been generally considered one of the most perfect, namely, the pecking reaction of chicks. Morgan and Thorndike are correct in asserting that this reaction is imperfect at birth—not " very nearly " perfect as Morgan thinks, but very imperfect. But Thorndike [1] doubts the *fact* of improvement. "As a matter of fact," he writes, " the pecking reaction may be as perfect at birth as it is after 10 or 12 days' experience." I shall have to

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[1] Thorndike, E. L.: The instinctive reaction of young chicks. *Psych. Rev.*, 1899, vol. VI, p. 285.

side with Morgan here and insist that the pecking reaction improves in accuracy after birth. Whether, now, this is a case of perfecting through habit, involves a still further problem, that of the relation of habit to the instinct. One sometimes speaks of the *modifiability* of an instinctive action like that of pecking, but wherever this term has been employed in this paper in connection with instinct no more has been implied than the objective fact of improvement in accuracy, an increasingly successful adjustment of parts in a more comprehensive function. The problem still remains, Is this development dependent upon practice, or is it the natural functional correlate of structural maturation independent of practice? Swallows are reported to be able to fly without previous practice. If the pecking of chicks could be successfully inhibited for a week's time without doing violence to the normal physical condition of the animals, would the accuracy of the reactions at the end of that time average 36.67 on a scale of 50, the average for our lot of twenty-one? There is evidence in support of the belief that such chicks would very quickly be pecking with average efficiency, without anything like the amount of practice chicks would have had by this time when growing naturally. In other words, improvement does not depend entirely upon practice. How much of the improvement does depend upon practice? All of it, one is led to believe from Morgan's pages. " Steadying of the inherited organic apparatus " through preparatory efforts means improvement through habit. Besides, overestimating, as he did, the degree of perfection of the instinct at birth, he has left less room for maturation and the effects of practice than there really is. So far as the facts are concerned, the most one can say is that the development of the pecking instinct proceeds somewhat without practice and is hastened by it. Maturation and use run along in time together. No means has yet been devised of measuring the amount either factor apart from the other contributes to the development of the pecking reaction.

The importance attached to individual acquisition as a factor in development seems on the whole to become increasingly restricted. The theory of the non-transmission of acquired characters enormously narrows its scope in phylogenetic development. Perhaps we shall discover its lesser importance in ontogenetic development. The drinking reaction, for example, is more self-dependent than we have hitherto supposed. The pecking reaction suffers the supplementation of habit, one may well believe, when it does not demand it. It remains to be shown to what extent these instincts are typical of instincts in general. But even if it should be established that acquisition contributes relatively little, environment would still remain a powerful factor in development. The animal begins life with an hereditary endowment in interaction with the environment. One is necessary to the other. In the economy of an organism there is no reaction without stimulation. And not only is the environment a system of energies without which natural tendencies of the organism cannot be realized, but it is a selective system. What tendencies shall be realized will be determined by what stimuli are provided. Heredity and environment are not opposites, but complements.

PART II. ACQUIRED REACTIONS

I. Introduction and Statement of the Problem

From the study of the modifiability of reactions that are made prior to experience and are supposed to be based on inherited neuro-muscular co-ordinations, our interest now shifts to a study of the development of reactions that depend upon no such hereditary dispositions in the nervous system, but are individually acquired. It was one of the aims of this investigation to discover not only whether reactions to certain optical stimuli or stimulus-complexes are modifiable, but also to determine the rate of modification; in other words, to describe the progress of habit-formation in quantitative terms.

Modifiability was tested by the so-called discrimination method. Never more than two possibilities of selection were offered to the animal at one time. The conditions were so arranged that the chick's natural tendency to react to confinement and solitude by efforts to escape furnished the necessary random activity. When, after a certain number of trials, the animal reacted selectively to one of two constant form or size or color stimuli, for neither of which it displayed a preference before training began, the process of habit-formation was adjudged completed. By selective reaction is here meant the ability to react without error to a constant stimulus for an arbitrarily fixed number of times.

The adoption of the discrimination method followed directly from the results of Yerkes' work with the dancing mouse. I have appropriated his method, my contribution being merely an adaptation of the method to the study of chicks. So much for the problem in a general way.

II. Apparatus

The apparatus used was a fan-shaped reaction box built of wood and painted brown. Fig. 8 shows the ground plan, fig. 9 the perspective. The method of construction was as follows. On a base 88 by 95.5 cm. a convenient point near one edge was selected from which as a center, with radii of 38.64 cm. and 69 cm., respectively, arcs of circles were described. This center later became the point from which the chick started at each trial, and around which the entrance box was built. The nearer arc marked the location of the cards first approached by the chick; the more distant one outlined a boundary of the apparatus. The box was made with four compartments, but only the two inner ones were used in these experiments. Removable partitions (J, fig. 8) made possible this use of only a limited portion of the box. The height of the apparatus was 20 cm., inside measurement. The covering consisted of two lifting doors, one over the entrance box A and the other over the rest of the apparatus. These were made of light wooden frames and wire netting, and were so arranged that they lifted on their hinges directly away from the experimenter as he stood at the entrance box. The mesh of the netting was 3 cm.—as large as conditions would permit, so as to interfere with the light as little as possible. The exits H were closed with removable galvanized sheet iron sliding doors that fitted from above in vertical grooves. The end of the box about G was closed with wire netting of .86 cm. mesh. Grooves at this end also provided for wooden screens inside the wire of sufficient height to conceal the flock of chicks in a cage just beyond and below the experiment box from the chick reacting. Two sets of cards were used, one at D and another at F. The card-carriers at F projected 2.55 cm. from the walls, making it impossible for the exit H to be seen from the chamber C.

Following the ground plan in fig. 8 and the path of a chick through the apparatus from the entrance box A, the remaining dimensions and details may be clearly supplied. From the entrance box A, 16 by 20 cm., the chick was released by a wire screen door of .86 cm. mesh that was raised and lowered in its grooves at B by the experimenter. This retaining screen was shaped so that its lower edge coincided with an arc of a circle constructed from the center above referred to. The width of the opening at B was 10 cm. The first cardholders were at D, the passage ways through which were 9.33 cm. wide. Through D the chick passed into the electric chamber E, the floor of which was crossed with copper wires 1 cm. apart, so arranged that they formed an interrupted circuit which could be closed by the chick when the current was on by its stepping simultaneously on two adjoining wires. Out of E the chick passed through the opening F, 8.5 cm. wide, the position of the second card. From G there was an outlook through the wire netting

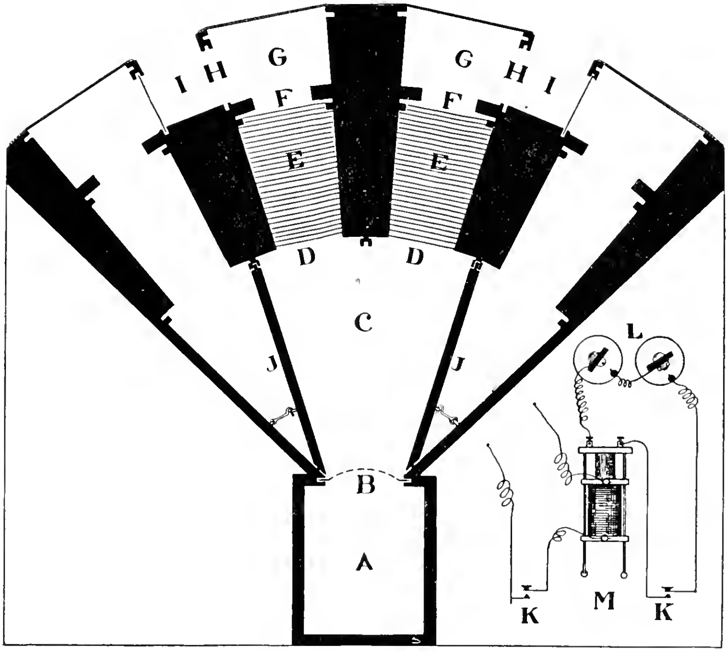

FIGURE 8—Ground plan of apparatus for testing habit-formation. A, entrance box; B, wire-screen door; D and F, location of card-holders; E,E, electric chambers; G, H, I, way out of box; K, electric key; L, electric battery; M, inductorium.

upon the flock of chicks in the cage below and also an outlet through H which was 8.5 cm. wide. The door of galvanized sheet iron could be inserted here to close the exit when desired. Once in I, the chick joined the rest of the flock by passing down over the door of the cage that was turned up toward this end of the apparatus at an angle of about 45 degrees. The dimensions and details were the same by either of the routes a chick might take from A to the cage. K indicates a key by which the circuit was made and broken. The current was supplied by

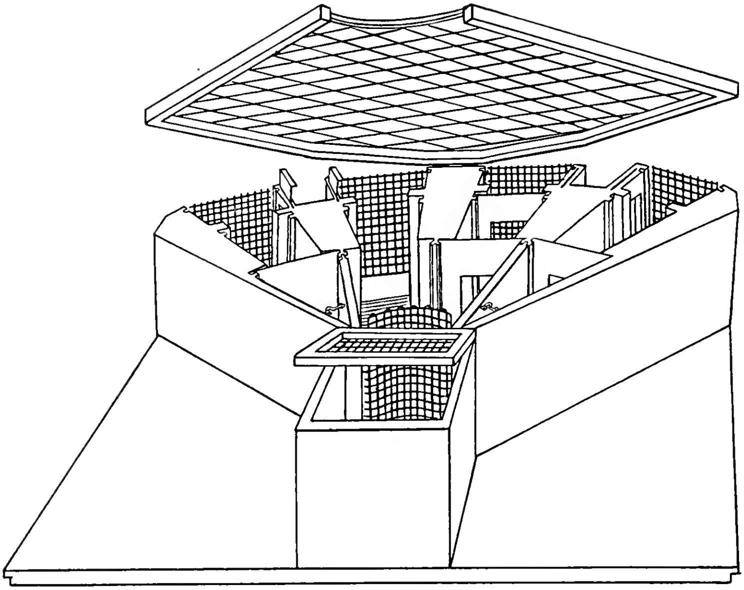

FIGURE 9—Perspective of apparatus for testing habit-formation, ground plan of which is presented in fig. 8.

a no. 6 Columbia dry cell which was connected with the primary coil of a Porter inductorium, the secondary coil of which was in circuit with the ends of the two wires that were wrapped parallel to each other about floors that were fitted into the electric chambers E. During the tests the apparatus was so placed that the entrance box was nearest the source of light and the sides of the apparatus were symmetrically situated with reference to the two windows that admitted the light. The cards used at D were 14.25 x 19.5 cm. and those at F 13.5 x

18.75 cm. In all color work the openings in the two sets of cards were the same in size, 8.5 cm. wide and 11.5 cm. high. These rectangular openings were cut in the lower part of the card in such a way as to leave equal margins of color on either side of the entry way.

III. Method

For a test of the reactions to color, form or size the appropriate cards were placed in the card-holders. For example, if reactions to black and blue were to be tested, one might start with a black card in each of the holders at D and F, right, and two blue cards in the corresponding holders on the left. The cage in which the animals lived was carried to a position with reference to the table upon which the apparatus sat such that one of the wire netting doors of the cage would turn back toward the exit-end of the apparatus as above described, and form an easy passage-way from the reaction box to the cage.

The chick to be experimented upon, marked and numbered, was carried from the cage to the entrance box. When placed in A, it soon acquired the habit of crowding up near the wire netting door, standing at a point equidistant from the two cards exposed at D. It also soon ceased pecking at the wire covering or flying against it, if it happened at first to try this way of escape. The work had not gone very far before the plan was rigidly adhered to of not releasing a chick from A until it made an effort to escape by urging toward the screen. Sometimes this meant a delay of several minutes, but it seemed useless to spend time with a chick that did not react negatively to the confinement or isolation. Further, care had at all times to be exercised that a chick be not kept struggling in A. Results were vitiated if this occurred. I feel sure that discriminating ability deteriorated as the response to the isolation of the reaction box approached too near in one direction the passivity of indifference, or in the other the activity of excitement. I have watched the record of indifferent chicks recover from a lapse when the response to isolation was accentuated by sufficiently prolonged solitary confinement between trials; on the other hand it is easy to point to numerous instances where a record has been marred by undue excitement. I concluded from experience, that much the wisest plan was to watch for an incipient struggle to escape, and to lift the door just when the impulse had begun to gather force. There is a nice middle ground here that gave the best results. There were great individual differences in the animals. Some stood about for a while before the impulse to escape seized them, others rushed immediately toward the screen door. The experimenter stood back of the entrance box between the two windows of the room, and, after releasing the chick from A, remained as quiet and motionless as possible until the animal found its way out of the apparatus. I had practically no success with the device Yerkes used with the dancing mouse, the card by which he gradually forced the animals toward the electric box. Chicks that won't work without force won't work with it, is a rule that can be generally relied upon. After the animal had escaped to the cage, the experimenter secured it again, brought it back to the entrance box, and the procedure as described above was repeated.

At the beginning of a set of experiments the animal was familiarized with the apparatus, as well as tested for its preference of the stimuli presented in the card-holders, by a number of " preference trials," usually one series, which consisted of ten trials. Sometimes a second series was given. These series are denoted in the tables by A and B, respectively. During the preference trials the exits at H were both left open, the two sets of cards were alternated right and left after each trial, and no electric shock was used. To show the readiness with which the chicks reacted in the preference trials as well as to suggest the availability of the animals for certain kinds of labyrinth training, I present below as typical the average time in seconds for each preference trial, from one to ten, of chicks nos. 32, 33, 38, and 39, Group I, at the beginning of their black-blue work: 69.2, 24.1, 18.1, 3.8, 3.4, 2.6, 2.1, 1.9, 2.2, 1.9. Chicks thus tested for an experiment were continued in that experiment, unless they were found to have a preference .for the stimulus to which it was desired they should form the habit of positive reaction. A chick that revealed a preference for this stimulus prior to training was rejected.

After the preference trials had proved a chick satisfactory, it was subjected to the regular conditions of training. The "wrong" side of the apparatus was closed at the exit and the animal was given a shock if it entered the electric chamber on that side. This was done by quietly pressing the key previously referred to. The shock was not severe enough to cause the chick to jump from the wires or chirp on receiving it. It was found that a shock from a current value of about 1.69 amperes with the secondary coil set at 5.5 according to the scale on the inductorium, proved most generally satisfactory. Here again there were individual differences in sensitiveness among the chicks, but in the main the above shock brought results without being injurious, and had no more effect on the chicks than to start them from their position, occasionally causing one to lift a foot from the wires. The floor of the entrance box was kept wet so that the feet of the chicks would be in a condition to receive the shock with regularity.

At first a chick usually ran right over the wires and on to the front netting, from which there was a full view of the other chicks in the cage. With the chick in this position on the "wrong" side, it was found best to wait until it happened upon the right road out by its own random activity. Some times the wait on the first training trial was ten minutes, but such a delay was exceptional. The young chicks, as a rule, were active and soon acquired the habit of withdrawing from the "wrong" side promptly. The draft on the experimenter's time after the training was well under way, averaged about 1.5 minutes per reaction, including everything. No trouble was experienced with hesitancy on the part of the chicks to return over the electric wires. Of course they were never shocked on the return passage.

In a series of trials the positive card was shifted right and left in this order: r, l, r, l, r, r, l, l, r, l. Thus each card in each series was displayed the same number of times on the right- and left-hand sides. When the chick had made a series of errorless reactions with the above changes of cards, it was tested for another perfect series with a different order and an equal number of rights and lefts. If no errors were made this time, a third series with still a different sequence of changes was given, when, if the chick reacted without error, the process of habit-formation was pronounced completed.

In none of the work with this apparatus was it necessary to starve the chick or even to keep it excessively hungry. It is my opinion that hunger did not play a more important part than the reaction to confinement and solitude. True, it is easy to show that, as a rule, a chick with a full crop is not so good material for an experiment like this as one not so well fed, but these animals while being experimented upon did not always rush about for food as soon as they had reached the cage.

IV. Experiments

In these experiments on modification thirty-eight chicks were used. The work was done from Dec. 15, 1907 to June 30, 1908. To test the interrelation of habits of response to optical stimuli, the necessity arose of discovering at least two methods of measuring modifiability in this sense mode. It was desirable in the case of any one method that the stimuli bear such a relation to each other that the average chick could complete the training within a reasonable time, and that the time should be as nearly as possible constant for different chicks. The feasibility of the electric shock and satisfactory conditions and devices for training the chicks were determined upon after several hundred preliminary trials in a crude reaction box. The apparatus shown in figures 8 and 9 was constructed on the basis of experience in these preliminary tests, combined with the suggestions afforded by the apparatus of Yerkes[1] and that of Hamilton[2] used in similar experiments. Means for retaining the animal in the entrance box until it made movements to escape, permitting it meanwhile to be within range of the stimuli; the location of these stimuli at a suitable distance from the point of release; the open screen overlooking the cage—these features were planned with characteristic activities of the chicks in mind. Releasing the chick too soon or too late at any given trial produced unsatisfactory results. If the cards were too near, the pulse of activity often carried the animal into the electric box before the card stimuli had wrought the proper effect. And when the animal had made an error and had arrived at the closed exit, the chicks in the cage below acted as an additional stimulus to escape. The animals readily found the exit through H when the door was open.

A. Color

In all the color work the reflection method with the Bradley standard colored papers was employed. Hue, tint, and shade

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[1] Yerkes, R. M.: The dancing mouse. New York, 1907, p. 92.

[2] Hamilton, G. V.: A study of trial and error reactions in mammals. *The Journal of Animal Behavior,* 1911, vol. I, p. 33.

are described only by reference to the catalogue name or number of the papers. Measurement of tint (or brightness) was attempted in only a few special cases. The purpose of these experiments at their inception was not to investigate the color reception of chicks, but to test modification of behavior. However, the reactions to reflected colored light proved so interesting that a slight digression from the central interest of the research was later made in the effort to gather some new facts in this closely related field.

Chicks were tried first with Bradley black and white. Most of the first tests involved many elements of irregularity. In some the right and left exchanges of cards were not balanced in the series. In others, chicks had been shocked too severely and either hesitated about entering the electric boxes or balked completely. Again, work was carried over from the preliminary to the new apparatus. The best of these first results are presented below. Chick no. 7, after being given preference trials which were of questionable value, was regularly trained to avoid white and go to black.[1]

TABLE 8

BLACK-WHITE REACTIONS

CHICK NO. 7. HATCHED 12/10, '07. SEX, F.[2]

Series[3]	Date	Right	Wrong
1	Jan. 8	11	9
2	" 10	13	7
3	" 11	13	7
4	" 13	10	10
5	" 14	12	8
6	" 15	9	11
7	" 16	7	13
8	" 17	18	2
9	" "	18	2
10	" 20	17	3
11	" "	7	3
12	" 21	17	3
13	" 22	19	1
14	" 23	17	3
15	" 24	9	1
15	" "	10	0
16	" 25	20	0

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[1] In all the tables of results in discrimination work the stimulus to which a chick was forming the habit of positive reaction is each time mentioned first. It is to be assumed that the animals were without previous training unless a definite statement to the contrary is made.

[2] All sex determinations were made by dissection.

[3] In some of the preliminary work the regular 10-trial series was doubled.

In table 9 are presented the results obtained from chick no. 9 under conditions exactly similar to those under which no. 7 was tested. No. 9, however, was trained to accept white and reject black.

TABLE 9

White-Black Reactions

Chick no. 9. Hatched 12/10, '07. Sex F.

Series	Date	Right	Wrong
1.	Jan. 9	11	9
2.	" 10	9	11
3.	" 13	13	7
4.	" 14	12	8
5.	" 15	13	7
6.	" 16	14	6
7.	" 17	20	0
8.	" "	10	0

Now, if some animals were going to require, as no. 8, 310 tests besides preference trials to complete the black-white training, working with this habit would consume too much of the experimenter's time. An objection to the white-black habit lay in the preference prior to training that chicks showed for the white. If a combination of visual stimuli could be discovered for neither of which the chicks showed any marked preference, such a combination would commend itself for use, provided the time required to form the desired habit of reaction should be fairly uniform among different chicks and conveniently short. The combination, orange and white, was tried with the result shown in table 10. The work of chick no. 12 was devoid of the irregularities spoken of above.

TABLE 10

Orange-White Reactions

Chick no. 12. Hatched 12/10, '07. Sex, F.

Series	Date	Right	Wrong
A and B	Jan. 29	11	9
1.	" 30	6	4
2.	" 31	6	4
3.	Feb. 1	10	0
4.	" 3	9	1
5.	" 4	9	1
6.	" 5	10	0
7.	" 6	10	0
8.	" 7	10	0

This record was the cleanest and most promising so far, but was offset by the results obtained from experiments conducted concurrently upon no. 10. The latter chick, in a period of training twice as long as that given to no. 12, failed to acquire a perfect habit of response to orange. The preference trials in each case were satisfactory.

TABLE 11

ORANGE-WHITE REACTIONS

CHICK NO. 10. HATCHED 12/10, '07. SEX, M.

Series	Date	Right	Wrong
A and B	Jan. 29	10	10
1	" 30	5	5
2	" 31	4	6
3	Feb. 1	5	5
4	" 3	4	6
5	" 4	5	5
6	" 5	4	6
7	" 6	4	6
8	" 7	5	5
9	" 8	6	4
10	" 10	9	1
11	" 11	8	2
12	" 12	8	2
13	" 13	9	1
14	" 14	7	3
15	" 15	9	1
16	" 17	9	1

Chick no. 8 was given more searching preference tests and then trained on black-blue.

TABLE 12

BLACK-BLUE REACTIONS

CHICK NO. 8. HATCHED 12/10, '07. SEX, M.

Series	Date	Right	Wrong
A	Jan. 27	Orange 13	Blue 27
B	Jan. 28	Black 6	White 14
C	Jan. 28	Yellow 7	Blue 13
D	Jan. 29	Black 6	Yellow 14

		Black	Blue
1	Jan. 29	2	8
2	“ 31	1	9
3	Feb. 1	1	9
4	“ 3	2	8
5	“ 4	3	7
6	“ 5	6	4
7	“ 6	4	6
8	“ 7	8	2
9	“ 8	7	3
10	“ 10	8	2
11	“ 11	8	2
12	“ 12	10	0
13	“ 13	10	0
14	“ 14	10	0

Preference tests B and D, table 12, indicate a natural preference for the brighter of the two cards. The orange-blue and yellow-blue preference tests brought to light interesting data. The yellow here was very light, much brighter than the comparatively dark blue, not only as judged directly by the human eye, but as tested by the flicker method. Particular attention is called to these first reactions to blue for, in so far as this paper has anything to contribute to the study of color vision, the interest will largely center in and results will turn upon the reactions of the chicks to blue.

The training of no. 8 on the black-blue was now carried through with the result detailed in table 12. Within a reasonable number of trials, 140, including the final three perfect series, the chick nicely developed the habit of selecting the black. It was thereupon decided to adopt the black-blue combination for a more searching test, with a view to its use in the determination of the rate of modification, the permanence of habit, and some of the effects of training.

Chicks nos. 16, 17, 18, 19, and 20 were selected for this work. From all appearances they were normal chicks, and were chosen at random from the healthy specimens in a flock of seventeen. They were twelve days old when given their preference tests. In all tests prior to those reported in table 13 but one set of cards was used, the cards at D, figure 8. In this set of experiments, after series 2, an additional pair of cards was placed at F, whereby shock and color stimuli were presented simultaneously and not successively only, as in the previous experiments. In table 13 the rate of decrease of error or the rapidity of modification is shown in the column, “average number of errors." On the basis of these results with black-blue there seemed to have been developed one habit of response to optical stimuli that would serve both for a measurement of the rate of modification in the chick and, when used along with another method yet to be discovered, as a test of the interrelation of modifications.

TABLE 13

BLACK-BLUE REACTIONS

CHICKS NOS. 16 TO 20. HATCHED 2/5, '08.

		No. 16 Sex, F.		No. 17 Sex, F.		No. 18 Sex, F.		No. 19 Sex, F.		No. 20 Sex, M.		Av. No. of errors
Series	Date	R	W	R	W	R	W	R	W	R	W	
A	Feb. 17	5	5	5	5	3	7	4	6	5	5	5.6
1	" 18	3	7	3	7	1	9	6	4	4	6	6.6
2	" 19	3	7	3	7	5	5	5	5	6	4	5.6
3	" 20	6	4	7	3	2	8	3	7	6	4	5.2
4	" 21	9	1	8	2	8	2	6	4	8	2	2.2
5	" 22	7	3	10	0	5	5	6	4	8	2	2.8
6	" 24	9	1	9	1	9	1	6	4	9	1	1.6
7	" 25	6	4	10	0	7	3	10	0	10	0	1.4
8	" 26	10	0	10	0	9	1	10	0	10	0	0.2
9	" 27	10	0	10	0	10	0	10	0	10	0	0.
10	" 28	9	1			9	1					0.4
11	" 29	10	0			10	0					0.
12	Mar. 1	10	0			10	0					0.
13	" 2	10	0			10	0					0.

The persistence of habits and their effects, as well as the bearing of the results upon the problem of color vision, will be discussed separately in a later section of the paper. For the present, interest is confined to certain aspects of the process of modification, and the question as to whether the reaction of the chick is determined by the quality as well as the intensity of the color stimulus is not a matter of special concern. The term color is used simply to denote a certain stimulus, with no implication that the chick's reactions are affected by variations in wave-length of the ether vibrations.

Let us turn now to the search for a second method of measuring modification.

B. Form

To test the animals' responses to forms, black cards, cut as previous cards, were used in the regular card-holders of the apparatus. The cards bore two-dimensional forms above the openings through which a chick had to pass on its way out of the apparatus. That is, forms were cut out of white paper and pasted midway between the two sides and a little below the top of the card. The chicks were first tested with a square and a triangle of equal area. The triangle had a base of 8.13 cm. and an altitude of 6.35 cm. The square was 5.08 x 5.08 cm. No. 11, a chick that had succeeded in acquiring the black-white habit to the point of making one error in the last twenty trials, reacted in the square-triangle test as shown in table 14.

TABLE 14

REACTIONS TO FORM

CHICK NO. 11. HATCHED 12/10, '07. SEX, F.

Square-Triangle

Series	Date	Right	Wrong
A	Jan. 31	5	5
1	" "	1	9
2	Feb. 1	3	7
3	" 3	4	6
4	" 4	6	4
5	" 5	6	4
6	" 6	4	6
7	" 7	7	3
8	" 8	5	5
9	" 10	2	8
10	" 11	4	6
11	" 12	6	4
12	" 13	2	8
13	" 14	3	7
14	" 15	6	4
15	" 17	4	6

Not only were the results here purely negative, but one had only to watch the chick to become convinced that the probability of its forming the habit of selecting the square was almost nil.

No. 13, a chick that had acquired the white-black (darkened [1]) habit perfectly, was tried at the same time by the same method in this form test with the result shown in table 15.

No. 13 showed no signs of improvement and the experiment was discontinued. The square-triangle combination was discarded for a " design " that was placed at the top of the cards. This time the cards in the apparatus were white and the forms upon them black. On one set of cards were pasted, vertically

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[1] The electric chamber on the side of black was covered with cardboard.

and 2.5 cm. apart, two parallel bands of black paper, each band being rectangular in form and measuring 4.2 x .9 cm. On the other set of cards two black bands of equal area and the same material were fastened at right angles to each other and in this wise (Λ). Chick no. 21 was tried first with this combination of forms, but with negative results. No. 15 was tested at the same time. It showed no improvement after 60 trials and from that on the continuous training plan was used. On Mar. 1 it was given 160 trials. The regular system of card exchanges was disregarded and one setting of cards was allowed to remain during several successive trials to see if the chick might thus hit upon the habit of selecting the vertical bars. Sixty trials were given in a similar way on Mar. 2 and as many more on Mar. 3, with negative results.

TABLE 15

Reactions to Form

Chick no. 13. Hatched 12/10, '07. Sex, F.

Triangle-Square

Series	Date	Right	Wrong
A	Jan. 30	5	5
1	" 31	3	7
2	Feb. 1	4	6
3	" 3	8	2
4	" 4	5	5
5	" 5	6	4
6	" 6	3	7
7	" 7	5	5
8	" 8	4	6
9	" 10	6	4
10	" 11	7	3
11	" 12	2	8
12	" 13	5	5
13	" 14	7	3
14	" 15	6	4
15	" 17	5	5

The plan of having forms at the tops of the display cards was then abandoned and another scheme employed. This time display cards were made of gray cardboard and the forms were presented as openings in the cards through which the chick had to pass on its way out of the apparatus. In one set of cards a circular opening was cut the diameter of which was 8.47+cm. In the other set of cards a rectangular opening was cut whose base was 6.35 cm. and altitude 8.89. The circle and the rectangle were constructed as nearly as possible of equal areas. The regular manner of training was resumed and the reactions of chicks 15, 22, and 23 to the circle-rectangle combination were tested. At the risk of being tedious I present the results in detail, for whether or not the ability to react selectively in this case would have demonstrated the dependence of the reactions on the element of form, it did not seem unreasonable to expect the chick to develop a habit of reacting differently to stimuli as different as these.

A glance at tables 16, 17, and 18 reveals only negative results. The chicks soon came to a point in these form tests where they did not make an effort to escape from the box. Precaution was taken to see that the electric shock was not too severe. Previous experience in the color experiments had shown that a chick occasionally received a shock of too great intensity and thereafter hesitated about entering the electric chambers. But the shock for nos. 15 and 23 ran as low as 6 to 6.5 on the scale of the inductorium, and did not reach a greater intensity than 6.5 for no. 22. The regular shock, as stated before, was 5.5. Just prior to the discontinuance of the tests, no. 22 would approach the display cards, hesitate, at times shake its bill, and go no further. The expedients of moving a card over the top of the apparatus from the entrance box toward the

TABLE 16

REACTIONS TO FORM

CHICK NO. 15. HATCHED 2/5, '08. SEX, UNDETERMINED

Circle-Square

Series	Date		Right	Wrong
A	Mar.	6	4	6
1	"	"	2	8
2	"	"	2	8
3	"	"	3	7
4	"	"	4	6
5	"	7	4	6
6	"	"	4	6
7	"	"	2	8
8	"	8	2	8
9	"	"	4	6
10	"	"	6	4
11	"	"	5	5
12	"	9	5	5
13	"	"	4	6
14	"	10	3	7

TABLE 17

REACTIONS TO FORM

CHICK NO. 22. HATCHED 2/5, '08. SEX, F.

Circle-Square

Series	Date	Right	Wrong
A	Mar. 9	4	6
1	" 10	4	6
2	" "	5	5
3	" 12	5	5
4	" "	5	5
5	" 13	4	6
6	" "	2	8
7	" 16	6	4
8	" "	4	6

TABLE 18

REACTIONS TO FORM

CHICK NO. 23. HATCHED 2/5, '08. SEX, UNDETERMINED

Circle-Square

Series	Date	Right	Wrong
A	Mar. 9	4	6
1	" "	9	1
2	" 10	2	8
3	" "	6	4
4	" 12	2	8
5	" 13	6	4
6	" "	6	4
7	" 16	8	2
8	" 17	5	5
9	" 19	4	6
10	" 20	5	5

chick and of forcing him gently from behind were tried without effect. The chick simply "gave up," as my note has it.[1]

C. Size

The search for a second method of measuring modification of behavior was continued in an investigation of the reactions of the chick to size differences in two dimensions, difference in form being excluded. The plan was adopted of having openings in gray display-cards through which the chick had to pass. The openings in one set of cards were 6.35 cm. wide and 8.89 cm. high; those in the other set 8.89 cm. wide and 12.44 cm. high.

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[1] Later, during some work as yet unpublished, I found a chick that acquired the circle-square habit when the experiment was conducted in a dark-room. Opal glass was electrically lighted from behind and the above forms, cut in black tin screens, permitted illuminated areas of these shapes to be exposed to the chick.

The openings were the same in shape and one was approximately twice the size of the other. The experiment was undertaken with chicks no. 24 and no. 25, and completed with the result detailed in table 19. The training was finished quite satisfactorily and within a reasonable time limit, so the method seemed available for further use. Five control series were given to check out the influence of brightness. It is manifest that with equal illumination on the faces of the display-cards, which was roughly secured by adjustment of the shades of the two windows that admitted light to the room, the electric box back

TABLE 19

Reactions to Size: Small-Large Openings

Chicks nos. 24 and 25. Hatched 2/5, '08

Series	Date	No. 24 Sex, M. R	No. 24 Sex, M. W	No. 25 Sex, F. R	No. 25 Sex, F. W
A	Mar. 17	5	5	3	7
1	" 18	0	10	3	7
2	" "	3	7	(frightened?)	
3	" 19	5	5	4	6
4	" "	8	2	6	4
5	" 20	7	3	7	3
6	" "	7	3	5	5
7	" 21	8	2	3	7
8	" "	10	0	6	4
9	" 23	10	0	10	0
10	" "	10	0	10	0
11	" 25			9	1

Control Tests

Series	Date	No. 24 R	No. 24 W	No. 25 R	No. 25 W
Card of small opening brighter, and its electric box brighter:					
1	Mar. 24	9	1		
Card of large opening brighter, its electric box brighter:					
2	Mar. 24	9	1		
Cards equally illuminated, electric box of small opening made the brighter by illumination of electric light:					
3	Mar. 24	9	1		
Card of small opening brighter, electric box of large opening made much darker by overhead cardboard:					
4	Mar. 24	10	0		
Cards equally illuminated, electric box of large opening made the darker by overhead cardboard:					
5	Mar. 25			10	0

of the large opening would be brighter than that back of the small one. The angle at which the cards stood to each other, together with the position of the windows with reference to the cards, made it possible to vary the brightness of the two cards independently, and that of the electric boxes so that the electric box on the side of the brighter card could be made also the brighter box. A cardboard over an electric box was also used to screen off light. Within the degrees of variation employed, the chicks continued to select the smaller opening regardless of the relative brightness of the faces of the cards or the electric boxes. When both electric chambers were covered with a ground glass plate and a 2 c.p. electric light was adjusted over the electric box on the side of the small opening, no. 24 approached as usual the small opening, hesitated a moment, glanced about the apparatus in the vicinity of the card, and then slowly entered. (See control test 3, table 19.) Control 5 exhibits the same general relations as 3, but without the use of electric light. The pronounced variation, even to a different quality of light, did not inhibit the selective reaction. In control series 4 the electric box on the side of the card having the large opening was darkened considerably by cutting off the light from above with a piece of black cardboard. The figures for this series of reactions, 10–0, in comparison with the 9–1 records in the other series, represent but do not express fully the difference in readiness with which the chick responded. This series repeated control series 1 with greater difference in the relative brightness of the electric boxes. The conclusion seems to be justified, on the basis of these results, that the chicks were responding selectively to one of two objects of different size. Of course the control of other possible determinants of reaction, such as odor, would have made this conclusion more certain. The small-large habit was now adopted to be used in conjunction with the black-blue habit for an experimental test of the effects and interrelation of habits.

D. To What Extent Has Training General Value?

After an experimental test of the influence of one labyrinth habit upon the formation of another, Yerkes[1] concludes that "the acquisition of one form of labyrinth habit may facilitate

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[1] Yerkes, R. M.: *Op. cit.*, p. 261.

the acquisition of others." "For the student of animal behavior, as for the human educator, it is of importance to learn," he writes, "whether one kind of training increases the efficiency of similar forms of training." The question for which an answer was sought in the work about to be reported is closely related to the problem which Yerkes set for himself, but is concerned with the more general value of training: How does acquired ability to react perfectly to one kind of element or complex affect the acquisition of ability to react to a quite different element or complex?

Among certain organisms a particular act once acquired is more easily re-acquired. A particular act once acquired may facilitate the acquisition of a similar act, similar meaning here a relation of partial identity. Now the question naturally arises, As two acts are less and less similar, what effect does the acquisition of one have on the later acquisition of the other? This raises the problem of formal discipline, capable, surely, of solution by experiment, but not yet solved. It has been suggested that there may be "two kinds or aspects of organic modification in connection with training; those which constitute the basis of a definite form of motor activity, and those which constitute the bases or dispositions for the acquirement of certain types of behavior."[1] The data upon which this suggestion is based would allow us to say nothing definite about "the acquirement of certain types of behavior" not of the original *labyrinth form*, which Yerkes used. But at that the general value of training has been experimentally demonstrated, in so far as different labyrinths are different objects, even different objects of the same kind. Although there is a degree of generality here, it is so slight that the training value involved would no doubt ordinarily be classified as specific. If no two particular stimuli are identical, then, practically speaking, much specific training has general value, which does not mean, however, that this generality of value may not rest at bottom on specific modifications. This must be our conclusion when we look at the matter from the side of content as opposed to function, stimulus as opposed to reaction. Practically, it cannot be denied that in some organisms certain kinds of training do have value for certain other kinds. The question awaiting answer in the

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[1] Yerkes, R. M.: *Op. cit.*, p. 261.

present state of our knowledge is, Between what kinds of modifiactions and to what degree is there transfer? Few will dispute the assertion that there may be dispositions preceding and underlying the acquisition of a particular act which are not identical with those that are at the basis of its actual performance. Indeed the former may no doubt be congenitally present, with or without the actual ability to perform. In a similar manner, of course, one may think of an acquired neurological disposition "predisposing" the individual to certain new activities. And within what range? That is our problem.

To bring a particular case to a test, two comparable groups of four chicks each were chosen, Group I consisting of chicks nos. 32, 33, 38, and 39, Group II of chicks nos. 34, 35, 36, and 40. All the chicks were of the same brood, hatched April 13, 1908. None of them had any other training prior to or during the course of these experiments. Uniformity in method was strictly adhered to. The chicks of Group I were given the black-blue training to the point where they made no errors for three successive days, ten trials per day. Then the chicks of both groups entered together into the size training. During the course of the development of each habit one setting of the cards was used for the corresponding trial of all the animals. For example, in the black-blue work, the black card occupied the positions r, l, r, l, r, r, l, l, r, l, in each series until an errorless series was reached. At the first setting of the cards—black right, blue left—the chicks of Group I went through one at a time until each animal had to its credit one reaction. Then the cards were exchanged to the second position and the chicks again taken as before.

As a precaution which seemed advisable, the secondary coil of the inductorium was adjusted at 6 to begin with in the black-blue training, and it was continued thus throughout. In the later size training a shock of the same intensity was employed at the start and at the beginning of the ninth series this was raised to 5.5 on all the chicks alike.

The order of training was this. When the chicks of Group I were twelve days old, work was begun with them, and they were trained until they responded errorlessly with a positive reaction to black. On May 11, by which time this group had finished the color work, these animals with those of Group II were introduced into the size training. Table 20 shows the course of modification of response to the color stimuli. Only the errors appear in this summary.

TABLE 20

Errors in Black-Blue Reactions

Chicks nos. 32, 33, 38, and 39. Hatched 4/13. '08

Group I		32 Sex, F.	33 Sex, M.	38 Sex, M.	39 Sex, F.
Series	Date	W	W	W	W
A	Apr. 25	5	5	5	5
1	" 26	6	7	7	7
2	" 27	3	3	5	4
3	" 28	1	3	3	2
4	" 29	0	3	2	4
5	" 30	0	2	1	2
6	May 1	0	1	2	0
7	" 2		1	1	1
8	" 3		0	1	0
9	" 4		0	0	0
10	" 5		0	3	0
11	" 6			0	
12	" 7			0	
13	" 8			0	

These chicks really do not vary so much in the modifiability of their behavior as the figures might indicate. No. 38 became excited during the tenth series, which may explain its lapse. The rapidity with which no. 32 finished the work is noticeable. No chick before or afterwards in my experiments excelled this record of 30 trials exclusive of preference and perfect series. But it is sufficient for our present purpose simply to show clearly the perfection of the training that preceded the formation of the second habit, without extended discussion of the other characteristics of the modification.

Following the completion of this training of Group I, both groups were introduced into a size experiment, as described above. Table 21 reveals the progressive development of the second modification for each group in the column of average daily number of errors. The total of these averages for Group I amounts to 66.3 for the sixteen days training; for Group II, 70.1 during the same period. Curves I and II, fig. 10, exhibit graphically the rate of decrease of error for the corresponding groups. The record of each group in the preference tests is included in the curves. In a comparison of results for the two groups two things especially must be taken into consideration, (1) the natural preferences before training began and (2) previous training. In regard to the first, Group II had to overcome a stronger preference for the larger of the two openings. The chicks of Group I took the smaller opening more often than those of Group II, perhaps because in general the black-blue training inclined chicks to accept the stimulus of lower brightness value, which in this case has been shown to be on the side of the smaller opening. The previous brightness training here came into conflict, however, with the natural(?) tendency to pass out by the larger opening, which may be something more than a brightness preference, and thus may be explained the small difference between the two groups in the results of the preference trials. As to the second point above, Group I, besides acquiring the black-blue habit, had become habituated to the general conditions of the apparatus in such a way that adjustment to the new conditions of the size experiment must have

TABLE 21

Record of Errors

Reactions to Size: Small-Large Openings

Hatched 4/13, '08

		Group I					Group II				
Series	Date	32	33	38	39	Av.	34	35	36	40	Av.
A.	May 11	6	7	5	3	5.3	5	5	7	8	6.3
1.	" 12	8	5	9	7	7.3	8	9	5	9	7.8
2.	" 13	6	7	6	7	6.5	6	9	10	5	7.5
3.	" 14	6	5	6	8	6.3	6	7	5	7	6.3
4.	" 15	7	7	4	7	6.3	5	5	7	7	6.
5.	" 16	5	5	5	7	5.5	7	8	6	7	7.
6.	" 18	5	4	6	3	4.5	6	6	4	6	5.5
7.	" 19	7	7	2	1	4.3	3	4	3	6	4.
8.	" 20	5	8	2	3	4.5	2	6	1	5	3.5
9.	" 21	3	5	4	2	3.5	5	4	1	8	4.5
10.	" 22	4	7	3	2	4.	3	3	3	6	3.8
11.	" 23	6	3	2	2	3.3	1	2	2	6	2.8
12.	" 25	4	6	2	4	4.	2	3	0	4	2.3
13.	" 26	1	1	1	1	1.	1	2	4	5	3.
14.	" 27	1	2	1	2	1.5	1	2	3	4	2.5
15.	" 28	0	1	4	1	1.5	1	1	1	4	1.8
16.	" 29	2	1	5	1	2.3	1	0	1	5	1.8
		Total av. 66.3					Total av. 70.1				

been somewhat facilitated—through a lessening of the tendency to general excitement during the first tests, if in no other way. In view of these considerations there is no conclusive evidence that the previous training of Group I with black-blue facilitated the formation of the small-large habit, albeit Group I averaged 5.4% less errors per day than Group II.

It should be stated in connection with the above size work that the results indicate difficulty of acquisition. The behavior of the chicks pointed in the same direction. So, any more general conclusion than we have ventured would have to be made subject to this further fact. It ought also to be pointed out that chicks of the same age are not always of the same size. The members within each group were of unequal size when six weeks old. Yet, fortunately for our experiment, the groups remained comparable as to size, individual for individual, throughout the tests. This matter is vital to the experiment, for naturally chicks of different sizes could pass through the small opening with different degrees of ease.

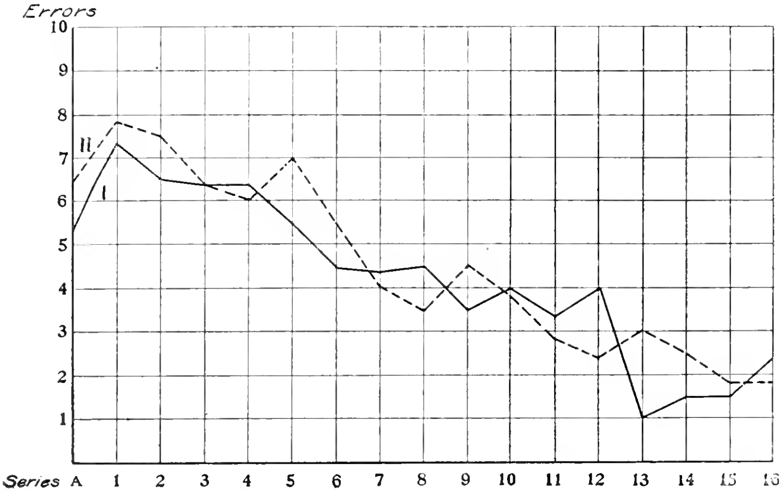

FIGURE 10—Rate of modification in size training, arranged to test the effect of previous color training. Curve I shows the rate of acquisition by Group I of the small-large habit after having acquired the black-blue habit; Curve II represents the rate of acquisition of the same habit by Group II, the same number and the same age as the chicks in Group I, but without previous color training. Preference tests on first day. Distances along axis of abscissae represent series; along axis of ordinates, average number of errors.

But the conclusion as to the general efficiency of the black-blue training should not rest alone upon a comparison of the rates of modification in the two groups of chicks. Having learned in the course of the experimentation with the black-blue habit, from data which will appear later, that this modification persists for some time with relatively slight change, it seemed of value to investigate the relation of the size training to the color training by means of the so-called memory test.

TABLE 22

THE NON-INTERFERENCE OF MODIFICATIONS

Training in Black-Blue					Training in Small-Large			Persistence of the Black-Blue Modification			
No.	Age	Sex	Trials	Errors	Age	Trials	Errors	Interval	R	W	First selection
32	12	F	30	10	28	160	70	32	10	0	Black
33	12	M	70	20	28	160	74	30	10	0	Black
38	12	M	100	25	28	160	62	31	4	6	Blue
39	12	F	70	20	28	160	58	30	9	1	Blue

Table 22 exhibits the results of this test. The table shows the age of the chicks of Group I when the work on black-blue was begun, 12 days; the number of trials necessary to complete the training, exclusive of preference and final perfect series; the number of errors made in the course of this training; and also the corresponding age, trials and errors for the size training. The interval, thirty days or more in each case, is the number of days between the date when the black-blue modification was pronounced perfect and the date upon which the memory test was given. Of course sixteen days of this interval were occupied with the development of the small-large habit.

The reactions of the chicks to black-blue in the persistence tests are detailed in the columns R and W. Chicks nos. 32 and 33 made perfect records, no. 39 made an error on its first trial, being thereafter perfect, while the reactions of no. 38 seemed to show no trace of the original modification. The results altogether weigh in favor of the view that the modifications with which we have dealt proceed quite independently of each other. By consulting table 26 it will be seen that the persistence of the black-blue habit in these chicks after 30 days measures fully up to the average made by other chicks that had not had intervening training. If it be objected at this point that one should expect the small-large training to exert an influence in the direction of strengthening the black-blue modification, I agree, in so far as brightness is concerned, but the inference is that something more than brightness was involved in each habit. That color and not brightness was the effective element in these tests of persistence I have not shown. The results are offered in their present stage for their possible value as a suggestion for method. It is not too much to expect relative permanency of the black-blue habit even if the brightness relations of the first training were reversed in the second. Though both forms of training are habits of response to optical stimuli, they are probably quite separate from each other in their development. Physiologically, this likely means the formation of separate neural bases. For our explanations we look to the central nervous system. Judd[1] observes that "Discrimination is not a process of impression." "The raw materials for adaptation, the impressions, are there very early, waiting for the individual gradually to adjust himself to them." Discrimination depends upon the ability of the individual to react specifically. Capacity to discriminate is linked with the capacity to react. If this be true, the animal's scope of reaction will determine the limits of its modifiability. According to this view, the grouping of elements to form a single object of reference in reaction derives its unity from the co-ordination in a single active brain process. This does not ignore the fact that the structure of the end organs will also define in advance the range of objects that may be discriminated. Impressions to be distinct must be accompanied by distinctive neurological dispositions. "In short," says Judd again, "so far as this raw material for development which presents itself in the form of impressions is concerned, it must all be worked over and connected with individual reactions before it can be regarded as really assimilated by the developing individual."

But let us return from theory to facts.

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[1] Judd, C. H.: Genetic psychology for teachers. New York, 1903, p. 153 ff.

E. Some Effects of Modifications

In table 12 were pointed out the natural color preferences of chick no. 8: white in preference to black, blue to orange, blue to yellow, and yellow to black. The peculiarity of the reactions to blue was mentioned. If blue be supposed to have a higher brightness value for chicks than for humans, the chick's behavior might be satisfactorily explained on the ground only of brightness of stimulus. Further experimentation was undertaken with a view to an explanation of the above apparent irregularity. No. 11, a chick which had been trained on black-white and had progressed so far that in its last series of twenty successive trials it made but one error, was tested for its preference on the combination of colors listed in table 23. Eight days had elapsed between the date of the 19–1 series and these color preference tests.

TABLE 23

Preference Tests After Black-White Training

Chick no. 11. Hatched 12/10, '07. Sex, F.

Series	Date	Right	Wrong
	Jan. 21	Black 19	White 1
A....................................	Jan. 29	Orange 8	White 2
B....................................	Jan. 29	Black 10	Blue 0
C....................................	Jan. 29	Blue 6	White 4
D....................................	Jan. 29	Yellow 8	White 2

This record reports the tests in the order in which they were given, as do other records. Again the reactions to blue seemed somewhat surprising. That blue should be rejected as freely as white, when appearing with black, and that blue and white should be accepted almost indifferently, are not results that one should expect. These facts seem to confirm the hypothesis that blue has a special brightness value for the chick.

Further investigation followed with six other chicks, incidental to the direct line of investigation. Table 24 shows the first preference reactions of chicks nos. 17, 18, 20, 32, 33, and

39 to black-blue. The preference tests are not representative of our chicks in general, for those chicks that already had a preference for black were rejected because they were not suitable for the special purposes of the experiment of which this black-blue training formed a part. There were a few of these. But this does not affect in the least the point that I wish to make in connection with the effects of training. The state in which the black-blue modification persisted at the time of the later color preference tests is shown in the columns under "Persistence." The tests on blue-white, black-white, blue-yellow, blue (tint no. 1) -yellow, blue-blue (tint no. 1) were given in the order named and, in all but two cases, immediately following the persistence tests. The most striking feature of these results is again the character of the reactions to blue. If brightness were the only factor, a chick trained to black-blue would be expected thereafter to react positively to the less bright of two stimuli, other things being equal, when a different combination were presented. But chicks that one minute accepted black and rejected blue, that is, selected the card of lower brightness value, the next minute accepted white and rejected blue. How shall we explain this behavior if we consider merely the

TABLE 24

SOME EFFECTS OF TRAINING

			Preference			Persistence			Preference after Training										
No. of chick	Age	Training	Black	Blue	Interval	Black	Blue	Interval	Blue	White	Black	White	Blue	Yellow	Interval	Blue (tint no. 1)	Yellow	Blue	Blue (tint no. 1)
17	12	Black-Blue	5	5	30	10	0	2	4	6	10	0	3	7					
18	12	"	3	7	30	8	2	0	3	7	8	2	2	8					
20	12	"	5	5	30	10	0	2	3	7	9	1	1	9					
32	12	"	5	5	32	10	0	0	0	10	3	7	0	10	3	1	9	1	9
33	12	"	5	5	30	10	0	0	0	10	6	4	0	10	1	0	10	5	5
39	12	"	5	5	30	9	1	0	2	8	5	5	1	9	1	5	5		
49	39	None	1	9											1	10	0		
51	39	"	1	9											1	7	3		

brightness values of the stimuli? After black-blue training the chicks quite commonly rejected this blue no matter with what other color it was in combination. It may be suggested that after the long period of training the chicks respond to a particular brightness value, the blue amounting to a certain degree of gray. But no. 32 and no. 33 rejected blue (tint no. 1) when it was used in combination with the much brighter yellow.

The method of training with the electric shock frequently makes the stimulus to which it is attached the emphatic one. In a word, the chicks thus trained may not be guided in their reactions by the color through which they escape, but by the color in connection with which they are shocked. This reaction is one primarily of rejecting blue, rather than of accepting black. It is indicated by such reactions as those of nos. 32, 33, and 39 to black-white after having been trained to black-blue. When white replaced the blue of the original training combination, the stimuli became almost indifferent to the chicks. Again, the same chicks seemed indifferent to the color presented with blue. When required to react to blue-white there was no hesitancy, the response being one of getting-away-from-the-blue-no-matter-what-the-other-color. For data see table 24.

All the chicks did not behave so, however. A comparison of the corresponding reactions of nos. 17, 18, and 20 is instructive. These animals, when white replaced blue as above, responded definitely and positively to black, and were quite lost when white accompanied blue. With these chicks black seemed to be the guiding stimulus.

It is sometimes said that negation is affirmation, but is this true in any proper psychological sense? Naturally, avoidance of one object means the acceptance of some other object—in the sense that leaving one place means going somewhere else. But does the "somewhere else" need to be defined as a constituent element of the avoiding reaction? Or, upon the occurrence of a positive response, is it necessary to consider the point of departure, which is objectively definable, of course, as a part of the process? The point of departure in the latter or of arrival in the former case does not appear to be essential.

Passing now from the standpoint of stimulus to that of reaction, why should a positive response be regarded as a simultaneous negative response? As antagonists may they not mutually exclude each other? But only in so far as a positive reaction essentially includes a negative one and *vice versa, is* affirmation psychologically negation.

There still remains another aspect of the relation between rejecting and accepting, their possible necessary concomitance. But if, with innervation of a given motor center, there is, according to the Muensterbergian action theory, a simultaneous inhibition of the antagonistic motor center, we are bound to think of real affirmation and real negation as distinct functions, for inhibition is not negation.

What, then, shall we say of our method as a "discrimination method?" From the point of view of behavior discrimination is selective reaction. In this sense the Yerkes method is a discrimination method.

It is interesting to observe the result when neither black nor blue are in the test combination presented after the training. No. 44 on May 22 completed the black-blue habit with three errorless series. On June 6 its persistence test was black, 10; blue, 0. The same day its preference tests on orange-white resulted 5–5. The daily training on orange-white, continued from this date, progressed as follows: 7–3, 8–2, 7–3, 10–0, 10–0, 10–0. No. 43, the same age, began black-blue training on the same date as no. 44 and completed the work the day after no. 44 with three perfect series. Its persistence test on June 6 resulted also 10–0. But when tested on the same day for its orange-white preference prior to the training on this combination, its record was orange, 10, white, 0. The figures thereafter were 9–1, 9–1, 9–1, 10–0, 10–0, 10–0. It is apparent in both these cases that the black-blue training strikingly predisposed the chicks to react positively to the darker of the two stimuli in the second combination. It cannot be urged in regard to no. 44 that, either on account of ready modifiability or an easy combination, this was simply a case of rapid learning unassisted by the previous acquisition, first, because orange-white, as indicated by earlier tests, is not so easy a combination; and secondly, the rate of acquisition by this chick was only average, nine days' training having been required for it to complete the black-blue habit.

The important exception to the general rule for brightness training, namely, that when the color which the chick was trained to avoid was presented in combination with a new color, the chick continued its specific avoiding reaction regardless of the relative brightness values of the stimuli, demands, I believe, that color quality as well as intensity be assumed as a determining factor in the reactions of these chicks.

F. The Persistence of Modifications

Hints of the material about to be presented have necessarily been dropped in the discussion of previous topics. Yerkes [1] publishes in his work on the dancing mouse a valuable table of results on "Measurements of the Duration of a Habit." Commenting on this data, he says, "It is safe, therefore, to conclude from the results which have been obtained that a white-black or black-white discrimination habit may persist during an interval of from two to eight weeks of disuse, but that such a habit is seldom perfect after more than four weeks." If one should assume that the chicks depended upon the element of brightness only, the results obtained for them in our black-blue tests would be comparable with the black-white and white-black records of the mice, provided one allowed for age differences, as well as for the fact that the discrimination, assuming the human standard, was made more difficult for the chicks on account of the smaller difference in the brightness of the two stimuli.

The chicks in these tests (see table 25) were placed in the entrance box in the manner followed in the original experiments and allowed to escape from the apparatus to the cage. The cards were exchanged after each trial, that is, regularly alternated right and left. No shock was given and both exits remained open throughout. There was a noticeable difference in the behavior of the chicks in the apparatus after the interval. Instead of smoothly going to work they usually hesitated a few moments and craned their necks about before starting for an opening. The same kind of phenomenon was noticeable, ordinarily, in the behavior of a previously trained chick when lifted in the hand after an interval of some weeks during which it had not been handled. Whereas the animal had come to submit freely and without struggle in the course of the original training, now, when grasped over the back, it sometimes kicked,

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[1] Yerkes, R. M.: *Op. cit.*, p. 256.

chirped, or attempted to make flapping movements with the wings. For the tests of persistence, excitement of this kind was avoided as much as possible.

In estimating the value of the results printed in table 25, it must be remembered that chicks nos. 32, 33, 38, and 39 had 16 days' size training in the interval. Also, nos. 43 and 44 had orange-white training to perfection between the first and the second persistence tests.

TABLE 25

The Persistence of Habit

Chick	Sex	Training	Days' interval	R	W	First selection
16	Female	Black-Blue	30	10	0	
17	"	"	30	10	0	
18	"	"	30	8	2	Black
19	"	"	30	7	3	"
20	Male	"	30	10	0	
24	"	Small-Large	19	6	4	Large
25	Female	"	17	6	4	Small
32	"	Black-Blue	32	10	0	
"	"	"	55	8	2	Black
33	Male	"	30	10	0	
"	"	"	51	9	1	"
34	"	Small-Large	71	9	1	Small
38	"	Black-Blue	31	4	6	Blue
"	"	"	48	5	5	Black
39	Female	"	30	9	1	Blue
43	"	"	14	10	0	
"	"	"	21	10	0	
"	"	"	77	10	0	
44	Male	"	15	10	0	
"	"	"	22	10	0	

Of eight mice which Yerkes trained in black-white or white-black, only two showed perfect persistence of the habit after an interval of four weeks. Of nine chicks trained in black-blue and tested in a similar way after 30 days, five obtained perfect records.

The behavior of no. 34 in the reaction box equipped with the size cards 71 days after the completion of the original training furnished a nice commentary on the "intelligence" of the animal. This chick, standing naturally, was 19 cm. high, measured to the highest point of its back. So large that the larger of the two openings would permit its passing out with difficulty, it crouched at the smaller opening and attempted to go through it at every trial but the last. Each time, as soon as it got its head through the small opening and was just beginning to struggle, it was brought back to the entrance box for the next trial. The record of its behavior found in table 25 is made subject to the irregularity reported below. The result of this persistence test is the same as that in its last training series. It would be difficult to reach any trustworthy conclusion in regard to the persistence of the small-large habit from the data at hand, for these data have to be considered together with a certain defect in the adjustment of the apparatus. When the persistence tests of nos. 24 and 25 were made, these chicks were so large that they had to *squeeze* through the smaller opening. For the test of no. 34 the small opening was made slightly larger and a dimension of the larger opening altered to preserve similarity of shape.

TABLE 26

The Rapidity of Modification and its Permanence

Black-Blue Training

Chick	Age	Sex	Trials	Errors	Interval	Persistence	
						R	W
16	12	F	100	28	30	10	0
17	12	F	60	20	30	10	0
18	12	F	100	35	30	8	2
19	12	F	60	28	30	7	3
20	12	M	60	19	30	10	0
32	12	F	30	10	32	10	0
33	12	M	70	20	30	10	0
38	12	M	100	25	31	4	6
39	12	F	70	20	30	9	1
Index of modifiability						72.2	

For the assistance it may be to others in estimating the value of these tests of the persistence of modifications, it should be stated that some of the chicks were in poor physical condition when the tests were made. In the confinement of the laboratory few chicks remained in normal physical condition after eight to twelve weeks.

It is interesting to study the above data on the persistence of habit in connection with the number of trials and errors in the original training series to see if any correlation exists between the rapidity of acquisition and its permanence or retention. In table 26 the necessary items are set side by side. One often hears the pedagogical byword, "Come easy, go easy." This certainly does not apply to the chicks tested. Of three animals that required 100 trials to perfect the black-blue modification, one made a perfect persistence test; of two that required 70 trials, one made a perfect record; of three that required 60 trials, two made perfect tests; and the chick that completed its work in the shortest time also made a perfect record. The number of trials given in the table is exclusive of preference and final perfect series. In the error column is given for each chick the total number of errors in this number of trials. Of five chicks that made twenty or less errors, four had perfect persistence tests; of four that made more than twenty errors, one had a perfect persistence test.

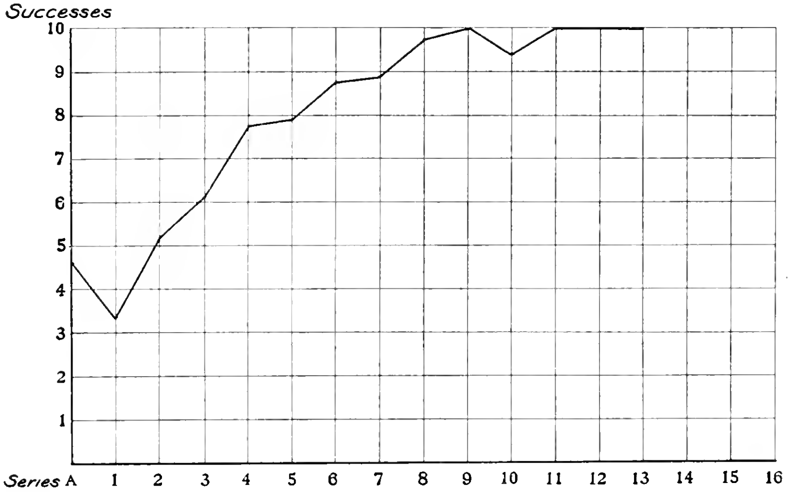

FIGURE 11—The success curve for nine chicks of the same age in black-blue training, plotted from averages based on data given in tables 13 and 20. Distances along axis of abscissae represent series; along axis of ordinates, right or successful trials.

One may well question the appropriateness of the expression "trial and error" intended to be descriptive of this method of learning. If the number of errors is included in the number of trials, as for example in this paper, then the original term is awkward if not illogical. These animals learn through successes as well as failures, and the sum of the number of both equals the whole number of trials. In this sense the method is more accurately described as a method of success and failure. Again, if the word " trial " in the above expression is meant to refer to the principle of random activity, and " error " to learning based on the avoidance of harmful stimuli, still " trial and error " is an inadequate descriptive term. One could as well say the general law is, " Prove all things; hold fast that which is good." If the term selection be construed broadly enough to include both the positive and negative aspects, then trial and selection appears on the whole to be a more satisfactory name for this type of modification.

If the " index of modifiability," to borrow Yerkes' term and definition, be considered " that number of tests after which no errors occur for at least thirty tests," the index of modifiability of these Barred Plymouth Rock chicks, under the conditions described, is 72.2.

The rate of modification for the same nine chicks is set forth graphically in fig. 11. This is a success curve plotted from data in tables 13 and 20. The averages upon which the curve is based, including the preference test, are as follows: 4.7, 3.3, 5.2, 6.1, 7.8, 7.9, 8.8, 8.9, 9.8, 10, 9.4, 10, 10, 10. It is quite possible that valuable accretions to our knowledge of habit and instinct may come through a careful study of the course of development of reactions of both types and a comparison of the quantitative relations involved. I offer the curve of the development of the complete pecking co-ordination (fig. 7) and that of the development of the black-blue modification (fig. 11) as suggestions for the beginning of a more specialized investigation.

SUMMARY AND CONCLUSIONS.

The early post-embryonic life of the chicks continued the scope of activities already begun in the egg. The alternations of passivity and activity, the lifting movements of the head combined with stretching movements of the legs, the occasional reflex forward thrust of the bill followed usually by movements of the mandibles, loud chirping along with other violent activity, —all these were common aspects of the behavior of chicks just before as well as immediately after hatching. The pecking reaction might have assisted in the process of exclusion, but by far the most common reaction while the chick was struggling in the egg was the lifting movement of the head and bill. This reaction actually broke shell and tore confining membranes.

The chicks, left to develop naturally in the vicinity of food and water, usually found the water by fortuitous pecking or by performing the drinking movement in imitation of other chicks. By imitation here I mean that the performance of drinking by one chick in the presence of another sometimes stimulated that other itself to perform the drinking act. I reach this conclusion on the basis of incidental observations in the course of the study of other problems. I have no doubt that a special study of this point will bear out the above conclusion. Chicks kept without drink until the third day did not perform the drinking reaction by accident or imitation only. The reaction was elicited by a variety of objects before drink of any kind had touched the bill of the chicks, showing that, when the need of the organism became sufficiently imperative, the drinking reaction appeared in response to many of the same kind of stimuli as the unpracticed pecking reaction. The drinking instinct does not "have to be supplemented by imitation, accident, intelligence, instruction, etc., in order to act." And it is not improbable that the "sight of still water" will be found to evoke this reaction.

The few tests that were made to determine the effect on the pecking reaction of disuse during the first two days of the life of the chick seemed to show (1) that the development of the instinct was retarded by disuse, and (2) that the retardation was quickly overcome with use.

The stimulus for the pecking reaction did not have to be some object of a size convenient for eating. The bill of the chick was used as a testing organ.

Pecking situations were found in which the reaction to one stimulus exerted an inhibitory effect on the reaction to another.

The assumption that chicks do not peck at or eat food when they cannot see it is not supported by the experimental data submitted in this paper. The chicks did peck at and eat food when the light was excluded.

The pecking instinct was investigated primarily to discover the meaning that should attach to such terms as perfection, accuracy, or congenital definiteness, when applied to this response. Pecking is a co-ordination of three reactions,—striking, seizing, and swallowing. The amount of improvement from day to day of the complete co-ordination, not only, but of the components separately, was measured. Records were taken up to the twenty-fifth day. The pecking improved in accuracy very rapidly during the first two days, reaching by the beginning of the third day an efficiency numerically represented by 29.29 on a scale of 50; by the beginning of the eleventh day an efficiency of 40.10 was attained; and during the rest of the period of measurement the degree of accuracy ran no higher than 42.57. The improvement was retarded more by errors in seizing than by errors in swallowing, and more by errors in swallowing than by errors in striking. After the third day the imperfection of seizure remained greater than that of the other two reactions combined. The striking reaction, seldom widely erroneous, improved rapidly and without relapse, closely approximating perfection by the fifth day,—a degree of accuracy that might easily have inspired belief in the perfection of the pecking instinct.

It did not appear that the effect of social influence was such as to increase the rate of improvement in accuracy of the pecking reaction. It may be that the change in the mode of functioning of the organism due to the presence of others was in the direction of increasing the intensity and rapidity of the reactions, without increasing their rate of improvement in accuracy. Such a variation would have selective value, inasmuch as the animal would get more food in a given time, even though the pecking were no more accurate.

The important exception to the general rule for brightness training, namely, that when the color which the chick was trained to avoid was presented in combination with a color other than that used in the original training, the chick continued its specific avoiding reaction regardless of the relative brightness values of the stimuli, demands, I believe, that color quality as well as intensity be assumed as a determining factor in the reactions of the chicks.

The chicks, without much doubt, responded selectively to one of two objects of different size.

The results of the form tests reported were purely negative.

There was no conclusive evidence that previous formation of the black-blue habit facilitated the formation of the small-large habit.

The tests of retention of the black-blue habit after size training, which intervened between the original training and the retention tests, at least suggest a method that may be useful in studies of the interrelation of habits.

The method of training with the electric shock frequently made the stimulus to which it was attached the emphatic one. In such a case the chicks were not guided in their reactions by the color through which they escaped, but by the color in connection with which they were shocked. That is, the reaction was negative to blue, not positive to black, when this occurred in black-blue training. Psychologically, it seems, negation is not affirmation.

Of nine chicks perfectly trained in black-blue, five made perfect persistence tests after an interval of thirty days.

In the case of the same tests of retention, rapidity of modification was positively correlated with permanence of modification.

For these nine chicks the "index of modifiability" was 72.2.

"Trial and error" is an unsatisfactory name for this method of learning.

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BEHAVIOR MONOGRAPHS

Volume 1, Number 2, 1911 Serial Number 2

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ROBERT M. YERKES
AND
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THIRTEEN FIGURES

A report prepared for the Committee of the American Psychological Association on the Standardizing of Procedure in Experimental Tests

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CONTENTS

INTRODUCTION

In 1907 we were asked by a Committee[1] on the standardization of psychological methods, appointed by the American Psychological Association, to attempt to devise "a standard procedure for testing color vision in animals." This we undertook to do. Four years have been devoted to the task, and during that time the scope of the investigation has been extended to include methods of studying the perception of (a) light (colorless), (b) size, (c) form, and (d) distance, as well as (e) color. We thus broadened our task because knowledge of the light vision of an animal is necessary for the intelligent study of its color vision, and, further, because it seemed to us highly desirable that closely related methods should be employed in the quantitative investigation of the several aspects of vision in an organism.

We beg leave now to submit to the Committee a full report of our researches. Although we feel encouraged by the progress which we have made in our search for highly controllable methods of studying the several aspects of vision, we realize that the methods which we recommend as standard procedures should be accepted rather as improvements upon procedures now in common use than as new and perfect methods. Indeed, we would urge the desirability and the fundamental importance of continuous efforts to improve upon our present methods

It is with pleasure that we express our indebtedness and gratitude to the following individuals and scientific firms for varied assistance.

Especially in connection with the spectral color apparatus, several physicists have aided us greatly. In fact, the construction of the apparatus would hardly have been possible without the aid of Professors Millikan and Gale of the University of Chicago and Professors R. W. Wood, A. H. Pfund, and J. A. Anderson of the Johns Hopkins University. For mechanical assistance we thank Mr. C. M. Childs, mechanician attached to the Physical and Psychological Laboratories of the Johns Hopkins

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[1] Consisting of Professors Angell, Judd, Pillsbury, Woodworth, and Seashore.

University, and Mr. William Gaertner of Chicago. Mr. B. Spencer Greenfield, formerly mechanician in the Harvard Psychological Laboratory, has aided us in many ways, but especially by making drawings of the various parts of our apparatus.

For information and advice on varied topics we thank Professors G. H. Parker, H. W. Morse and G. W. Pierce of Harvard University; Doctor Louis Bell, consulting electrical engineer, Boston; Professor J. W. Baird of Clark University; Professors Edward L. Nichols and E. B. Titchener of Cornell University; Mr. A. J. Marshall and Mr. G. A. Anderegg of New York; Mr. Willard Greene; Doctors P. G. Nutting and W. W. Coblentz of the United States Bureau of Standards; Mr. James Wallace of the Cramer Dry Plate Company; Eimer and Amend; Metz and Company; the National Electric Lamp Association; Mr. J. G. Biddle, and the Arthur H. Thomas Company.

The late Professor W. A. Nagel of the University of Rostock, master of the technique of physiological optics and throughout his life a specialist in the problems of vision, was especially painstaking in his efforts to further our investigation. His death in the prime of life leaves with us a keen sense of personal loss. We desire to express our appreciation of the man and the scientist.[1]

During the early portion of our investigation, we profited by the valuable assistance of Doctor E. G. Congdon. He worked especially on the problems of ray filters. The authors wish to emphasize the importance of Doctor Congdon's share in the investigation. Except for the fact that he is not in any way responsible for the methods and apparatus which we have during the past two years decided to perfect and recommend as standard procedures, his name should appear as a joint author of this monograph.

Professor Yerkes, who was charged by the Committee with the general direction of the work, is chiefly responsible for the preliminary portion of the report and for the method and apparatus

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[1] After this manuscript had been written, with the exception of the final descriptions of the light and color apparatus, there appeared in Tigerstedt's *Handbuch der physiologischen Methodik* an admirable review and discussion of "*Methoden zur Erforschung des Licht- und Farbensinns*" by Professor Nagel. Since Professor Nagel in his paper presented some of the material which we had intended to publish, it has seemed to us desirable to omit certain portions of our report, as originally planned. We especially commend Professor Nagel's discussion to those who are interested in human vision.

recommended for the study of "*light vision.*" To Professor Watson chiefly belongs the credit for the method and apparatus herein described and recommended for the study of "*color vision.*"

We have attempted, in this report, first, to indicate pointedly the principal merits and defects of several of the more important and commonly employed methods of studying vision, and, second, to perfect and recommend, *for all intensive quantitative investigations*, a procedure for testing light, size, form, and distance perception, and a procedure for testing the various aspects of color perception. It is our hope that this monograph may prove of service to other investigators by enabling them to avoid the use of eminently unsatisfactory, although commonly used, methods, and by facilitating the adaptation to their special needs of what we judge to be the more promising types of procedure.

At the outset, it is essential that we emphasize the ground upon which we recommend certain procedures for standardization. We have neither discovered nor devised perfect methods; we have merely done our best to propose methods whose scientific value is obvious and whose possibilities of improvement seem almost unlimited. Our standard procedures are recommended only for thoroughgoing, intensive, quantitative work. Simpler and more conveniently manipulated apparatus may be used in the case of preliminary exploratory work. We do not wish to discourage the use of crude and relatively uncontrollable methods for the study of vision, but we do most emphatically recommend that these methods be abandoned as soon as the rough problem-defining portion of an investigation has been completed. The employment of colored papers, colored yarns, painted backgrounds, and similar conditions, for the testing of color vision may yield valuable qualitative results, and they may be used to advantage if the experimenter realizes and clearly states that his control of the visual conditions of his tests is extremely imperfect. In this methodological investigation, it has been our aim to perfect procedures which shall vastly increase the experimental control and describability of the visual stimuli to which an organism is subjected.

Without further introduction, we shall present our results in accordance with the plan given in the table of contents.

I. METHODS OF INVESTIGATING *LIGHT* VISION

1. Sources of stimulus

A source of stimuli for the study of *light* vision[1] in animals should fulfill four important requirements which may be designated as naturalness, controllability, constancy, and measurability.

(1) Naturalness.—The source should yield light which is identical with, or closely similar to, daylight or sunlight in quality. Or, in other words, stimuli which are used for the investigation of the visual capacity of an animal should be "familiar" or "natural" to the animal. As has been pointed out by Nichols, "the normal stimulus of the eye is diffuse daylight and artificial stimuli which depart widely from it either as to intensity or quality are sure to be unsatisfactory and are likely to be injurious."[2] We may expect natural or normal reactions only when stimuli to which the animal is accustomed are employed. This is the principal reason for the use of daylight and sunlight, instead of artificial light, in experiments on vision.

(2) Controllability.—The source of light should be, so far as is possible, under the control of the experimenter. This requirement applies to both quality and intensity, but it is especially important in connection with work on *light* vision that the intensity of the stimulus be accurately controllable.

(3) Constancy.—The source under given conditions should yield light whose quality and intensity are constant. No known source fulfills this requirement. Certain of the high temperature electric lamps are most nearly satisfactory.

(4) Measurability.—The light which a given source produces should be readily and accurately measurable in terms of visual (e. g., photometric) and energy (e. g., radiometric) units. *In the employment of visual, and all other stimuli, it is desirable to obtain three sets of measurements: the psychological (sensation-unit), the physiological (stimulus-unit), and the physical (energy-unit).*

With respect to their relations to the four requirements which lights used for experiments on vision should fulfill we shall

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[1] Frequently termed "brightness" vision.

[2] Nichols, E. L. Daylight and artificial light. Illuminating Engineer, 1908.

now examine the most important and widely available natural and artificial sources of light.

a. The sun.—For the eyes of most animals, it is well known that daylight and sunlight are the natural photic stimuli. Indeed, it is in connection with the reception of such stimuli that the eye has developed. As pertinent evidence of the truth of this statement we may mention the fact that the maximum of the luminosity curve for the human eye and that of the energy curve of sunlight lie in the same region of the spectrum.

The sun fulfills neither the second nor the third of our four requirements: it is uncontrollable experimentally and inconstant. To a degree which few untrained observers realize, the composition or color values of daylight and sunlight vary with the condition of the atmosphere, the altitude of the observer, the hour, and the season. Like statements may be made concerning intensity, for at mid-day the light is many times more intense than at morning or evening, and during the summer it is likely to be more intense than during the winter. These considerable variations in quality and intensity, in connection with the fact that no human experimenter is able to control them accurately, render the sun unsatisfactory as a source of stimuli for the *quantitive* study of light vision. For *qualitative* investigations it is invaluable because of its naturalness.

In naturalness the sun is preferable to all other sources of stimuli; with respect to controllability and constancy it is surpassed by several artificial sources; and in measurability it is as satisfactory as most other sources. If we could devise satisfactory ways of controlling the quality and intensity of sunlight, it obviously would be ideal for the study of vision.

b. Nernst lamps.—The Nernst glower yields a light which is qualitatively and intensively fairly satisfactory for the study of vision. In quality its light, although less like daylight than that of the open arc, is about as satisfactory, all things considered, as that of any artificial source at present available.[1] It, therefore is likely to prove reasonably natural. Its spectrum is continuous, but rather weak in the violet.

The quality and intensity of the Nernst light is to a high

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[1] Progress in the art of artificial illumination is so rapid that what is written to-day may be misleading to-morrow. The statements in this report must be read with the understanding that they were true in the year 1910.

degree controllable by the experimenter. On a well controlled circuit, the life of the Nernst glower is six hundred hours for the direct current and eight hundred hours for the alternating current, regardless of position. During the first two or three hundred hours of the life of a "glower" the intensity of the light yielded by it diminishes rapidly (10-15 per cent). A new lamp should be allowed to burn for several hours before being used for quantitative experiments. During the mid-life period of the Nernst it is possible, by accurately regulating the current, to obtain light which is fairly constant in quality and intensity. As a rule it is desirable to mount the Nernst glower separately in order to avoid the influence of the "heating coils" upon the quality of the light.

Measurements of quality and intensity can be made as readily with this lamp as with any other source of light. The use of from one to six glowers, according to the demands of the investigation, renders intensities of from 50 to 500 c. p. obtainable.

As compared with the sun, the Nernst lamp is somewhat less satisfactory in respect to the naturalness of its light, vastly more satisfactory with respect to controllability and constancy, and equally satisfactory with respect to measurability. It is, of course, to be noted that it can not be used when high intensities of illumination are required. For more than five hundred candle power the sun and the electric arc are more practicable sources of light.

On the whole the Nernst glower commends itself to us as highly satisfactory for experiments on vision and for the photic stimulation of lower organisms. Its adaptability, stability, and efficiency are important considerations. For *quantitative* work on vision, with stimuli of medium intensities, it certainly is preferable to the sun and to most artificial sources of light.

For detailed information concerning the performance, characteristics of light, prices, etc., of this glower we refer the reader to the Bulletins of the Engineering Department, National Electric Lamp Association of Cleveland, Ohio, to "Lectures on illuminating engineering," Baltimore, The Johns Hopkins Press. 1911, vol. 1, p. 72, to "The Standard handbook for electrical engineers" (2d ed., 1908), and to various publications of the Nernst Lamp Company, Pittsburg, Pa.

c. Tungsten lamps.—This form of incandescent lamp yields a light, which, under favorable conditions, is as satisfactory qualitatively as that of the Nernst glower. In naturalness it may therefore be classed with the latter. The lamp is highly efficient and its light reasonably well fulfills the requirements of controllability, constancy, and measurability. The normal life of the tungsten is about eight hundred hours, and during this period the intensity of the light diminishes by eight to ten per cent. This decrease is barely half that of the Nernst. With the aging of its filament, the quality of the tungsten light changes somewhat, but not so markedly, it would seem, as that of the carbon incandescent. The filament is brittle when cold and there is considerable risk of breakage in moving the lamp quickly, but when hot it is tough and flexible and the lamp may be handled safely.

For the quantitative study of light vision we recommend the tungsten incandescent lamp (1) because it, as nearly as any other reasonably convenient artificial source, meets the requirements of naturalness, controllability, constancy, and measurability, (2) because it is efficient, inexpensive, easily cared for, and adaptable, and (3) because, when carefully seasoned and used, its quality and intensity do not vary greatly during the mid-life period.

It should be emphasized that, in contrast with the Nernst, the tungsten lamp exhibits a steady decrease in intensity during its life, instead of relatively rapid decrease at the beginning and end of the life-history and constancy during the mid-life period. This fact renders the Nernst lamp preferable to the tungsten for certain purposes.

Valuable information concerning tungsten lamps,[1] which are now manufactured in a great variety of forms, may be obtained from the Bulletins of the National Electric Lamp Association, No. 6A, No. 6B, No. 6D, No. 6E. These Bulletins may be obtained from the Engineering Department of the National Electric Lamp Association, 4411 Hough Avenue, Cleveland, Ohio. R. W. Hutchinson's "High-efficiency electrical illuminants and illumination," New York, 1911, also is useful.

d. Carbon incandescents.—Of the numerous forms of carbon

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[1] The tantalum lamp has seemed to us less satisfactory for our purposes than the tungsten, and detailed consideration of it is therefore omitted.

incandescent lamps, the metallized filament lamp is, for our purposes, the most satisfactory. All carbon lamps yield a yellowish light, which tends to become reddish with age, and they exhibit a greater sensitiveness to fluctuations in current than does the tungsten. In neither quality nor intensity are carbon lamps as constant as tungsten and Nernst lamps. We recommend them only in case the other lamps are not available, or, for some reason, prove impracticable.

e. Carbon arcs.—The carbon arc as a source of light is valuable for experiments on vision which require high intensities. For all other purposes the Nernst and the tungsten are preferable. The crater of the arc yields a light whose spectrum is continuous and whose quality approaches sunlight more nearly than that of any other artificial light. The light of the arc itself, as contrasted with that of the crater, presents a banded spectrum which is especially intense in the violet. Intensity variations are almost always great, except in the crater of the arc, and it is difficult to control them. These defects render this form of lamp slightly, if any, more satisfactory than the sun for the quantitative investigation of *light* vision. It should be stated, however, that the arc lamp is eminently satisfactory when the light from the crater alone is used.

The faults mentioned above are at their minimum in lamps of the "baby arc" family, to which belong the Siva arc, the Lilliput, the Midget, and other lamps. They are small carbon arcs, used chiefly in Europe, which under high pressure furnish an excellent quality of light in fairly uniform intensity. Unfortunately, none of these arcs burns well out of the horizontal position.

f. Acetylene lamps.—The quality of acetylene light is fairly satisfactory, but its intensity is with difficulty kept constant. In the absence of electricity, this form of lamp may be used to advantage for many tests of vision.

g. Gas lamps.—The light is likely to be over-strong in orange and yellow. Under carefully chosen conditions, in the absence of electric lights, incandescent gas lamps may be used for tests of vision.

h. Oil lamps and candles.—Like the light of the gas flame, that of oil lamps and candles is likely to be over-strong in yellow. With respect to constancy, controllability, and measurability, both oil lamps and candles constitute fairly satisfactory sources, provided the intensity of light needed is not high.

Tables 1 and 2 [1] present data concerning the color- and intensity-values of the sources of light which are most commonly used. It is needless to state that these data are not highly accurate.

TABLE 1

COLOR OF COMMON ILLUMINANTS

Illuminant	Color
Acetylene	Nearly white
Arc light (enclosed)	Bluish white to violet
Arc light (open)	White
Candle	Orange yellow
Carbon incandescent (below voltage)	Orange to orange red
Carbon incandescent (normal voltage)	Yellowish white
Gas light (open flame)	Yellowish white to pale orange
Gem metallized filament incandescent	Nearly white, slightly yellowish
Kerosene lamp	Orange, slightly yellowish
Nernst lamp	White
Mantle burner	Greenish white
Sky light	Bluish white
Sun (high in sky)	White
Sun (near horizon)	Orange red
Tantalum	White
Tungsten	White

TABLE 2

INTENSITY OF LIGHT SOURCES IN CANDLE POWER PER SQUARE INCH OF ILLUMINATING SURFACE

Source	Intrinsic brilliancy	Remarks
Opal shaded lamps (electric)	$\frac{1}{2}$ to 2 c. p.	
Frosted incandescent lamps	2 to 5	
Candle	3 to 4	
Gas flame	3 to 8	Varies widely
Oil light	3 to 8	
Mantle burner	20 to 25	Probably too low
Acetylene flame	75 to 100	
Enclosed arc lamp	75 to 200	Depending on globe
Incandescent lamps (carbon)		
Carbon 4.0 watts per candle	300	
Carbon 3.5 watts per candle	375	
Carbon 3.1 watts per candle	480	
Gem metallized filament incandescent, 2.5 watts per candle	625	
Tantalum incandescent	750	
Tungsten incandescent	1,000	
Nernst lamp (bare)	800 to 1,000	
Open arc lamp	10,000 to 100,000	(200,000 in crater)
Sun on horizon	2,000	
Sun at 30° elevation	500,000	
Sun at zenith	600,000	

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[1] These tables are taken from "Data on illumination." Bulletin of the Engineering Department of the National Electric Lamp Association, No. 7, June 1, 1907.

i. Recommendations concerning sources for tests of LIGHT *vision.*—In view of the above considerations, and a multitude of others which space limitations force us to omit, we offer the following recommendations concerning sources of stimuli for the investigation of light vision.

(1) That for all strictly accurate quantitative work the tungsten, or the Nernst, be used, in its mid-life period, and on a well-regulated circuit.

The lamps should be burned on a rheostat circuit at a voltage slightly below the optimal (2–3 volts for 110 volt direct current lamp), so that as the efficiency diminishes with age (as is shown by frequent photometric tests), an increase in voltage will serve to maintain the lamp at its standard efficiency. This precaution, and method of obtaining a constant intensity, is especially advantageous in connection with experiments which must be continued for weeks and in the midst of which it is inadvisable to change lamps.

Attention is called to the following important points in connection with the use of tungsten and Nernst lamps. (a) The lamp should be well seasoned and in perfect condition; (b) it should have been burned under constant pressure for from ten to one hundred hours, according to the type, before being employed in quantitative experiments; (c) the current should be carefully regulated during use of lamp; (d) by frequent metric tests the experimenter should discover variations in the quality or intensity of the light yielded by a lamp, and he should replace it as soon as he detects marked changes, such for example as those indicating the end of life.

(2) That the sun be employed as a source for check or comparison experiments, in order that the normal reaction of the animal shall be observed with certainty. That experiments with sunlight or daylight be performed at the same hour each day, preferably toward noon, and under as nearly identical atmospheric conditions as are obtainable.

(3) That in case of the inaccessibility of an electric current, acetylene or gas be used under carefully controlled conditions.

(4) That for qualitative, as distinguished from quantitative, experiments, sunlight or daylight be employed in the study of *light* vision.

2. Measurements of stimulus

Measurement of the photic stimuli employed in a quantitative study of vision is essential. Only on the basis of exact statements concerning the values of stimuli can the conditions of an observation be reproduced and the reliability of the observation determined.

Two varieties of measurement are available at present for students of visual reactions. They may be designated as (a) the psycho-physiological, and (b) the physical. As one of the most important examples of the former variety of method we have photometry; as a typical example of the latter method, radiometry.

Photometry involves optical comparison of two illuminated areas, one of which is the standard and the other the compared area. This comparison results in a measurement of the visual stimulus in terms of a conventional unit of light (candle-power, hefner, carcel). The method, in all of its forms, is dependent upon the visual capacity, training, and the special skill of the observer who attempts to use it. For this reason, and others only less important, it is usually desirable to supplement photometric measurements of photic stimuli by measurements of their value in terms of energy. Hence the pertinence of physical methods.

Determination of the value of photic stimuli in terms of heat units by a radiometric procedure has proved feasible. Radiometry yields a measurement which is relatively independent of the visual peculiarities of the observer, and it therefore supplements in an invaluable manner the results of photometry.

a. Photometry of white light stimuli.—It is difficult to obtain accurate measurements of the stimuli employed in investigations of vision which are conducted in daylight. But whenever a dark-room is used, it is possible to employ photometry profitably. We shall limit our recommendations to dark-room measurements.

The Lummer-Brodhun prism photometer,[1] with a standardized

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[1] Brief descriptions and prices of the various forms of the Lummer-Brodhun photometer may be found in the " Photometrische Apparate " catalogues of Franz Schmidt and Haensch, Berlin, Germany. The catalogues may be obtained, and importations satisfactorily made, through Mr. James G. Biddle, 1114 Chestnut Street, Philadelphia, Pa. See also Stine, W. M., " Photometrical measurements," New York, 1904.

tungsten lamp as a source,[1] is recommended for use in connection with the methods of investigating vision whose adoption, subject to all possible improvement, we urge.

The Hefner amyl-acetate lamp provides a photometric standard which is unsatisfactory because of its yellowish color. In all cases, qualitative (color) difference between the standard and the photometered light should be avoided.

If an electric standard is inaccessible, a standard candle may be employed.

In case the Lummer-Brodhun photometer is not available, some cheaper form, (for example, the Bunsen)[2] may, with care, be used to advantage. It is, however, high time that we students of animal behavior realized that the quantitative investigation of a problem can be made worth while only by the employment of the best methods of measurement which are available. The employment of the most precise instruments for the investigation of vision can not be too strongly urged.

For the determination of extremely low intensity values (threshold stimuli) in limited spaces, we recommend that the Lummer-Brodhun screen be used in connection with a rotating sector. By means of the latter the intensity of the standard may be reduced to any desired amount.

We further recommend that the values of lamps be given in candle power (c. p.) and the value of stimuli in candle meters (cd. m.).

b. Radiometry of white light stimuli.—"Light is not a simple multiple of radiation, but a complicated function of its quality, quantity, and duration."[3] For this reason, measurements of the energy of light are of uncertain value in physiology and

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[1] Standardized electric lamps may be purchased of the General Electric Company, Harrison, New Jersey, or of the Electrical Testing Laboratories, 80th Street and East End Avenue, New York, and the latter will make special photometric determinations, at rates obtainable on request. Problems relating to units of measurements and standards may advantageously be referred by the inexperienced investigator to the National Bureau of Standards, Washington, D. C., S. W. Stratton, Director.

[2] For an excellent discussion of "photometric units and standards" and "the measurement of light" the reader is referred to *Lectures on illuminating engineering*, Baltimore, The Johns Hopkins Press, 1911, vol. 1, pp. 387–506. These two volumes of lectures present also invaluable information concerning the characteristics of sources of light.

[3] Nutting, P. G. The Luminous equivalent of radiation. Bull. U. S. Bureau of Standards, 1908, vol. 5, p. 262.

psychology. Nevertheless, it seems highly desirable that energy measurements be made to supplement our photometric data.

Of the various radiometric devices and methods[1] which are at our command, the radiomicrometer and the selenium cell have been at least partially adapted to our needs and tested in investigations which are now in progress.

Concerning the former instrument Coblentz writes: "The radiomicrometer is essentially a moving coil galvanometer having a single loop of wire with a thermo-junction at one end. This instrument was invented independently by d'Arsonval[2] and by Boys.[3] The former used a loop, one part of which was silver and the other was of palladium. The latter used a junction of bismuth and antimony, which was soldered to a loop of copper wire.

"The sensibility of the Boys instrument was given as $\frac{1}{10\,000\,000}$ to $\frac{1}{94\,000\,000}$ of 1°. From subsequent work with other radiation meters in which this high degree of sensitiveness has never been attained, it would appear that the sensibility of the radiomicrometer was overestimated."[4]

Professor G. H. Parker is at present using for the measuring of photic stimuli, as applied to organisms without highly developed visual organs, the Boys radiomicrometer essentially as it is described by Adams.[5] As he later will publish a description of the method, with the results of his experiments, we need add merely a comment.

The radiomicrometer is certain to prove useful in connection with studies of *light* vision. It is not sufficiently sensitive to enable us to measure directly extremely weak stimuli (threshold or approximations thereto), and it can not be used at all unless a highly stable base is available.

The selenium cell[6] has been classed among the "selective

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[1] Coblentz, W. W. Instruments and methods used in radiometry. Bull. U. S. Bureau of Standards, 1908, vol. 4, pp. 391–460.

[2] d'Arsonval. Soc. Franc. de Phys., 1886, pp. 30, 77.

[3] Boys, C. V. Phil. Trans., vol. 180, pp. 159.

[4] Coblentz. Loc. cit., p. 395.

[5] Adams, J. M. The transmission of roentgen rays through metallic sheets. Proc. Amer. Acad., 1907, vol. 42, p. 673 ff.

[6] Pfund, A. H. The electrical and optical properties of metallic selenium. Physical Review, 1909, vol. 28, pp. 324–336.

Stebbins, Joel. The color-sensibility of selenium in cells. Astrophysical Journal, 1908, vol. 27, pp. 183–187.

radiation meters."[1] It is extremely sensitive, as compared with the radiomicrometer, and it has the great advantage of being serviceable where only a moderate degree of stability is possible. In an adaptation to our needs made by Professor A. H. Pfund, the selenium cell is now being tested by Professor Watson. In view of the results obtained, the apparatus promises well for measurements of both light and color stimuli. It provides a convenient means of equating any two *light*, *size*, or *form* stimuli with respect to intensity of *light*. The measurements may be made quickly as well as accurately. Subsequently, if it prove desirable, determinations of the photometric values of the stimuli may be made. In as much as it promises to be especially valuable in connection with studies of color vision, further description will be reserved for our section on the measurement of chromatic stimuli.

We recommend that photometric measurements of *light* stimuli be supplemented by radiometric measurements, obtained by the use of some form of radiomicrometer, selenium cell, or other heat meter.

3. Application of stimulus to animal

a. Common methods.—There are almost as many methods of applying achromatic stimuli as there are investigators. Many of the methods in common use are excellent for qualitative investigations, but few, if any, are satisfactory for quantitative work.

The type of method[2] most in evidence depends upon the reflection of varying amounts of light (natural or artificial) from the surfaces of paper, wood, glass or metal. White, grey, and black papers and cardboards are extensively used as visual testing materials. They are unsatisfactory in that it is extremely difficult to describe accurately the conditions of stimulation and almost as difficult to control or modify them.

b. Method recommended.—The method which it is our purpose to describe in Section III as a standard procedure for testing

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[1] Coblentz. Loc. cit., p. 454.

[2] Graber, V. Grundlinien zur Erforschung des Helligskeits und Farbensinns der Tiere. Prag und Leipzig, 1884.

Small, W. S. An experimental study of the mental processes of the rat. Amer. Jour. Psychol., 1899, vol. 11, p. 80, p. 133; 1900, vol. 12, p. 206.

Kinnaman, A. J. The mental life of two *Macacus rhesus* monkeys in captivity. Amer. Jour. Psychol., 1902, vol. 13, pp. 98–148, 173–218.

the light vision of an animal involves the presentation, in a dark-room, of two visual areas which differ only in intensity of illumination. These visual areas are obtained by illuminating semi-opaque glass plates with a standard source which is placed on the opposite side from the animal. The chief advantages of this general method of presenting *light* stimuli, in contrast with the reflection methods which are usually employed by psychologists and often by physiologists, are three: (1) The visual stimulus can be controlled accurately with respect to intensity; (2) it may be photometered and radiometered with accuracy; (3) other visual factors than intensity of *light* may be excluded or kept constant; (4) other factors than the visual may be excluded or controlled more certainly and satisfactorily than in the case of most methods.

While recognizing the value of the commonly employed methods as means of obtaining certain kinds of information about the *light* perceiving capacities of an organism, we wish to urge the use of more accurately controllable and measurable stimuli in all quantitative investigations.

II. METHODS OF INVESTIGATING VISUAL SIZE, FORM, AND DISTANCE PERCEPTION

1. Size perception

Students of vision have investigated the perception of size, with few exceptions, by means of crude methods; and the results of such quantitative studies as have been made by excellent methods can not be compared because of fundamental differences in experimental procedure. It has been our purpose to devise a method which shall be adaptable; which shall yield accurate quantitative results; and which shall render possible and profitable the direct comparison of results obtained with different animals.

Size perception, or the ability of an organism to detect differences in size, has been studied chiefly by "the method of the discrimination of objects" (boxes, blocks, balls, glasses, etc.) on the basis of difference in size. Thus, for example, an animal is tested by being required to select the smaller of two boxes in order to obtain the reward of food. The method has many advantages—like all other reasonably well planned qualitative methods—but it does not and can not, as ordinarily used, enable us to determine with accuracy the limits of an animal's ability to perceive difference in size. In other words, it does not lend itself to the thorough investigation of size perception.

We wish to recommend a method whose chief defect, apparently, is unnaturalness, and whose prominent advantages are accurate controllability and describability.

This, in brief, is the method. In a dark-room, and by means of the apparatus described below in Section III, two visual areas are simultaneously exposed to view. These areas differ only in size, and with respect to this character they are under the control of the experimenter. Differences of the compared stimuli as to form, color, light, texture, position, odor, which exist and in varying degrees influence the results obtained by common methods, are largely or wholly excluded by our standardized apparatus.

2. Form perception

The statements made concerning size perception apply also to form perception. The procedure recommended, and for which the necessary apparatus is described in Section III, p. 17, involves the use of standard plates in which are cut openings in the shape of circles, hexagons, squares, and triangles.

3. Distance perception

Few students of vision have considered the problem of distance perception in animals.[1] This is rather because of the difficultness of the task than because the problem lacks interest or importance. We have made some preliminary attempts to devise a satisfactory method of dealing with the subject, but we are not prepared at present to make recommendations. It seems to us especially important that this visual factor be studied in connection with *color* vision.

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[1] Thorndike, E. L. The instinctive reactions of young chicks. Psychol. Review, 1899, vol. 6, p. 284 ff.

Waugh, K. T. The rôle of vision in the mental life of the mouse. Jour. Comp. Neurol. and Psychol., 1910, vol. 20, p. 572 ff.

Yerkes, R. M. Space perception of tortoises. Jour. Comp. Neurol. and Psychol., 1904, vol. 14, p. 17 ff.

III. DESCRIPTION OF STANDARDIZED APPARATUS AND METHOD FOR THE STUDY OF *LIGHT*, SIZE, FORM, AND DISTANCE PERCEPTION

Without wishing to dictate to any experimenter either details of apparatus or methods of experimentation, we present the following description of a mechanical device and of an experimental procedure which in our experience yield excellent results.

1. *Light* or "brightness" apparatus

This apparatus consists of three chief parts: (1) A light box, fig. 1, A; (2) an experiment box suited to the animal to be tested, fig. 4; and between the two (3) a stimulus adapter, fig. 3, by means of which two illuminated areas are simultaneously exposed to view.

The wooden light box, A, is divided into two compartments, C and D, by the partition, B. The sides, ends, and partition of the box are $\frac{7}{8}$ inch planed and seasoned lumber. The inside dimensions are as follows: length, 3 meters; width (between sides) 52 cm.; depth, 30 cm. The bottom is $1\frac{3}{4}$ inch planed stock, dowelled and glued. It is made 2 feet longer than the box, as a provision for the support of the experiment box.

To the middle partition of the box are hinged two lids, E and F, of $\frac{7}{8}$ inch lumber.[1] The edges of the box and lids are grooved and rabbeted. When the lids are closed the two compartments, C and D, are light-tight with respect to one another.

Two cast-iron carriages, G and H, carry incandescent lamps which serve as sources of photic stimuli. Each carriage rides on a pair of steel tracks, IJ and KL, placed on the floor of its compartment.

To the floor of each compartment is attached a Starrett (Athol, Mass.) steel tape, M and N, from which the position of the source of light may be read directly in millimeters.

In order that daylight, instead of artificial light, may be used when it seems desirable, a hole 12.7 cm. in diameter is cut in the end of each compartment. These holes are fitted with Aubert diaphragms as shown at O and P, fig. 1.

The completed apparatus carries a system of ball-bearing pulleys, cords, and levers (not shown in fig. 1) by means of

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[1] The drawing for fig. 1 was made while the lids were hinged to the sides. Later it was found desirable to hinge them to the middle partition. We recommend the latter form of construction.

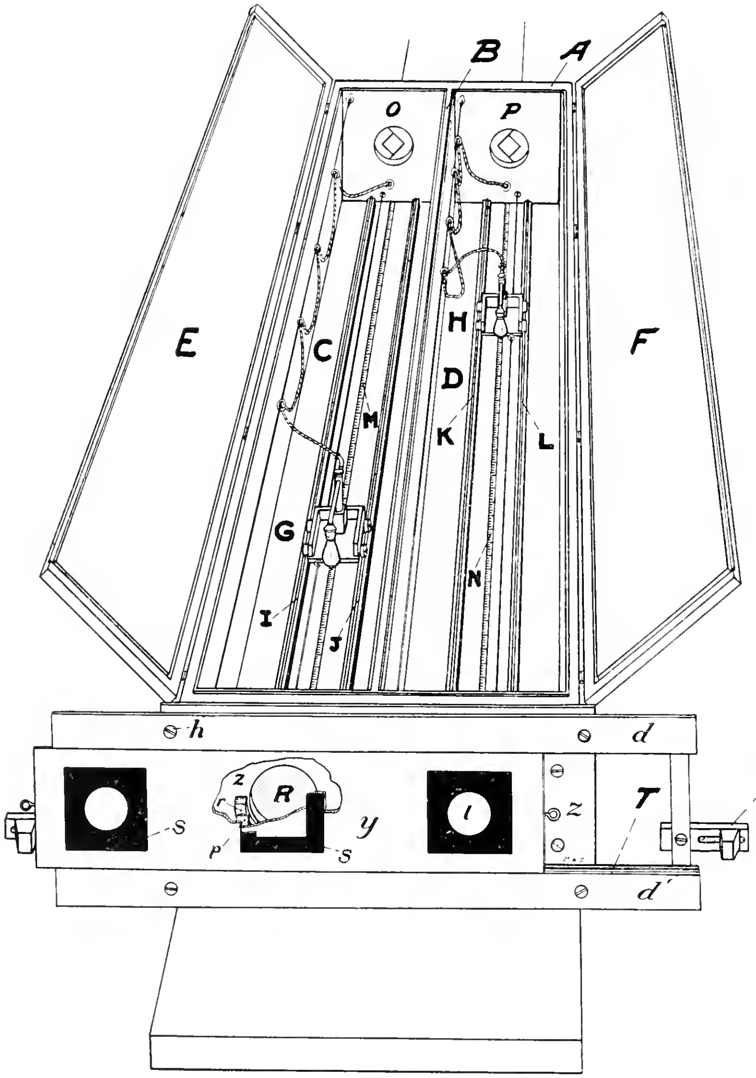

FIGURE 1.—Perspective of *light* or "brightness" apparatus. A, light box; C, D, compartments of A; B, partition between C and D; E, F, lids of A; G, H, metal carriages carrying tungsten lamps; IJ and KL, tracks for G and H; M, N, Starrett steel millimeter tapes; O, P, apertures covered by Aubert diaphragms; R, Bausch and Lomb cooling cell in light box; d, d', metal straps; y, aluminum plate sliding between d and d'; T, tracks for y; V, stop for y; z, steel plate bolted to wooden end of light box; h, screws attaching y to z; s, s, standard brass stimulus plates; p, brass frame about aperture in y; r, hard rubber ring screwed to p.

which the experimenter may shift the lamp carriages without approaching the light box or experiment box. Fig. 2 presents

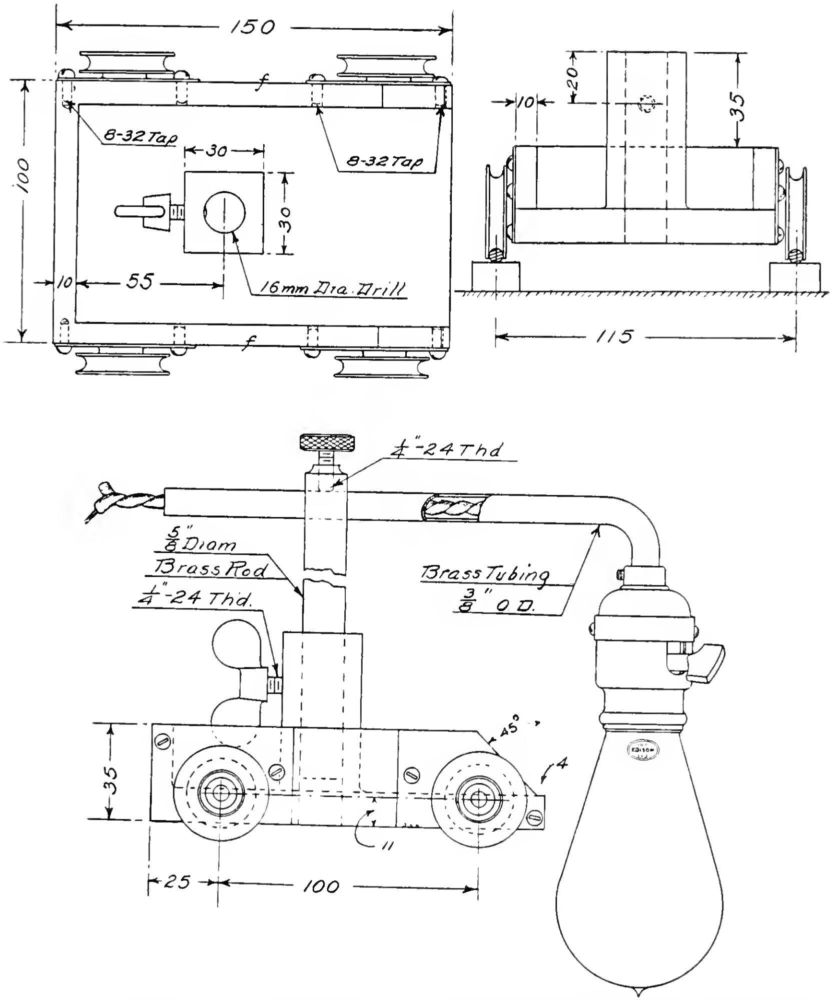

FIGURE 2—Construction drawings for lamp carriages. Dimensions, unless otherwise specified, are given in millimeters. Castings for the base of carriage may be obtained through the writers.

construction drawings of the lamp carriages. The rollers were obtained from Francis Keil & Son, New York. They are known as ball-bearing sheaves no. 17074. These rollers neatly fit a track made by soldering, or screwing, a 3-16 inch diameter coppered iron rod to the broader side of a $\frac{1}{2}$x$\frac{3}{4}$ inch coppered iron bar. The weight of this track is sufficient to hold it in position, but it may advantageously be lightly secured to the floor of the box at two points. If the rod be screwed, instead of soldered, to the bar, it is well to insert a strip of $\frac{1}{8}$ inch felt between them, throughout their length, to diminish the noise of the moving carriage.

Against the experiment box end of each compartment of the light box is placed a water cell (R, fig. 1) to serve as an adiathermal screen. The cooling cells used by Bausch and Lomb in their projection lanterns prove satisfactory. They are circular metal cells of at least 11 cm. diameter with a water space of 4.8 x12.5 cm.

The stimulus adapter is a device by means of which the experimenter is able to regulate the size, form and position of the visual stimuli. It appears as the front (end) of the light box when the experiment box, fig. 4, is removed. In fig. 1 it is shown as a unit and in fig. 3 construction drawings are provided.

A steel casting $\frac{3}{8}$ inch thick, carefully planed, and firmly bolted to the light box is shown at z, fig. 1. This sheet of steel contains two circular apertures, 10 cm. in diameter, through which the light passes from the light box to the experiment box.

To the metal plate z, the stimulus adapter is attached by four bolts, one of which is labelled as h in fig. 1.

The essential parts of the stimulus adapter are: (1) a metal frame composed of the straps d and d′, fig. 1, and the two vertical straps, e, fig. 3. The inner edges of the horizontal straps are rabbeted and into them is fitted (2) the aluminum plate y, which slides smoothly on a pair of tracks, k, fig. 3, which are screwed to d and d′. Y moves on six rollers, m, n, o, fig. 3. It contains three windows, each 12 cm. square, located 27 cm. apart (center to center). These windows receive the standard stimulus plates described below. (3) Back of each window is attached by four small screws a square frame of 1-16 inch sheet brass, p, fig. 1, 9.3 cm. on its inner edges and 13.3 cm. on its outer edges. A flange is thus created which serves to hold; in each window, (4) a brass plate, s, fig. 1, 12x12 cm. and 1-16 inch thick. This plate contains an accurately cut opening.

It is held firmly in position by two screws through diagonally opposite corners of the metal frame p. At any time by loosening the screws (v. fig. 3) the experimenter may readily remove a plate and replace it by another with an opening of different

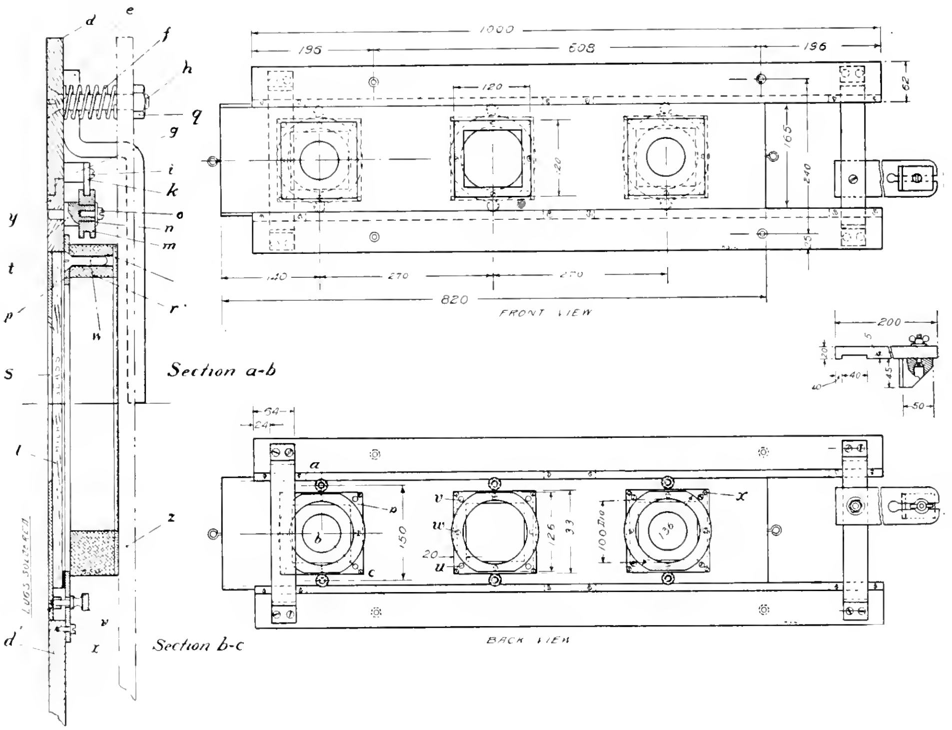

FIGURE 3—Construction drawings for stimulus adapter. Dimensions in millimeters. *Front view. Back view*; p, brass plate framing the aperture in aluminum plate y; u, head of one of the two screws which serves to hold opal glass plate firmly against standard brass stimulus plate (the other screw is in the corner diagonally opposite); v, one of the two screws which serves to hold standard stimulus plate in position (the other is in the corner diagonally opposite); w, screws attaching hard rubber ring to p; a-b, and b-c indicating sections. *Section a-b*; d, d′, metal straps with rabbeted edge for aluminum plate y; e, strap connecting d and d′; f, steel spring on h, bolt tying d to z; g, brass collar for screw, i, which attaches brass track, k, to d; m, n, o, t, parts of brass roller which enables y to move on track; p, brass plate framing aperture in y; r, hard rubber ring about aperture; w, screw attaching r to p; s, standard brass stimulus plate. *Section b-c*; l, plate of flashed opal glass.

size or form. The set of standard plates is fully described in connection with table 3, p. 23. Between the frame p, and the standard plate, s, is inserted a piece of opal flashed glass, l.

This serves as a diffusing surface and constitutes the stimulus area. It is held against the brass plate, s, by two screws, u, fig. 3. (6) To the metal frame p is screwed from the front at w, fig. 3, and three other points, a ring of hard rubber, n, 1.8 cm. thick, 2 cm. wide with a circular aperture 10 cm. in diameter. To this rubber ring is glued a ring of piano felt about ½ cm. thick. These hard rubber and felt rings serve to fill in the space between the metal front, z, of the light box, and the aluminum plate, y, which carries the stimulus plates. (7) By means of the bolts, at h and corresponding positions in the three other corners, the stimulus adapter may be brought into the necessary proximity to z to prevent light from passing from one stimulus opening to the other, between z and y. Each of the four bolts (h) at the corners of the stimulus adapter carries, between z and y, a coiled spring, f, fig. 3, which serves to press y away from z. By putting the proper amount of pressure on the four springs the experimenter can so adjust the surfaces of the rings of piano felt to the planed front of the steel plate z that the light can not pass between the two, while, at the same time the surfaces may be moved over one another freely whenever it is necessary to move y. (8) At either end of the frame of the stimulus adapter a stop, V, fig. 1, is attached so that y shall not run beyond the track T.

The most important part of the "brightness" apparatus is the set of accurately made brass stimulus plates which is briefly described in table 3.

The set, as used by us at present, consists of twenty-six plates. Others may readily be added as they are needed. These plates fall into three groups: (1) the light perception plates—three plates with a 6 cm. circular opening and three with a 5 cm. circular opening. This provides a plate for each of the three windows of the stimulus adapter with a diameter of either 5 or 6 cm. (2) The size perception plates—this group consists (including those of group 1) of plates with circular openings which, between 6 cm. and 5.5 cm., differ by 1 mm. in diameter, and between 5.5 cm. and 3 cm. by 5 mm.[1] (3) The form perception plates—there are in this group four plates whose open-

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[1] In case an animal should prove able to discriminate slighter differences in size than 1 mm. it would be necessary to cut additional plates, but this may readily be done.

ings differ in form while being equal in area. They are (a) the 6 cm. circle; (b) a hexagon 3.299 cm. on the side; (c) a square 5.317 cm. on the side; (d) and an equilateral triangle 8.081 cm. on the side. The area of each opening is 28.2743 sq. cm. In

TABLE 3

Description of Standard Stimulus Plates. Each Plate is a 12 cm. square of 1-16 inch Acid Blackened Brass, Containing an Accurately Cut and Centered Opening.

Description of Openings

Use	Form	Diameter or side	Area	Number of plates needed
To test Light Perception	Circle	6.000 cm.	28.2743 sq. cm.	3
	"	5.000 cm.	19.6350 sq. cm.	3
To test Size Perception	The 6 and 5 cm. circles (as above) and			
	Circle	5.900 cm.	27.3397 sq. cm.	1
	"	5.800 cm.	26.4208 sq. cm.	1
	"	5.700 cm.	25.5176 sq. cm.	1
	"	5.600 cm.	24.6301 cm. sq.	1
	"	5.500 cm.	23.7583 sq. cm.	2
	"	4.500 cm.	15.9043 sq. cm.	1
	"	4.000 cm.	12.5664 sq. cm.	1
	"	3.500 cm.	9.6211 sq. cm.	1
	"	3.000 cm.	7.0686 sq. cm.	1
To test Form Perception	Circle	6.00 cm.	28.2743 (as above)	
	Hexagon	3.299 cm. (side)	"	1
	Square	5.317 cm. "	"	2
	Equil. triangle	8.081 cm. "	"	2
	Openings inscribed in 6.000 cm. circle			
	Hexagon	3.000 cm.	23.382	1
	Square	4.243 cm.	18.003	2
	Equil. triangle	5.196 cm.	11.691	2
			Total..................	26

addition to the above there are provided three forms which are inscribed in the aperture of the 6 cm. circle. They are (a) a hexagon 3.000 cm. on the side; (b) a square 4.243 cm. on the side; and (c) an equilateral triangle 5.196 cm. on the side.

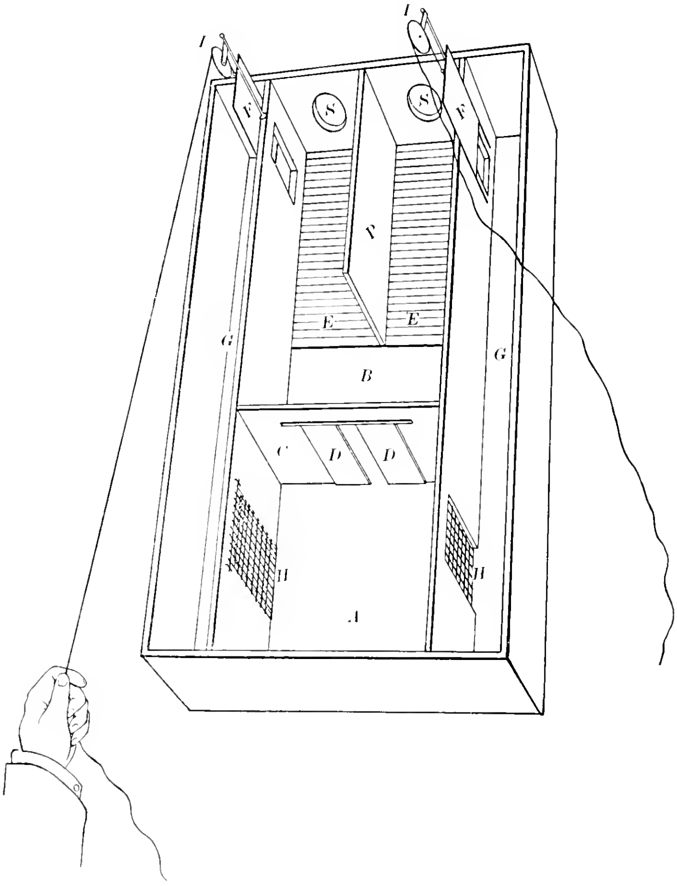

FIGURE 4—Experiment box for brightness apparatus. Planned for kittens. A, entrance chamber; B, discrimination chamber; C, partition; D, D, sliding doors; E, E, electric passage-ways; P, partition; S, S, stimulus apertures; F, F, doors for exits from E, E; I, I, pulleys for cords from I, I; G, G, alleys to A; H, H, swinging doors.

The experiment box differs from the light box and the stimulus adapter in being a variable. The latter are permanent and may be used for the study of any animal. The former, in every case, must be adapted to the animal. The particular experiment box represented in fig. 4 happens to be one which was made for experiments with kittens. It is extremely simple. The essential parts are the entrance chamber, A; the discrimination chamber, B; a partition, C, between A and B, with a pair of sliding doors, D, D; the identical passage-ways, E, E, the floors of which consist of a slab of slate wound with phosphor bronze wire so that the animal can, when necessary, be given an electric shock; the partition, P, between the electric passage-ways; the stimulus areas, S, S, which during experiments are approximated to the two opal glass plates, of the stimulus adapter; the doors (and doorways), F, F, which remain closed except when the experimenter raises them by means of cords running over the pulleys I, I; the alleys, G, G, which, through H, H, give access to the entrance chamber.

This experiment box is by no means perfect. It is described in this connection merely for the purpose of exhibiting the relations of the several portions of the apparatus.

TABLE 4

List and Approximate Cost of Parts of "Brightness" Apparatus

Light box	$ 25.00
Lamp carriages	6.00
Lamp rods and adjusters	2.50
Aubert diaphragms [1]	
Tracks	5.00
Millimeter tapes (Starrett)	3.00
Cooling cells	10.00
Steel plate for end of light box	8.00
Stimulus adapter	25.00
Standard stimulus plates (each $.75)	19.50
Sheaves, cords, levers	5.00
Experiment box	5.00
Lamps, rheostat, meters	$50.00–100.00
Total cost, exclusive of last item	$124.00

The apparatus can undoubtedly be made, now that the plans have been perfected, for about one hundred dollars.

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[1] No estimate of cost of the Aubert diaphragms is given because we have not as yet designed accurate forms thereof.

2. Points of method

The use of the "brightness" apparatus involves a number of important points of method.

The sources of light should be well seasoned tungsten lamps burned on a carefully regulated circuit, and every precaution should be taken to avoid sources of error from reflection within the light box.

The stimulus area (i.e., the illuminated window of opal glass which is framed by an accurately cut standard plate) should consist of a carefully selected piece of "flashed opal glass."[1] As this glass varies in thickness and contains imperfections, it is absolutely essential that the three windows of the stimulus adapter be fitted with pieces which are as closely matched as possible. Unless great care be exercised in selecting and placing the diffusing glasses the value of the apparatus is certain to be impaired. The lights must be centered with the stimulus windows, and these, in turn, with the openings into the experiment box. It is desirable that the experiment box be so arranged that the photic stimulus may be measured photometrically and radiometrically just as it appears to the animal. Since the value of the method which we are proposing depends upon the comparison of two photic stimuli which differ from one another, in a certain definite amount, with respect to some one character, it is important that every precaution be taken to keep the stimuli separate. This means that the apparatus must in effect be double, the one half being wholly beyond the photic influence of the other.

Discrimination by difference in the degree of illumination of the two passage-ways of the experiment box should be prevented by covering the portions of the passage-ways near the stimulus windows with black velvet. In some cases it is likely to prove necessary to arrange a truncated cone of dead black velvet about each stimulus area. Thus the animal can be forced, in its attempts to discriminate in favor of the right passage-way, to depend solely upon a visual difference in the two illuminated windows.

In its perfect form the "brightness" apparatus should enable the experimenter to present two visual stimuli which differ from

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[1] This glass is obtainable through Semon Bache and Company, West and Hubert Streets, New York, at 40 cents per square foot, in cut sizes.

one another in a definite, constant, measured way with respect to some one characteristic, and only one. It should, further, enable him to exclude all secondary and irrelevant sensory criteria by which the discriminative reaction of the animal might be influenced.

Account must be taken, in any accurate visual tests, of the animal's degree of visual adaptation. This must be controlled. It is necessary, therefore, to control carefully, and to measure (a) the illumination of the experiment room between tests, and (b) the intervals of exposure to the influence of stimuli and to general illumination, or the lack thereof. No definite procedure can be recommended because the method must be determined by the characteristics of the animal under observation.

The stimulus adapter must be adjusted, between experiments, noiselessly, and the experimenter must keep himself beyond the range of vision of the animal as much as possible.

In order, then, that reasonably accurate and strictly comparable data concerning the *light*, size, form, and distance perception of animals may be gathered in different laboratories we recommend:

(1) That the simple discrimination method be employed by presenting to the animal simultaneously two photic stimuli, the one of which calls for a positive response and the other for a negative response.[1]

(2) That the following motives, singly or in combination, be considered, and if possible used as conditions favoring the establishment of the proper method of reacting: (a) Escape from the experiment box to a larger, more comfortable, and more natural (home-like) cage; (b) return to companions; (c) the obtaining of food by choice of a certain stimulus; (d) the avoidance of punishment—weak electric shock or other suitable form—for inappropriate reactions.

In our opinion it is desirable, for quantitative investigations, that conditions for the establishment of a habit be chosen with careful consideration of their constancy and controllability.

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[1] For full description of the discrimination method and various modifications thereof the reader is referred to the following publications:

Yerkes, R. M. The dancing mouse. New York, 1907.

Watson, J. B. Some experiments bearing upon color vision in monkeys. Jour. Comp. Neurol. and Psychol., 1909, vol. 19, pp. 1–28.

Casteel, D. B. The discriminative ability of the painted turtle. Jour. Animal Behavior, 1911, vol. 1, pp. 1–28.

The matter deserves as serious attention as does the method of presenting the stimuli which are to be discriminated.

(3) That preliminary, problem-defining investigations of vision be carried on with rough and ready methods, and that by means of the "brightness" apparatus systematic and detailed studies be made of the visual capacities of one, or a few, individuals of known life-history. Thus our results may be rendered intensive, accurate, and valuable for comparison with the data on human vision.

(4) That the visual stimuli be presented in an apparatus whose construction is in essentials like the one described.

(5) That light perception be investigated by the presentation of two visual areas (circular in form and either 5 or 6 cm. in diameter) whose photic values are accurately controlled and measured by the experimenter.

(6) That size perception be investigated by the presentation, similarly, of two visual areas whose only constant difference is in size. The stimulus adapter might carry, for example, a 5 cm. circle in the middle window, and a 6 cm. circle in each of the end windows. To the animal there could be presented either 6 cm. circle on right and 5 cm. circle on left, or the reverse, as the experimenter desired. Discrimination could be made to depend wholly upon ability to react to the size difference of the areas.

(7) That form perception be investigated by the presentation of two visual areas whose only constant difference is in form. The form plates have been so chosen that the two forms may be either equal or unequal in area. For example, a square and a circle both measuring 28.2743 sq. cm. may be used; or with the same circle may be used a square which may be inscribed in the circle.

IV. METHODS OF INVESTIGATING COLOR VISION

1. Sources of stimulus

The statements concerning the advantages and disadvantages of sources of light made on pages 4 to 10 apply, with certain qualifications, in this connection. In experiments on color vision we may use either a light capable of yielding, in fair intensity, any of the hues of the solar spectrum, or a light which, instead, yields a line spectrum. Since the particular method employed to obtain a monochromatic stimulus determines the nature of the source which may be used, it is necessary to make special recommendations for each of the several methods of investigating color vision.

For all color vision experiments it is highly desirable that the source provide a light which is natural (like sunlight in quality) constant, controllable, and measurable.

a. Sun.—Sunlight is perfect as to naturalness (quality) and it certainly should be used extensively for comparison experiments in connection with the use of artificial lights. For accurate quantitative experiments it is at present extremely unsatisfactory because of (a) uncertainty of supply, (b) fluctuations in quality and intensity, and (c) uncontrollability.

b. Nernst lamp.—The Nernst lamp yields a light whose quality is excellent and whose intensity, during the last half of the life of the glower, is fairly constant. What is lost in naturalness by the use of this source, instead of the sun, is more than compensated by the gain in constancy of quality, intensity and controllability. For qualitative experiments the Nernst glower is admirable, if intelligently handled; and for quantitative work it is probably the best source now available. It can not, however, be used for extremely high intensity work.

c. Tungsten lamp.—Of the medium power electric lamps the tungsten appears to be the most satisfactory for investigations of color vision which do not demand stimuli of high intensity.

d. Acetylene.—In the absence of electricity, the acetylene lamp may be used to advantage in the study of color vision.

e. Carbon arcs.—The crater of the open carbon arc yields a light of eminently satisfactory quality, but the remainder of the light is unsuitable for visual work. A well constructed arc-lamp, burning high grade carbons, on a well controlled circuit may be made to supply a large amount of light of satisfactory quality and in fairly constant intensity, provided the crater alone be used.

f. Recommendations concerning sources for tests of color vision.—In general, as sources of light for the study of color vision we recommend the following in order of preference (a) sun, (b) open carbon arc, (c) Nernst, (d) tungsten, (e) acetylene. These sources are not, however, equally suitable for all methods.

Some are especially valuable for low intensities of light; others for high intensities.

As sources which are especially strong in certain portions of the spectrum we recommend:

For red, orange, and yellow: Sun (low); mercury arc; amyl-acetate lamp; sodium flame; combustion gas lamps; oil lamps.

For green: Mercury arc; welsbach.

For blue and violet: Skylight; enclosed carbon arc; mercury arc.

2. Methods of obtaining and applying stimulus

Of the many methods by which chromatic stimuli may be obtained for experiments on vision we shall discuss the values of only those which seem to us practicable in the present state of our knowledge. For convenience of description we have classified the methods under the three rubrics of *reflection*, *transmission*, and *dispersion*. There are in reality, for our purposes, two physical phenomena which yield colored light: selective absorption, and the resolution of white light. The former gives the phenomena of object-color in nature; the latter exhibits itself in the rainbow, and in various ways through refraction and interference. In the case of selective absorption, the chromatic stimulus may come to the eye as reflected light (from the absorbing surface) or as transmitted light, if the medium be partially transparent. The phenomenon of selective absorption appears, in its two forms, in colored papers and colored glasses: the former yield chromatic stimuli by selective absorption and reflection; the latter by selective absorption and transmission.

We shall briefly consider, in turn, each of the three groups of methods.

a. The reflection method.—Here we class substances which, because of their capacity for absorption, reflect only a definitely limited range of wave-lengths. Chief among them, for our special purposes, are colored papers, colored cloths, and oil pigments on opaque substrata.

Colored papers.—These, in various forms, have long been used, and still are extensively employed in the study of human color vision. The most pertinent description of them would seem to be an enumeration of their merits and defects.

Merits: Availability in many colors and saturations (hues, tints, chromas);[1] cheapness, and convenience of handling;

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[1] Titchener, E. B. A text-book of psychology. New York, 1910, p. 54.

possibility of ready use in daylight, sunlight, or artificial light; naturalness of colors. The latter would seem to be a very important consideration, for colored objects in nature are seen in white light as colored surfaces, as are colored papers when used in daylight or sunlight.

Defects: Inconstancy of qualities in successive sets of the same manufacture; rapid fading under the influence of strong light; impossibility of changing quality, except by the substitution of another paper; extreme difficulty and inaccuracy of measuring either the wave-length or the intensity of the reflected light; impossibility of getting any desired quality of light.

As compared with spectral chromatic stimuli those obtained from colored papers are unsatisfactory (a) because they can not be well controlled with respect to color, saturation, and intensity (the number of papers is finite); (b) because they are not reliable either from day to day or from set to set, and (c) because it is practically impossible to describe them accurately as to color, saturation, and intensity.

In view of this list of defects, it seems impossible that papers should be extensively used in the future for quantitative investigations of color vision. They are invaluable for rough preliminary tests, for class-experiments, demonstration experiments, and, indeed, for all qualitative investigations which do not demand complete control and accurate description of the chromatic stimuli employed.

The characteristics of psychologically satisfactory colored papers are enumerated by Titchener. [1] In the opinion of the writers, spectral light is preferable even to the stimuli from papers which fulfill all of Professor Titchener's requirements. Our reasons for holding this opinion will appear in our description and discussion of the method which we recommend for the quantitative investigation of color vision.

A number of investigations of color vision in animals,[2] prominent among which are those conducted under the direction of

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[1] Titchener, E. B. Experimental psychology, vol. I, part II, p. 14.

[2] Kinnaman, A. J. Mental life of two *Macacus rhesus* monkeys in captivity. Amer. Jour. Psychol., 1902, vol. 13, p. 43.

Cole, L. W. and Long, F. M. Visual discrimination in raccoons. Jour. Comp. Neurol. and Psychol., 1909, vol. 19, p. 657.

Samojloff, A. and Pheophilaktowa, A. Ueber die Farbenwahrnehmung beim Hunde. Centralb. f. Physiol., 1907, Bd. 21, S. 133.

Professor E. C. Sanford at Clark University, indicate both the serviceability and disadvantages of colored papers in this kind of work.

In order of preference, we mention the following sets of papers:

1. The Hegg colored papers. (Pfister und Streit, Math. physikalische Werkstatte, Bern, Switzerland).—These are mixtures of oils on paper yielding the hues red, yellow, green, and blue. These hues are claimed to be equal in intensity and saturation for the human eye. The set is useful as a means of ascertaining, in a preliminary survey, whether an animal readily discriminates two hues which for us are of nearly the same intensity and saturation.

2. The Wundt colored papers. (E. Zimmermann, 21 Emilienstrasse, Leipzig, Germany.) A series including the various spectral hues and purple in a number of saturations (chromas).

3. The Hering colored papers. (R. Rothe, 16 Liebigstrasse, Leipzig, Germany. C. H. Stoelting Company, Chicago, Ill., American Agent.) A series of twelve strong colors, including purple.

Rothe supplies also a set of fifty neutral papers, ranging from white to black, but it is unsatisfactory.

4. The Bradley colored papers. (Milton Bradley Company, Springfield, Mass.) A useful series, including a great variety of colors and saturations.

Colored cloths.—Cloths, as secondary sources of chromatic stimuli have most of the defects and few, if any, more merits than papers. They are useful, under certain circumstances, for qualitative work.

Especially valuable in this class of reflecting surfaces, because it reflects only a small quantity of white light, is silk velvet. In experiments which demand change in the intensity of the chromatic stimulus without marked change in its hue or saturation this material, properly dyed, is superior to colored papers. A great variety of hues of silk velvet are on the market, but they are quite likely to prove unsatisfactory for tests of color vision because their dyes reflect, in varying amounts, light of different wave-lengths. Could we obtain a set of these cloths which reflected respectively only red, yellow, green, blue, and violet, we should be able to use them to advantage in many of our qualitative experiments on vision in animals. But they would not meet the fundamental requirements, controllability and describability.

Although for quantitative experiments the reflection method, in its available forms, is quite unsatisfactory, it is not to be discarded lightly, for it offers important conditions for the preliminary investigation of the nature of an animal's color vision which no other method furnishes. Above all, the naturalness of the stimulus, and of the conditions under which it may be applied, would seem to be important. We wish, therefore, to recommend the employment of papers, cloths, and oil pigments under suitable conditions, and with recognition of their limitations. No experimenter can reasonably hope to gain adequate knowledge of the visual capacity of an animal by the use of this method alone, although by means of it he may obtain knowledge which will enable him to formulate his problems and advantageously apply other methods to their solution.

b. The transmission method.—In this rubric we have tried to include all suitable means of obtaining chromatic stimuli by selective absorption and transmission. Among the most important of these means are glasses and gelatines ("dry filters") and solutions ("wet filters"). Before taking up these several types of absorption media, we may enumerate the chief merits and defects of the transmission method, in contrast with the reflection and dispersion methods.

Merits: Availability in many forms; cheapness, in comparison with all forms of apparatus for the dispersion method; convenience and simplicity of apparatus (this applies especially to glasses and gelatines—the so-called dry filters—it does not hold to the same extent of wet filters); the possibility of use in daylight and sunlight; ease of changing quality and intensity of stimulus independently, within certain limits; reasonable ease and accuracy of measuring wave-length and intensity of stimulus. (In the last two features the transmission method is infinitely superior to the reflection method.)

Defects: Inconstancy of qualitative values of commercial colored glasses and gelatines (this does not apply to solutions); more or less rapid fading (this renders unsatisfactory expensive sets of glasses); unnaturalness of the stimulus, as compared with colored papers, or cloths or other surfaces, viewed in sunlight (it is possible to use color filters in sunlight, but their light is not so satisfactorily applied thus as in a dark-room, and quantitative experiments are impossible); impossibility of obtaining readily any desired quality of stimulus.

Unlike the reflection method, the transmission method may be used fairly satisfactorily for quantitative work, for the stimulus may be accurately measured and it may be applied, in a dark-room, under simple controllable conditions.

Since animals in nature view colors mostly as colored objects seen in white light, it seems only fair that their color vision should be investigated under conditions similar to these, as well as under such conditions as are furnished by the clear cut and controllable methods of transmission and dispersion. The quantitative tests described in this report are open to the objection that the darkened room, in which they should be conducted, is an unnatural environment for most animals. In view of this objection, we believe that for rough qualitative tests of vision the reflection and the transmission methods may be employed to advantage in daylight or sunlight. But even in the case of qualitative experiments in sunlight, we recommend the transmission method over the reflection method because it enables the experimenter, first, to get a great variety of qualities (hues) and intensities; second, because it enables him to measure both the wave-length and intensity; and third, because it enables him, within narrow limits, to vary intensity independently of quality.

We shall now point out the special characteristics of a number of the substances which exhibit selective absorption and transmission.

Glasses.—Colored glasses are readily obtainable, but most of them, when used singly, are practically worthless as filters. There are two kinds in use: that in which the pigment is mixed with the glass, known as pot glass; and the variety which has a thin coating of pigment on one or both surfaces, known as flashed glass. The former in good quality, is more expensive than the latter. To these we might add the spectro-optical glass, a special kind of pot glass

Colored glasses may be described as ray filters in relatively stable and permanent form, convenient for handling. Unfortunately many colored glasses fade more or less rapidly in strong light. Their chief advantage over solutions for visual tests is portability.

At present the following are the most satisfactory colored glasses of which we have knowledge, together with sources of supply:

E. Grosse, Berlin, N. W. 52, Paulstrasse 5, supplies flashed glasses which yield red, yellow, green, blue, and violet light. These glasses are, on the whole, the most satisfactory of the flashed glasses which we have been able to obtain. Only the red, however, is monochromatic. By using combinations of the blue and violet glasses, it is possible to get a stimulus which contains no red or yellow. If monochromatic light is desired these glasses, with the exception of the ruby, are of no value.

Chance Brothers and Company, Birmingham, England, manufacture colored glasses which are used for signals, but examination indicates that except in combination they have no special value for our purposes.

The Central Scientific Company, 14-28 Michigan street, Chicago, Illinois, sells (a) plates of pot glass, and (b) plates of flashed glass. The latter they furnish in seven colors. Plates 10 cm. square, 11 cents each. These glasses, according to our spectroscopic examinations are not as satisfactory as those supplied by E. Grosse.

Schott and Genn, Jena, Germany, manufacture a high grade of colored glass (spectro-optical), much more expensive and also more satisfactory than the flashed or pot glasses of commerce. Their latest series consists of six colored glasses: "dark, medium, and light yellow, blue filter, green glass, and red filter." These may be obtained in different thicknesses, and, according to catalogue statements, in pieces not exceeding 5 cm. square. The price of pieces approximately 4 cm. × 4 cm. is about $1.25 each.

Glass filters greatly reduce the intensity of a chromatic stimulus and it is therefore necessary to employ with them an intense source of light. They are of extremely different values with respect to different wave-lengths.

For red one or two thicknesses of flashed ruby glass is excellent.

For yellow no colored glass, or combination of glasses, is satisfactory.

For green the same is true. A monochromatic green can not be obtained with any of the glasses, or combinations thereof, which we have examined.

For blue a glass may be obtained which transmits no red, but blue can not be obtained without some violet.

For violet there is no satisfactory glass or combination of glasses.

From these statements it is evident that among the colored glasses at present manufactured, it is extremely difficult to find satisfactory filters for use in the study of color vision. With commercial glasses it is easy to obtain two mutually exclusive chromatic stimuli (red and blue-violet for example), and it is possible to divide the spectrum into three mutually exclusive parts (red, yellow-green, blue-violet), but the search for the proper glasses, and combinations thereof, for the latter purpose is likely to prove discouraging and scarcely worth while, in view of the possibility now to be mentioned of obtaining good gelatine filters.

The ruby glass of Grosse we find perfectly satisfactory as a source of red light, and could equally good glasses be obtained for yellow, green, blue, and violet, our qualitative experiments on color vision would be greatly facilitated.

On the whole, it seems desirable that some one should attempt to discover formulae for a set of colored glasses which shall be as satisfactory as the ruby. The task is a difficult one, and, although we have considered undertaking it, we have not found time nor opportunity to do so.

Gelatines.—Color filters consisting of pigmented films of gelatine yield color stimuli by selective absorption and transmission. There are, so far as we know, no gelatines on the market which, when used singly, give monochromatic stimuli, but by combining certain of the films now available it is possible to obtain fairly satisfactory filters for red, green, yellow, and blue. There is no apparent reason why a standard set of gelatine filters which should yield respectively red, yellow, green, blue, and violet light should not be manufactured. They should be prepared with extreme care, according to definite formulae, by a reliable scientific firm, and the experimenter would need to be on his guard against fading, for one of the chief defects of gelatine films is their extreme liability to fade.

Spectroscopic, as well as spectro-photometric tests would have to be made frequently. But in spite of this, it seems to us desirable that a standard set of gelatine filters be manufactured. Such a set of films would possess almost all of the merits of colored papers, while enabling the experimenter to vary, somewhat, the intensity of his chromatic stimulus independently of its hue and saturation.

Available at present are the following sets of pigmented gelatine films:

Hanauer vereinigten Gelatoid Fabriken, Hanau, a. M. Germany, manufactures colored gelatine films, some of which, singly or in combination, are excellent. They may be obtained through the American Agent of the German firm, Henry Pfaltz, 300 Pearl Street, New York.

Queen and Company, 1211 Arch Street, Philadelphia, imports and sells a set of thirty gelatine absorption films, 3½ by 6½ inches, stained by chemically pure substances. They are too thin for our purposes, and in our tests proved of little value.

Zimmermann, 21 Emilienstrasse, Leipzig, Germany, supplies gelatine films for psychological purposes.

Filters are made, to order, by the Cramer Dry Plate Company, St. Louis, Missouri.

Dr. Louis Bell recommends the following formulae, on the basis of his experience:

For red: (1) Grubler's lichtgrün F. S.; (2) concentrated safranine, in gelatine films.

This double filter transmits pure red of 700 $\mu\mu$ wave-length.

For yellow: (1) Copper chloride (solution) in absolute ethyl-alcohol; (2) yellowish eosine (Berlin Anilinfabrik), in gelatine film.

This combination, solution and gelatine, filter transmits yellow of 560–590 $\mu\mu$.

For green: (1) Acid green (Cassella and Co.); (2) methyl orange III (St. Denis Co.), in gelatine films.

This double filter transmits green of 460–490 $\mu\mu$ (?).

For blue green: Methyl green, in gelatine film.

This transmits light of 450–490 $\mu\mu$.

For blue: (1) Alkali blue (Albany Color Works); (2) yellowish eosine (Berlin Anilinfabrik), in gelatine films.

This double filter transmits from 435 $\mu\mu$ to the ultra-violet.

Directions for making up gelatine or collodion filters from approved formulae may be found in works on photographic methods.[1]

The essential points of method may be stated. Lantern dry plates should be (1) fixed in a solution of hyposulphite of soda, (2) cleared in a ferricyanide and hyposulphite solution, if necessary, (3) washed thoroughly, and (4) immersed in the solution of the desired stain until the proper depth of color has been attained.

For the following practical and more specific directions, the writers are indebted to Mr. Willard Greene.

Select a heavily coated dry plate, fix, clear (if necessary) as above, wash for an hour in running water, and dry. Having prepared the dye solution according to formula, pour it into a tray about the size of the plate to be stained. Place one edge of the dry, or partially dry, plate in the solution and by tipping the tray, and at the same time lowering the plate, cause the solution to flow over it in an even wave. Leave the plate in the dye until it has attained proper depth of color. The time may be accurately determined by trial. Upon removal of the plate from the dye, rinse it in running water. Drain and then wipe lightly in both directions with soft surgical gauze to remove excess of solution. After a few minutes wipe again to remove surface moisture and then place on rack to dry.

When skill has been achieved in staining plates to the proper depth, a filter of more satisfactory quality may be made by coating optical glass with a carefully filtered and clarified solution of gelatine or collodion, and, when dry, immersing in the dye-solution for the proper length of time. Gelatine filters may be protected by binding plates of clear glass against them.

Solutions.—(Wet filters) Aqueous or alcoholic solutions of dyes and other substances exhibit selective absorption (the capacity to transmit only light of certain wave-lengths). The quality and intensity of the light transmitted depends upon the concentration of the solution and the thickness of the layer. Either singly or in series, layers of solutions which exhibit selective absorption may be used as ray filters. The absorption

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[1] Bolas, T., Tallent, A. A. K., and Senior, E. A handbook of photography in colors. New York and Chicago, 1900. Chapter 21. "The manufacture of color filters," pp. 157–160.

spectra of hundreds of solutions have been described.[1] We have ourselves examined many substances in our search for *single solutions* which should yield satisfactory monochromatic stimuli, but our efforts have not added materially to the knowledge of the subject.

Single solutions which transmit "monochromatic light" in fair intensity are rare. Indeed, a serious fault common to filters is the great diminution of the intensity of light. Except with a high intensity source it is impossible, in most instances, to obtain a narrow band of light of fair intensity. This defect is greatly accentuated when two or more layers of solutions (or glasses or gelatine films) are used side by side. Another serious defect of ray filters is the transmission of the infra red and ultra violet.

Wet filters have the advantage of being relatively easy to make. They have almost all of the advantages of dry filters, and their deterioration is a less serious matter because of the ease with which they can be renewed.

In order to insure "keeping" for a considerable interval, solution filters should be made up with distilled water which has been boiled for several minutes before dye is added. The addition of a few crystals of carbolic acid to solution after it has been cooled will prevent the growth of moulds.

For single solution filters, boxes of crystal plate, optical glass, or quartz, in certain standard sizes and shapes (or to order) may be obtained from E. Leybold's Nachfolger, Cöln a Rh., Germany. These cells are admirably suited to the needs of students of color vision who wish to obtain chromatic stimuli by means of wet filters.

For double or triple solution filters the Leybold glass boxes may be obtained on special order, with a single plate of glass between adjacent chambers.

We have designed a special unit cell which has many ad-

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[1] Kayser, H. Handbuch der Spectroscopie. Leipzig, 1905, Bd. III.

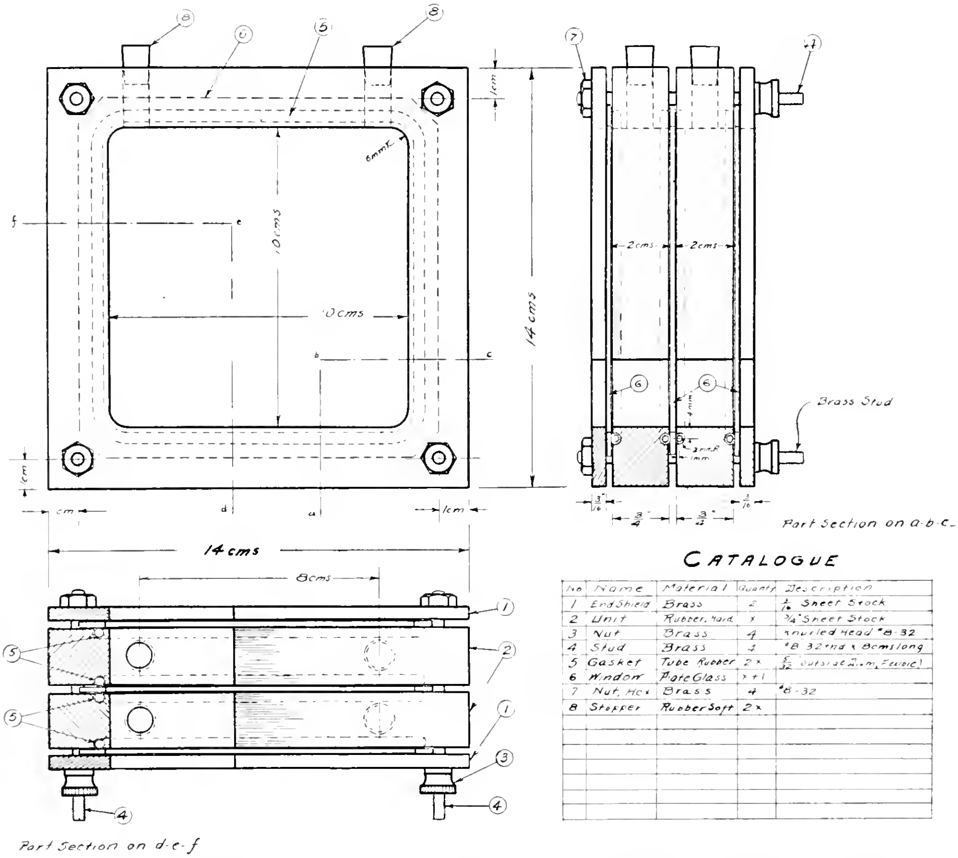
Uhler, H. S. and Wood, R. W. Atlas of absorption spectra. Washington, 1907. Carnegie Institution Publication, No. 71.

Jones, H. C. Hydrates in aqueous solution. Washington, 1907. Carnegie Institution Publications, No. 60.

Formánek, J. Die qualitative spectral analyse anorganischer Körper. Berlin, 1900.

Formánek, J. Spectral analytischer Nachweis kunstlicher organischer Farbenstoffe. Berlin, 1900.

vantages. It may be used for single, double, or triple solutions, and it is convenient to fill, empty, and clean. Any kind or thickness of glass may be used as transmitting plates, for the whole may readily be taken apart.



CATALOGUE

No	Name	Material	Quanty	Description
1	End Shield	Brass	2	1/16 Sheet Stock
2	Unit	Rubber, Hard	x	3/4" Sheet Stock
3	Nut	Brass	4	Knurled Head #8-32
4	Stud	Brass	4	#8 32 thd x 8cms long
5	Gasket	Tube Rubber	2x	5/32 Outside Diam. (Flexible)
6	Window	Plate Glass	x+1	
7	Nut, Hex	Brass	4	#8-32
8	Stopper	Rubber Soft	2x	

FIGURE 5—Unit absorption cell for ray filter. The drawings represent a double (two unit) cell.

In fig. 5 we present construction drawings for a two-unit cell of this type.

The essential parts of the cell are a solution chamber cut in a 14 x 14 x 2 cm. block of hard rubber; two 14 x 14 x .4 cm. plates of sheet brass; two plates of optical glass 12 x 12 cm.; two rubber stoppers; rubber tubing for gasket; four studs and nuts. The clear aperture of this cell is 10 x 10 cm. In the form used by us, it carries a 2 cm. layer of solution, but it may as readily be made for a 1 cm. layer.

At the outset of this investigation it was our ambition to select a set of wet filters which should yield the principal spectral hues in a satisfactory manner. This we have not succeeded in doing, and we therefore present the following formulae—all of which have proved satisfactory under certain circumstances—for the consideration of those who wish to experiment with wet filters.

The formulae of Landolt.[1]—These we have tested and found fairly satisfactory with respect to the quality of the light transmitted. The yellow is unsatisfactory because of the low intensity of the transmitted light.

Color	Thickness of layer in mm.	Aqueous solution	Grams of substance in 100 cc. of solution	Optical point of max. value
Red	20	Crystal violet 5 Bo.	0.005	665.9 $\mu\mu$
	20	Potassium monochromate.	10	
Yellow	20	Nickel sulphate + 7 aq.	30	591.9 $\mu\mu$
	15	Potassium monochromate.	10	
	15	Potassium permanganate.	0.025	
Green	20	Copper chloride + 2 aq.	60	533.0 $\mu\mu$
	20	Potassium monochromate.	10	
Light blue	20	Doppelgrün S, F.	0.02	488.5 $\mu\mu$
	20	Copper sulphate + 5 aq.	15.	
Dark blue	20	Crystal violet 5 BO.	0.005	448.2 $\mu\mu$
	20	Copper sulphate + 5 aq.	15	

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[1] H. Landolt. Das optische Drehungsvermögen. 2 Auflage, Braunschweig, 1898, S. 390.

The formulae of Parker and Day.—The following formulae were devised for the study of the reactions of organisms to chromatic stimuli in the Zoölogical Laboratory of Harvard University, but for obvious reasons they were not employed. We present them as given to us by Professor G. H. Parker, with his comments.

Color	Thickness of layer in mm.	Aqueous solution	Grams of substance in 1300 cc. of solution	Range in spectrum
Blue	20	Methylene blue	0.65	420-470 $\mu\mu$
Green	20	Napthol yellow S Lichtgrün F. S. Napthol green B	3.25 .39 .39	490-580 $\mu\mu$
Yellow	20	Napthol yellow S Napthol green B Ponceau P. R.	3.25 .39 .20	560-650 $\mu\mu$
Red	20	Ponceau P. R. Napthol green B Formyl violet S 4 B.	13.00 .20 .32	600-720 $\mu\mu$?

"All of these were used as single solution ray filters in plate glass containers, with the thickness of layer 20 mm. Tests with the radiomicrometer indicated that about one-third of the energy transmitted by these solutions was invisible (probably for the most part infra-red). We could find no satisfactory way to prevent this transmission of the invisible rays and therefore abandoned the use of filters in connection with studies of the influence of chromatic stimuli."

The formulae of Greene.—We have tested the following formulae, supplied by Mr. Willard Greene, and discovered that they may be used to advantage for certain experiments with animals. Several of them are very similar to those given by Professor Parker. We have used our solutions, however, in layers 10 mm. instead of 20 mm. in thickness.

Color	Thickness of layer in mm.	Aqueous solution	Grams of substance in 1 liter. of solution	Range in spectrum
Violet	10	Copper sulphate (c. p.)	25.00	–450 μμ
		Ammonia	10.00 c.c.	
Blue	10	Napthol green B[1]	.20	450–490 μμ
		Formyl violet S. 4B.	.20	
Green	10	Napthol yellow S.	2.50	510–550 μμ
		Lichtgrün F. S.	.30	
		Napthol green B.	.30	
Yellow	10	Napthol green B.	.30	560–610 μμ
		Napthol yellow S.	2.50	
		Ponceau P. R.	.15	
Red	10	Ponceau P. R.	10.00	600–700 μμ

Lithium carmine, in aqueous solution, yields a fairly satisfactory red.

R. W. Wood in his "Physical optics" (New York, 1905, p. 12), recommends the following methods of obtaining monochromatic light from the mercury arc.

He writes, "for long continued work, however, the most satisfactory light is the mercury arc,[2] from the radiation of which we can pick out by means of color screens . . . any one of the numerous bright lines. The following screens have been recommended for use with this form of lamp. The solutions are made with water, and contained in cells made by cementing glass plates to annular strips cut from heavy brass tubing.

Methyl violet 4 R (Berlin aniline fabrik) + very dilute nitrosodimethyl-aniline, transits wave-length 365. Methyl violet + chinin sulphate (separate solutions), the violet solution is made strong enough to blot out wave-length 4359. This screen transmits 4047 and 4078, also faintly 3984.

Cobalt glass + Aesculin solution, transmits 4359.

Guinea green B extra (Berlin) + Chinin sulphate, transmits 4916.

Neptune green (Bayer, Elberfeld) + Chrysoidine. Dilute

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[1] Dyes from H. A. Metz and Company, New York.

[2] Mercury lamps, made of fused quartz, may be obtained from W. C. Heraeus, Hanau, Germany.

the Chrysoidine sufficiently to just transmit 5790 and 5461, then add Neptune green until the yellow lines disappear.

Chrysoidine + Eosine transmits 5790. The chrysoidine should be dilute and the eosine added until the green line disappears."

For additional formulae and a thorough discussion of ray filters the reader is referred to the recent monograph of Nagel[1] and to Busck.[2]

Except when a light which gives a line spectrum is used for special purposes, as for example in the case of the mercury lamp, it is desirable to use as a source in work with the transmission method a white light of fairly high intensity. Sunlight, daylight, Nernst light, tungsten light, and acetylene light are likely to prove satisfactory. The sun is to be preferred as a source when naturalness is the chief desideratum; the Nernst or tungsten lamp, when constancy of intensity is important. The transmission method of obtaining chromatic stimuli is decidedly superior to the reflection method in that it permits (a) of the use of a greater variety of stimuli, (b) of the control of the quality and intensity of the stimuli to a greater extent, (c) of more accurate determinations of the wave-length used, and finally, (d) of the spectrophotometric measurement of intensity in a fairly satisfactory manner. On account of the unequal transmission of the infra-red rays by filters, radiometric measurements are of little value.

Dry filters are convenient for a great variety of experiments which demand neither stimuli of a single or closely restricted wave-length, nor extreme accuracy of measurement.

c. Dispersion method.—White light may, by various means, be resolved into a spectrum,[3] from which the experimenter may select and isolate light of the particular wave-length he desires to use as a stimulus.

We may mention, as especially convenient for use in studies of color vision, two mechanisms for the production of spectra: the diffraction grating and the prism.

Grating spectra are excellent for many of the investigations

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[1] Nagel, W. A. Methoden zur Erforschung des Licht und Farbensinns. Tigerstedt's Handbuch der physiologischen Methodik. S. 43-55.

Nagel, W. A. Ueber flussige Strahlenfilter. Biologisches Centralblatt, 1898, Bd. 18, S. 655.

[2] Busck, G. Ueber farbige Lichtfilter. Zeitschr. f. Psychologie und Physiol. d. Sinnesorgane, 1904, Bd. 37, S. 104-111.

[3] Baly, E. C. C. Spectroscopy. London, 1905

of human vision, but because of their low intensity, in comparison with prismatic spectra, they are less satisfactory than the latter where a wide range of intensities for a given hue is demanded. As soon, however, as it becomes possible to rule a large concave grating with short focus, the diffraction grating, in all probability, will supersede the prism, since with such a grating collimating and objective lenses would be unnecessary. The grating would have the additional advantage of rendering it possible to get a good yellow. This is extremely difficult with the prism.

Prismatic spectra seem to us, at present, the most satisfactory chromatic stimuli. We have therefore decided to use them in connection with our standardized apparatus for the investigation of color vision in animals.

The advantages which spectral stimuli obtained by "diffraction" or "refraction" have over chromatic stimuli obtained by "reflection" or by "transmission" (as used in this report) may be thus stated:

(1) They are perfectly under the control of the experimenter with respect to (a) color, (b) saturation, and (c) intensity.

(2) They are measurable, and therefore describable, with a degree of facility and accuracy which is not attainable in connection with other methods.

Inasmuch as the remainder of this report is to be devoted to the description of a method of using spectral light, it is needless to discuss the matter further at present.

3. Measurements of stimulus

Whatever the means employed for obtaining chromatic stimuli, they should be accurately describable in terms of wave-length (quality or composition) and intensity (psycho-physiological and physical).

As has been pointed out, it is practically impossible to describe stimuli obtained from surfaces which exhibit selective absorption and reflection. It is considerably less difficult, however, to describe stimuli obtained by the use of ray filters. Finally, it is possible to obtain highly satisfactory descriptions of the stimuli used in the "color" apparatus now to be described.

We recommend that in all quantitative investigations of color vision determinations be made (a) of the wave-length of the stimuli by means of a first-class spectroscope or spectrometer,[1] and (b) of the intensity of the stimuli by means of a good spectro-photometer and also, when grating or prism is used, by the use of a radio-micrometer or a selenium cell.[2]

V. DESCRIPTION OF STANDARDIZED APPARATUS AND METHOD FOR THE STUDY OF COLOR PERCEPTION

The apparatus we have finally decided to recommend as a standard for testing the color perception of animals was described in an early form in the April, 1909, number of the Journal of Comparative Neurology and Psychology, p. 1. In that form there were many objectionable features, such as the use of silvered mirrors, the projection of colored beams upon improperly ground glass surfaces, etc., all of which have been entirely eliminated in the present form.[3]

In its improved form the apparatus now affords:

(1) Means of selecting any two desired bands of homogeneous spectral light of constant and known wave-lengths. Furthermore, (a) the energy of each band is known in C. G. S. units and can be varied at will; (b) the distance between them is adjustable; (c) their right-left position can be interchanged at will.

(2) Means of splitting any single chosen beam of monochromatic light into two parts, in such a way that the two beams thus obtained are of the same wave-length, form and size, and are equal in energy. At the same time, (a), (b) and (c) under (1) apply here also.

(3) The possibility of substituting for either of the monochromatic bands a beam of white light of the same size and form as the homogeneous chromatic bands.

(4) The alteration of the saturation of any monochromatic band by the admixture of white light of known energy.

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[1] Further details are to be found on pp. 79–84, in the description of our standard procedure.

[2] See p. 79.

[3] On pp. 70–87 will be found a detailed description of the separate parts referred to here, together with a statement of their cost and the places where they may be obtained.

1. General description of the optical system

Fig. 6 is a diagram showing the path of the light. As it is drawn, the arc L is used as a source. The apparatus is adaptable for use also with sunlight or with a Nernst filament. When sunlight is used, the beam from a heliostat falls directly upon the condenser, K. When the Nernst filament is used it is mounted vertically 12 cm. from the slit S, and is focused upon S by means of a small concavo-convex lens of $\frac{3}{8}'$ aperture and $1\frac{1}{2}''$ focus (single achromat). Such lenses are ground to order for us by the Wollensak Optical Company, Rochester, N. Y.

It will be seen as the apparatus is here sketched for use with the arc, that the light from the crater of the positive carbon of the arc L falls upon the face of an achromatic condenser, K. This condenser causes a sharp image of the crater of the positive carbon to fall upon the slit S. The diverging rays of light issuing from this slit are made parallel by the collimating lens C. The parallel cylinder of light next strikes the face of a dense flint glass prism (60°), is refracted, and passing through the objective O, is brought to a focus in a series of colored images of S upon the double slit (at R and G, two beams are shown passing through this slit).

Immediately behind this double slit two total reflection prisms m_1 and m_2 are to be found. As shown in the diagram, they serve the purpose of bringing the red beam near to the green. It is absolutely necessary to keep the two selected beams within about 10 mm. of each other if the reversing and spacing devices which are later described are to work properly. It may be seen that the distance separating the two beams shortly after they issue from the double slit is determined by the separation existing between m_1 and m_2. Suppose, for example, one beam issues from the red region, and the other from the violet. Now, with the lenses and refracting prism at present in use, the separation would be, without the use of m_1 and m_2 about 6 cm. In order to bring the red over to the violet and have them in the same relation as are the red and green in the diagram, one has to draw prism m_2 over toward the violet beam until the red issues from m_2 parallel to the violet and 10 mm. distant from it. This device works equally well for any two selected beams widely separated. On the other hand, if the

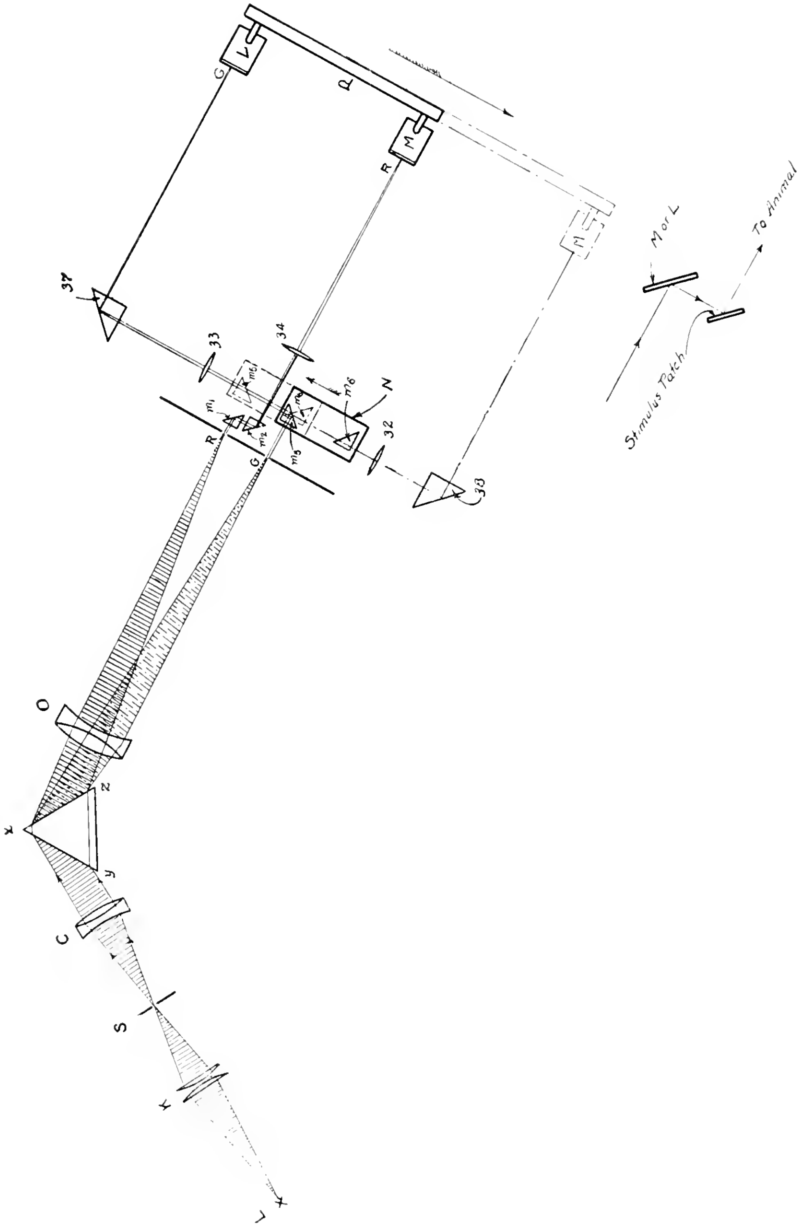

FIGURE 6—Diagrammatic sketch showing the path of the light. L, source; K, condenser; S, slit; C, collimator; X, Y, Z, prism; R and G, double slit openings. Behind R and G are to be found the system of total reflection prisms and small lenses used in spacing, reversing and projecting the monochromatic bundles. M and L are speculum mirrors for receiving the projected beams. The small diagram shows the path of the beams after reflection from the mirror.

beams lie very near together, as e. g., red and orange, the prisms m_1 and m_2 are unnecessary. Beams from regions lying very near together, e. g., two in the red, can still be spaced and reversed within the limits of the construction of the double slit (cf. p.62).

At times it becomes necessary to have two beams of exactly the same wave-length, for example, when one desires to test the difference limen for any given color (D. L.). The apparatus permits this with only a slight modification (not shown in the above diagram, but separately below—fig. 6A).

One allows a single beam to issue from the double slit and to fall upon a Wollaston double image prism, combined with two parallelopipeds of glass, the arrangement of which is shown in the figure. A, slit admitting the monochromatic bundle, B; C, Wollaston double image prism; D, one of the parallelopipeds of optical glass (equivalent to two total reflection prisms); E, one of the divisions of the bundle, B. This compound prism (designed especially for our work by Steeg & Reuter, Homburg, v. d. Höhe) yields us two parallel beams of light, 10 mm. between centers, of exactly the same wave-length and of equal energy. They can be spaced and reversed as are the red and green in fig. 6.

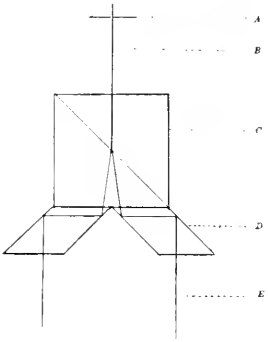

FIGURE 6A—Apparatus for obtaining two beams of same wave-length.

As may be seen from the solid line marked G, fig. 6, the green beam falls upon the face of the total reflection prism, m_5, passes through the small achromatic lens 33, strikes the total reflection prism, 37, whence it is reflected at right angles to fall upon the speculum mirror, L. It is reflected downward at right angles by this and made to fall upon a plaster of paris strip below, as is shown in the small auxiliary diagram. We thus have falling upon the plaster of paris surface a sharply focussed and magnified image of slit G. This image is always larger than the plaster of paris strip. The excess light passes down into a dark compartment and is absorbed.

The red beam, after passing through the small right angle prisms in the way already described, escapes behind the base of the prism m_5, passes through the small projection lens 34, thence to the speculum plate M, and down to the plaster of paris surface, as in the case of the green. As conditions are in the diagram, the red beam is on the left, the green on the right.

In order to reverse the position of the two colors, the slide N, bearing the prisms m_5 and m_6 must be pushed over to the right to take the dotted position. The green beam now engages the right angle prism m_6, is bent at right angles through lens 32 to meet prism 38, thence to a mirror and plaster of paris surface as before. After this change is made, the red beam is made to pass between m_5 and m_6. Its course is in no way changed by the shifting of the slide N; as conditions are now after the introduction of this change, the green beam is on the left and the red on the right. If only two speculum mirrors are used, the carrier P, holding them must be pushed over to the left to take the dotted position. If three speculum plates are used, no shifting of them is required (cf. p. 56). It is hardly necessary to mention that m_5 and m_6 are prisms of the same size and absorption value; that prisms 37 and 38 are likewise matched, and that lenses 32 and 33 are matched as to quality of glass, thickness, and focal length.

There are three convenient ways in which the energy of these beams may be altered: (a) by attaching iris diaphragms to the lenses; (b) by the interposition of a smoked wedge in the pathway of each beam, and (c) by the rotating sector or episcotister. The rotating sector is the easiest and most accurate method of the three. Figs. 7 and 11 show the arrangement for use with the episcotister cf. also p. 76).

The method by which a white beam of light equal in size and form to the monochromatic beam is made to fall upon the plaster of paris strip in place of either of the monochromatic beams is as follows: A Nernst filament is mounted vertically

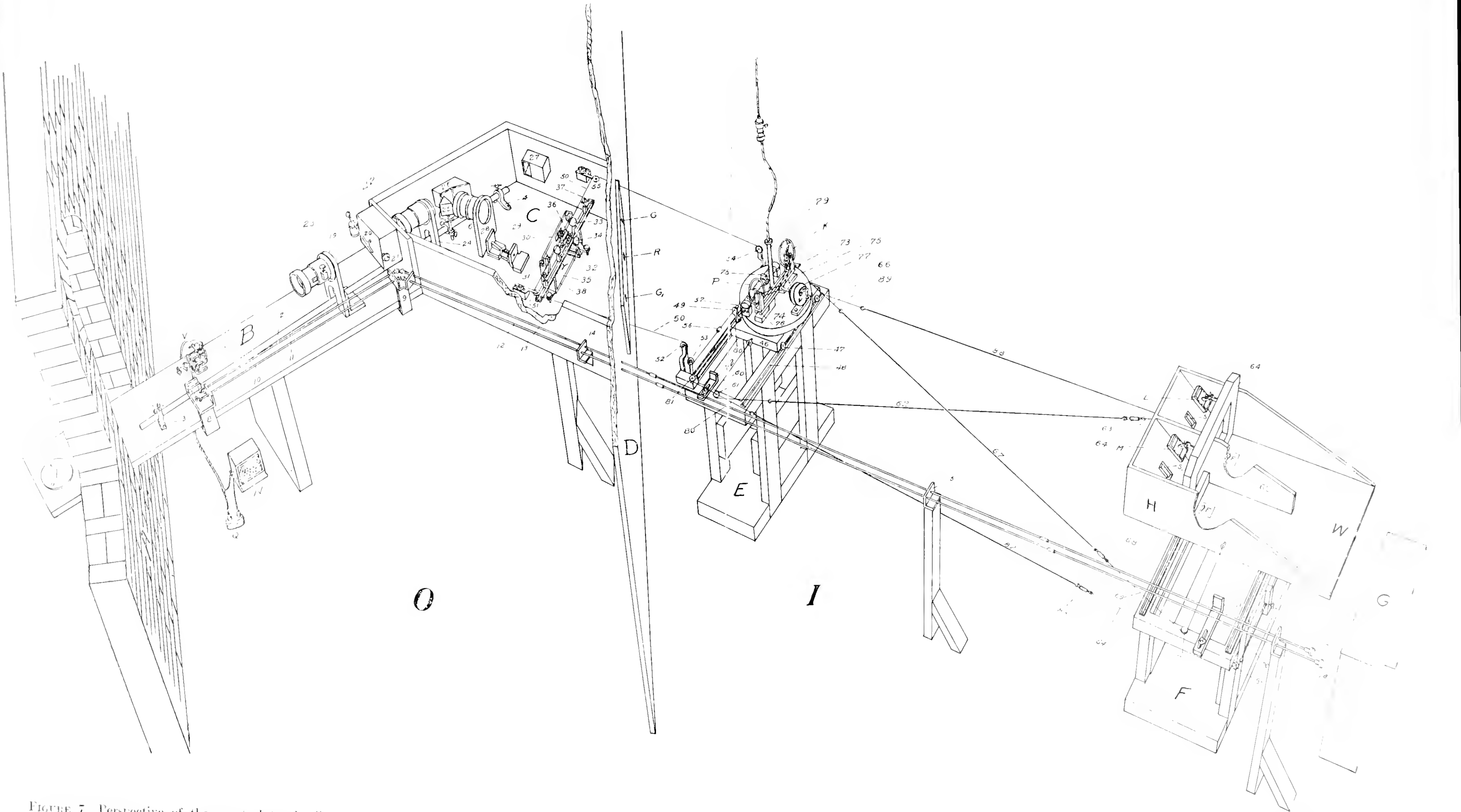

FIGURE 7. Perspective of the spectral "color" apparatus. On the table B is shown the arc, 5, the condenser 19 and the slit 20. Inside the compartment C is placed the collimator 24, the prism 25 and the object 28. The casting Y supports the selecting, spacing and reversing devices. The stand E supports the rotating sectors P and K and the motor 77 which rotates them. At W are shown the speculum mirrors M and the "stimulus-patches" S and S₁ which receive the monochromatic beams. The animal is placed at W and must make a choice of the two colors as evidenced by his passing to the right or the left of the tion 65 and opening the one or the other of the food boxes F or F₁.

in a 4″ cubical metal box. (At greater expense the Westinghouse Nernst lamp, see p. 5, may be mounted on the box in place of the filament. The lamp is far more convenient.) This filament is projected upon the plaster of paris strips by means of a short focus achromatic lens mounted in a tube attached to the box. The box can be shifted on a metal arm so as to exclude any one of the beams, and to project in its place a white beam upon the plaster of paris surface. This box is not shown in the diagram. It should be inserted immediately behind the partition D, shown in fig. 7, and consequently in front of the episcotisters. The episcotisters can then be adjusted so as to decrease the energy of this light to any desired amount. If preferred, a simple vertical optical slit may be mounted in the focus of the projection lens. The intensity of the beam may be conveniently and accurately controlled by the slit without the use of the episcotister.

The details of the mounting of the above optical system will now be taken up with the aid of separate drawings.

2. Description of the mounting of the apparatus

Fig. 7 shows the complete system ready for operation. Since the aim of our report is to present the working parts clearly enough to make duplication possible, the description which follows will be somewhat technical and detailed. Also there will be, necessarily, a certain amount of repetition in the descriptions, since fig. 7, showing the whole apparatus, is first taken up, and is followed by the description of the larger drawings of certain parts of the system. Figs. 6 and 7 will give a clear idea of the whole apparatus. Figs. 8-12 inclusive are given for the benefit of those who may desire to construct, or at least install the apparatus. Many important dimensions are not given, but the lenses and other optical parts obtainable differ so much that it seemed hardly worth while to give all the dimensions. Those which relate specifically to the control of the stimulus are everywhere given.

As shown in fig. 7, two rooms, *O* and *I* are devoted to the apparatus. *I* is a complete dark-room 25 feet long and 16 feet wide; *O* is a smaller room containing a window for the admission of sunlight. When either the arc or Nernst is in use, daylight is excluded from *O*. The dividing wall between *O* and *I* is marked by the letter D. The wall A is the outer wall of the building. It faces west (south is a far better exposure if it can be obtained). With a Fuess heliostat, sunlight may be obtained from about 1 P. M. to 4 P. M.

A shelf, B, 10″ wide and 2″ thick, supported upon heavy trestle work 20″ in height, projects through a window in the wall A. Continuous with this, at an angle of 120 degrees to it and in the same plane, is a much wider shelf, C. This latter shelf, about 30″ wide and 4′ long, is surrounded by walls 2″ thick and 12″ high. The compartment thus formed is supplied with a heavy wooden cover not shown in the diagram. Its shape is somewhat irregular, as appears in the figure. Most of the delicate parts of the apparatus are assembled here. It is lined with dark paper and is made light-tight and dust-proof. Where possible, it is very desirable to have the supports for the parts of the apparatus thus far described made of concrete.

Upon the end of shelf B, which projects through the wall A, is to be found a circular aluminum plate, 1, to hold the heliostat, when sunlight is desired. Two end supports, 3 and 4, screwed to the shelf, support a steel bar, 2. To this rod is attached an arc mechanism, 5, and a clamp, 6, which carries the prism table, 7, shown inside box *C*. Two castings, 8 and 9, carry $\frac{1}{4}$″ rods, 10, 11, 12 and 13, which are so geared that the arc may be controlled by the operator in the room *I*, by turning the knobs 17 and 18. These long rods are supported by means of castings, 14, 15 and 16.[1]

The incident beam (sunlight or arc) is made to pass through the condensing lens 19. This is a "second-hand" Perry portrait lens, 3″ aperture, 6″ focus, supplied with rack and pinion. It gives an image of the crater of the positive carbon upon slit 20. The width of the slit is controlled by the micrometer screw 21. The beam of light may be kept from passing through the slit when desirable by means of a little shutter, 22, electromagnetically actuated. The shutter can be operated by means of a switch placed near the operator at G.

After the rays pass through the slit they are made parallel by means of the collimating lens 24 (Voitländer portrait lens

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[1] While the ordinary 45° hand feed arc supplied with the controlling rods just described is satisfactory and cheap, the automatic lamp of Bausch & Lomb is much more convenient. When it is used no controlling rods, castings, etc., are necessary. (See p. 71.)

8″ focus, 3″ aperture, supplied with rack and pinion). The parallel rays then strike the face of a dense flint glass prism, 25, (face 4″ x 4″). The excess white light reflected from the face is thrown into the small dark box, 26.

The refracted beam passes through the objective, 28, (Zeiss "extra rapid" focus portrait lens, 3″ aperture, 20″ focus). This lens is not regularly supplied with rack and pinion, and is therefore mounted on a carriage, 29. This objective brings the beam to a focus on the silvered face of a vertically placed slit wall or table, 30. The mechanism of this is taken up separately in figs. 9 and 10. The wall carries four sliding jaws, which form two slits whose widths are adjusted by means of the micrometer screw-head, 31, and by one not shown in the cut. The casting, Y, which holds the slit-wall, also carries a metal track, 35. A metal support (see 22 of fig. 9) which may be fixed to the metal track 35 at any desired point, bears a sliding mechanism, 36, (N of fig. 6) for reversing the beams. The place of this reversing mechanism on track 35 varies slightly, depending on the monochromatic beams selected, but is shown in the cut as occupying the middle of the track. On each side of this is mounted a small projection lens, 32 and 33; near the ends of the track are mounted the prisms 37 and 38. A third projection lens, 34, is mounted upon a metal track projecting at right angles to the main track. (These numbers refer to the same objects as in fig. 6.) Two small prisms lying between lenses 32 and 33 are not clearly shown in this cut, but appear separately in fig. 9. The whole system mounted on Y, which selects, spaces and reverses the beams, will be made clear by reference to fig. 9.

Three small windows, G, R and G_1, 2″ x 2″ each, are made in the wall D, 25 cm. between centers. Only two of these windows are in use at any one position of the colors.

In room *I*, a stimulus carriage, H, is mounted upon the trestle-work F, so as to travel right and left. The rectangular wooden frame 64 carries the two 3″ x 5″ speculum mirrors, L and M, inclined at an angle of 45 degrees to the two incident beams. These mirrors are attached to the framework at a height of 14″ from the floor, W, of the stimulus carriage. The two mirrors reflect the beams vertically downward to the rectangular plaster of paris surfaces, S and S_1. F and F_1 show the two food boxes. A partition, 65, separates the two food compartments. In front of the stimulus carriage, H, is placed the bench G, upon which the experimenter sits.

Between wall D and the stimulus carriage, H, is shown the apparatus for the control of intensity, mounted upon the trestlework E. A heavy maple block, 46, 2″ x 12″ x 18″, is mounted upon four ball-bearing rollers, 47, so as to slide on track 48 parallel to and synchronously with the carriage H. A small metal spur, 49, is fastened to block 46. By means of this metal spur and the gut cord system 50, which is attached to the metal framework of the reversing mechanism 36, block 46 is made to operate the device for reversing the colors. The gut cord 50 passes around pulley 51, over and down 52, under 53 and under another one not shown in the cut, up and over 54, thence to 55 and back to the opposite side of the framework of the reversing mechanism. Two stops, 56 and 57, are attached to the cord in such a position that the spur 49 can throw the mechanism 36 to the right or left, depending upon the extreme right or left position of block 46. Since it has already been pointed out that this block moves synchronously with the stimulus carriage H it follows that a movement of H to the extreme right or left position serves to reverse the right-left relation of the two beams.

The block 46 is made to move synchronously with the stimulus carriage H by means of a heavy gut cord, 60, which passes over a pulley 61, connects with a small 3-32″ iron rod, 62, through turn-buckle, 63, with gut cord, 64, which runs over a fixed pulley (not shown) fastened to the framework supporting the track upon which carriage H runs, and is attached to the right-hand side of the carriage. With this single cord system in operation it will be seen that when carriage H is moved to the left block 46 is moved an equal distance to the left also. To the opposite end of the block 46 is fastened a similar heavy gut cord, 66, running over a fixed pulley not shown, but similar to pulley 61 on the opposite side, and connecting with the iron rod 67, through turn-buckle 68, with gut cord 69, over fixed pulley 70 to carriage H. It will be seen that this latter link system will not be operative when the carriage moves from the left to the right position, but that it does operate when the carriage is moved from the right to the left.

The extreme positions of carriage H are adjustable by means of a stop, 71, on the left-hand side, and by a similar stop on the right-hand side, which is hidden by the carriage. The extreme positions of block 46 are likewise limited by stops 72 and 73. When carriage H hits its left-hand stop, 71, block 46 hits its left-hand stop, 72. A similar condition obtains for the right-hand position of both.

In the center of block 46 is mounted a circular table, 74, free to rotate in a horizontal plane. On a diameter of this table and 4″ above it is mounted by means of two L-shaped blocks, 75, a metal track, 76, which carries the two episcotisters, P and K. The distance between centers of these episcotisters can be adjusted by clamping them at any desired position on the track. They are belted by means of small round leather belts or rubber bands to a small motor, 77, screwed firmly to the circular table 74. The speed of the motor can be controlled by the rheostat, 78, which is also screwed to the table. The wiring to the motor and rheostat is carried to the table through a ½″ brass tube, 79, which serves to keep the wires from interfering with the beams when the horizontal table is being revolved in order to change the relation of the episcotisters. The rotation of the circular table, and thus of the episcotisters, can be controlled by the operator at G, by means of a continuous cord system passing around a circular drum lying between block 46 and table 74, to which it is concentrically attached (not shown in this cut, but separately in figs. 11 and 12.) The cord system may be traced as follows: The gut cord 80 passes over a pulley, 81, to iron rod 82, to turn-buckle 83, to gut cord 84, to pulley 85, to iron rod 86, through a clamp 87, to another gut cord which runs over a pulley to a turn-buckle not shown, to iron rod 88, to gut cord 87, over pulley not shown, back to the drum.

a. Operation of the system—The purpose of these various pulley systems is to make the shifting of the colors and the control of their intensity absolutely automatic. The operator at G can reverse the colors by merely pushing the carriage to the right or left for a distance of 25 cm. At the same time, this movement of the carriage can be made to control the positions of the episcotisters. With the carriage at its extreme right position the green is on the right and the red on the left.

Episcotister K intercepts the green beam, while P intercepts the red. Shifting the carriage 25 cm. to the left, brings the green beam to the left and the red to the right, but episcotister P now intercepts the green, while K intercepts the red. Sometimes this is desirable. But suppose we desire to shift the position of the color without changing the relation of the episcotisters; one needs then merely to clamp the cord system controlling the circular table at 87. This will cause the circular table carrying the episcotisters to rotate 180° while the carriage H goes from one extreme position to the other. P will thus be made always to intercept the red, and K the green beam. It is desirable at still other times to use the full intensity of the beam. This is accomplished by first rotating the episcotister table 90° from the position shown in the drawing, and by releasing the clamp screw at 87. The episcotisters will no longer intercept either of the beams in either position of carriage H (see, for mechanism of episcotister table, p 66).

A somewhat more expensive but more satisfactory substitute for carriage H is a rectangular dark cabinet, fig. 8, 40″ high. 20″ thick by 40″ wide. The vertical framework of the cabinet is made of four pieces of oak, 3″ x 3″ x 40″, bolted together by heavy iron straps $\frac{1}{4}$″ thick, 3″ wide and 40″ long. The sides and top are covered with thin wall-board, coated with dead black paint. The inside of the cabinet is lined with dead black velvet, loosely glued to the sides. The three speculum mirrors, M, M_1 and M_2, are fastened by means of their brass framework to the strap Ba, 25 cm. between centers. The mirrors are inclined as before, at an angle of 45° to the incident beam. Below each mirror stands a metal box containing at its upper end the surface of opal glass or plaster of paris, upon which the beam coming from the mirror is to fall. The beams are admitted through the three windows, W, W_1 and W_2. The arrows show the course of the beams, G, Rd and G_1.

There are two sets of these metal boxes: one set of three, which permits the use of a plaster of paris surface, and another of three, of opal glass. For convenience we shall call these respectively "plaster of paris boxes" and "saturation boxes." The plaster of paris boxes are used in all cases where it is desired to give a stimulation of monochromatic light at maximum

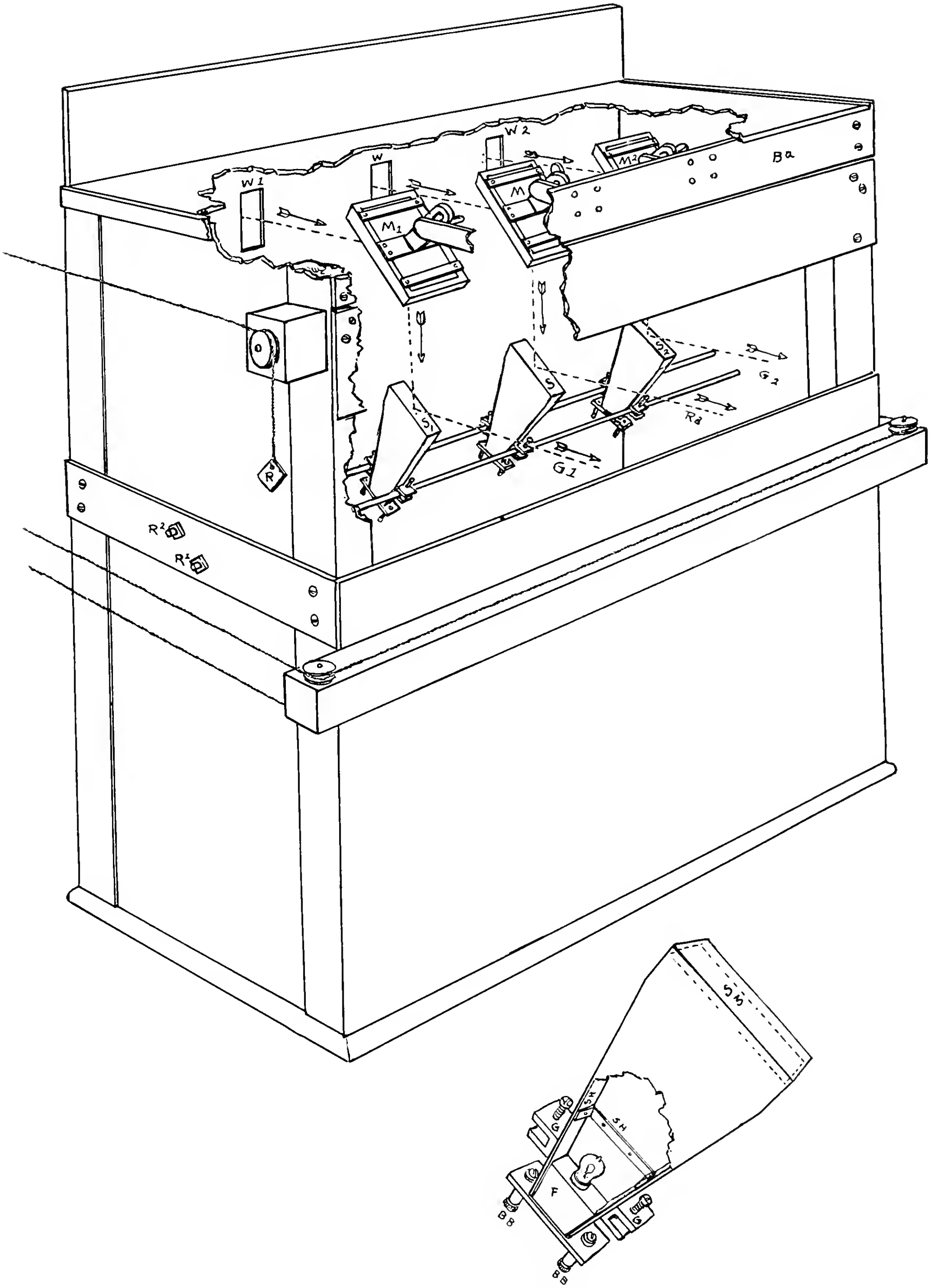

FIGURE 8—Sketch of dark cabinet and stimulus box. The colored bands are admitted through windows W^1, W and W^2. They pass to the mirrors M^1, M and M^2 and thence to the plaster-paris surfaces of the stimulus boxes S^1, S and S^2. The small diagram shows the details of the construction of the "saturation box." The ground glass surface S^3 receives monochromatic light from the speculum mirror above and white light from the tungsten miniature F, below.

saturation. The saturation boxes are employed when it is desired for purposes of control, to alter the saturation of the beam.

The above diagram shows the three saturation boxes in the dark cabinet in the position in which they are to be used. A separate drawing of the interior of the saturation box is shown below the cabinet. The boxes are first cast in brass; the walls are then shaped down until they are made as thin as possible, especially at the large end, which is practically knife-edged. This end is made rectangular, 7 mm. x 7 cm. A piece of opal glass, first ground with coarse emery upon the "flashed" surface (see p. 26) is then accurately ground by hand to fit the whole opening snugly (see dotted lines in small figure). It is then forced in (with flashed surface out) after the edges have been carefully blackened with dead black paint and allowed to dry. This gives a sharply defined surface for the beam coming from the speculum mirror to fall upon. On account of the shape of the box the excess light falls into the dark cabinet and is there absorbed.

The interior construction of this saturation box is clear from the drawing. A small block of wood-fiber, F, is fitted into the small end. A miniature lamp-socket is imbedded in this block, and the wires for its electrical connections are led outside to two binding posts, VB, BB; a small miniature tungsten lamp 1½″ c.p., 2 volts, is burned in this socket. This lamp should have practically a straight filament and should be burned constantly in one position. The tip of the bulb should be at the side and not at the end. The three lamps required are supplied with current by five 2 volt storage batteries. A separate sliding resistance is burned in series with each lamp. A volt meter reading 0–6 volts should also be placed in the circuit, in such a way that the voltage of each lamp may be tested separately. The lamp is burned always at a constant and known voltage. Immediately above the lamp a small shelf-support, SH, 2 mm. wide and 1-64″ thick, is shown; shelves of smoked glass are accurately ground and fitted into the opening. The intensity of the light can be easily and accurately controlled by this means. At a greater expense an Aubert diaphragm, adjustable from the outside of the box, may be inserted in place of the smoked glass.

The opal glass, S_3, is illuminated from below by this white light, and is at the same time illuminated from above by the beam of monochromatic light coming from the speculum mirror. The energy of the whole effective stimulus may be taken, or that of each component separately.

The plaster of paris boxes are identical with the former in size and shape. The whole upper end of the box, however, is filled with plaster of paris, in accordance with the following method: A good piece of plate glass is first selected. This is then ground with emery of coarse to medium fineness until the surface of the glass shows a uniform grinding. The large end of the metal box is inverted upon this. Dental plaster of paris, mixed with water until it begins to set, is poured into the box and allowed to stand 24 hours. The box is then carefully lifted from the surface of the plate glass, and all excess plaster of paris is removed with a damp cloth, great care being taken not to mar the diffusing surface. After the plaster is thoroughly dry it offers a splendid diffusing surface with a *minimum* of direct reflection. A small dust-proof cap should be kept over these surfaces when the apparatus is not in use.

The stimulus boxes have small metal guides, D and G, attached to their base, supplied with clamp-screws, by means of which the boxes are easily attached to the supporting rods, R^1 and R^2, passing through the cabinet. From the drawing it is clear that these boxes are inclined at an angle of 45°, so that the face of the diffusing surface is parallel to the face of the mirror. Thus, each part of the monochromatic beam passes through the same distance.

If one contrasts the use made of this cabinet with that of the stimulus carriage H, one sees that in the latter there are only two mirrors and two stimulus boxes, and that consequently the whole has to move from left to right, or *vice versa*, in order to catch the green beam as it is sent to the left or to the right by means of the reversing device. The cabinet, however, supplied with three mirrors and three stimulus boxes, remains stationary while the beams are reversed as before, either automatically by the movement of block 46 or by means of a light cord, R, directly connected with the reversing mechanism.

When the cabinet is used the animal is placed in a separate experiment box in front of it (see fig. 4 and p. 84). The cage containing the animal must be movable, parallel to the front of the cabinet for a distance of 25 cm. Probably the chief advantage of the cabinet comes from the fact that with it experiments may be carried out *in full daylight illumination.*

3. Description of color-spacing and reversing device

The various parts by means of which the two beams are selected, spaced, reversed and finally projected upon the plaster of paris surface, are all assembled upon the iron casting Y, fig. 9. This consists of a base ½″ thick and 3″ wide, mounted upon three levelling screws, two of which are seen in 1 and 2, and two uprights, 3 and 4. The upright pieces are notched on the back so as to support the metal track 5. This track consists of two ½″ square iron bars, 60 cm. long, bolted together parallel by straps, 6 and 7. The track is held to the uprights by means of clamps 8 and 9. It will be seen that the track can be clamped to the casting in any desired position to the right or left. In the central point in the length of this track, there is attached another short track, 10, normal to it. The front upper part of each of the uprights 3 and 4 is notched so as to receive the slit-wall 11, containing the double slit (see fig. 10). The front plate of this slit-wall is fastened to a rectangular frame, 12, made of ¼″ square brass rods. To the upper face of the lower horizontal bar of this frame is attached a grooved track, 13, the beveled sides of which are fastened to a horizontal plate by means of screws, two of which appear at 14 and 15.

Running in this grooved track are to be found two small prism tables, 16 and 17, which can be moved by hand and clamped in any desired position by arrangements not shown in the cut. To these tables are attached two total reflection prisms with 9 mm. face, 18 and 19 (m_1 and m_2 of fig. 6). The use to which these prisms are put is mentioned on page 47. The plate and frame holding the double slit mechanism is shown in front view in fig. 10.

In the present drawing is seen the back view of this double slit mechanism. The letters O, J, J_1, J_2, J_3, have the same significance as in fig. 10. In the back of the slit-wall is the window W, the slit jaws, J, J_1, J_2, J_3, slide in front of this. Jaws J_1 and J_2 are held firmly against the track by means of spring clips, c and d. The two slit openings described in fig. 10 are seen here from the back at Sg and Sr. These two slits admit the two selected beams, e.g., red and green.

The track 5 supports five 1″ square iron posts, 20, 21, 22,

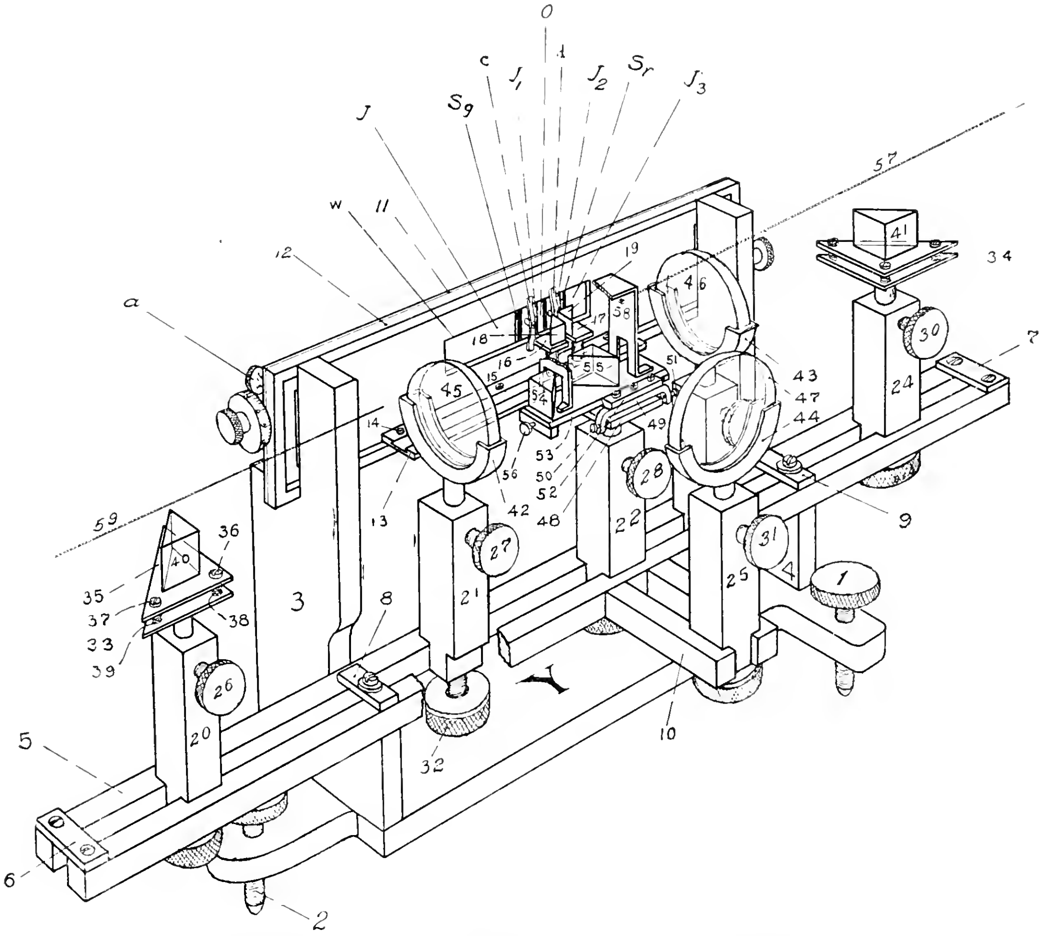

FIGURE 9—Perspective of the color selecting, spacing and reversing device. The selected bands are admitted through the slit openings, Sg and Sr. They are brought near together by total reflection prisms 18 and 19, reversed by prisms 54 and 55 and focussed by the small lenses 45, 46 and 47. The beams are spaced by the prisms 40 and 41.

23, 24, 25, which are first shouldered on their lower end so as to fit the opening between the bars forming track 5, and are then turned down to form a $\frac{3}{8}''$–12 screw. A knurled nut, 26, serves to clamp the post to the track. A gasket is placed between nut and track.

These posts are drilled with a $\frac{3}{8}''$ hole, and are supplied with clamp-screws, 27, 28, 29, 30, 31 and 32. Posts 20 and 24 carry prism tables, fixed directly to an upright $\frac{3}{8}''$ in diameter. 35 is another plate of the same shape and size mounted above 33 by means of three screws (clearance holes are drilled for these) two of which are seen at 36 and 37. The plate 35 is constantly pressed upward against the screw-heads by means of spiral springs, two of which are seen at 38 and 39, through which the screws run to the tapped holes in 33. It will be seen that this device enables one accurately to level plate 35, upon which is fixed the total reflection prism 40. The table on the opposite side, 34, is identical in structure.

Each of the uprights, 21, 23 and 25, carries a lens holder, 42, 43 and 44 respectively. These holders carry the three small achromatic projection lenses, 45, 46 and 47.

Post 22 supports the reversing mechanism, which consists of the fixed plate 48 mounted directly upon a $\frac{3}{8}''$ rod. An upper plate, 49, is hinged to this plate by means of pivot screws 50 and 51. The upper plate has a leveling device attached, similar to that just described for plates 34 and 35. The upper plate has two beveled strips, one of which is seen at 52, screwed to it so as to form a track which receives the sliding plate 53. The two 19 mm. total reflection prisms 54 and 55 (m_5 and m_6 of fig. 6) used in reversing the beams are cemented to this sliding track. The lateral movement of the slide is limited by two stops, one of which, 56, is adjustable. The sliding plate itself, 53, is moved from side to side by means of the light gut cord, 57, attached to a metal bridge, 58. This bridge is broken away in front for the sake of clearness. The opposite attachment for cord 59 is not shown. It will be remembered that this cord system is attached to block 46 (see p. 66).

a. The double-slit mechanism and calibration.—Fig. 10 is a horizontal drawing of the double-slit structure. It is constructed as follows: A heavy brass plate, A, 3-16″ thick, $2\frac{3}{4}''$ wide and 12″ long, is attached by screws, 1–9 inclusive, to a frame made of $\frac{1}{4}''$ square brass. The plate is slotted at Sl and Sl$_1$, so that it may be attached vertically by thumb-screws to the planed surface of the uprights of Y (page 61). A window wide enough to allow the whole spectrum to pass through, 1 cm. high and 8 cm. long, is cut in this wall. A part of this window is shown at O. The window is seen more clearly in the back view of the mounted slit, shown at W in fig. 9. The two thin metal strips upon which the scales Sc and Sc_1 are ruled, 6 mm. wide, 1.5 mm. thick and 20 cm. long, are beveled at an angle of 45°, and are attached above and below the window in such a way as to form a grooved track for holding the slit jaws. This track is indicated at 11 and 12. Two large slit jaws, J, and J_3 knife-edged along their vertical surfaces, slide in this track. Attached to these jaws are two shouldered nuts, K and K_1. By turning the calibrated screw-heads Cal and Cal_1, the two jaws may be made to advance or to recede. Without the addition of jaws J_1 and J_2 the apparatus may be used as a single optical slit. When these two jaws are inserted, a double slit is provided which allows two beams of monochromatic light to be admitted. These two jaws are also grooved to slide in tracks 11 and 12. They are held in their position by means of small vertical spring clips (c and d in fig. 9), fastened firmly to the center of each in such a way that the two ends of the spring work constantly against the back face of the slit-wall. The clip, combined with their snug fit in the grooved track, holds the jaws quite firmly in a vertical position. The jaws J and J_3 are provided on their front faces with indices, I and I_1, fig. 10, which give their position with respect to the scales Sc and Sc_1 respectively. These scales are needed for controlling the width of the slit and for setting the openings at desired positions.

After the apparatus has been permanently installed, it is very desirable to calibrate the double slit in terms of wave-lengths. For this purpose it is best to rule the scale Sc_1 for the whole of the length of the strip. With the slit in position one then burns in the lamp (using the *arc* between the two carbons, instead of the crater of the positive carbon as the *source*) a positive carbon soaked in a strong salt solution. A well-defined D-line appears, the position of which is noted on the scale. Several other metallic salts, e. g., lithium and barium, are then successively burned in the same way, and their lines noted on the scale. Some ten or twelve such determinations are sufficient to enable one to plot the wave-length curve of the

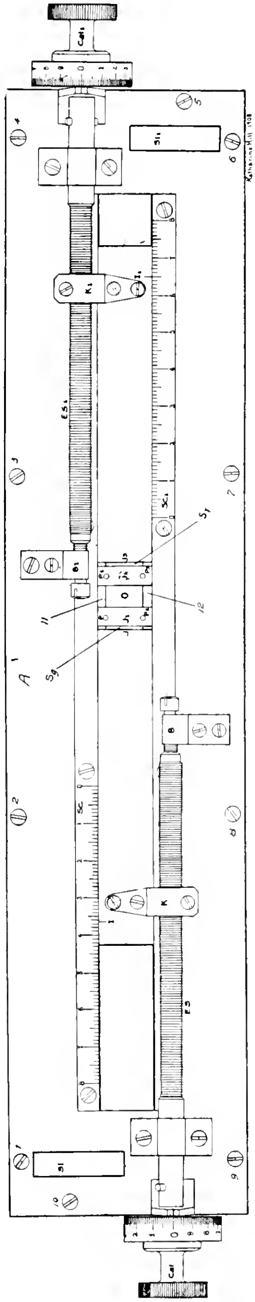

FIGURE 10—Double slit mechanism. The slit openings are shown at Sg and Sr. The width of these openings is controlled by the calibrated screw heads Cal and Cal^1. O is an opening variable in width. Its width depends upon the spectral regions which the slit openings admit.

whole spectrum in terms of the divisions on the scale, in exactly the same way as the curve for the scale of every spectrometer is plotted. The mercury arc gives very great assistance in this calibration. The wave-lengths admitted by any given opening can be immediately read off without the use of a spectrometer. Since several of the solar lines are also clearly visible upon the polished jaws of the slit, all one needs to do when the solar spectrum is used is to make the D-line of the solar spectrum coincide with the D-line of the spectrum obtained by the use of the brine-soaked positive carbon. The distribution of wave-lengths in the solar spectrum will coincide with that of the arc. Since the D-line can be so conveniently used, the apparatus should be tested every week or so, to see that the D-line always falls upon the same scale division.

In the actual setting of the jaws so as to admit the passage of the monochromatic beams through the slit, the following method must be used: In fig. 10 the jaw J, as shown by its index, stands at 3.65. Suppose we desire to admit some other portion of the spectrum, say that which would be admitted when the scale should read 6 for J and 5.9 for J_1 respectively; we bring the jaw J back until the index reads 6 or more. The small jaw J_1 is then moved up by hand to touch J. J is then screwed forward by the micrometer screw-head Cal until the index reads 5.9. J is then brought back until its index reads 6. An optically perfect slit is thus formed, 1 mm. wide. After J_3 and J_2 have been set in a similar way, an opening, O, is left between J_1 and J_2. This opening must be closed with black oiled skin, thin soft black leather or blackened tinfoil, or by some other pliable opaque material. Four little projections are to be found upon J_1 and J_2 for this purpose. They are marked P, P_1, P_2, and P_3. This strip should be fastened on before J_1 and J_3 are withdrawn from J and J_2 respectively. In the diagram the two slit openings are shown as Sg and Sr.

The jaws J_1 and J_2 are each 5 mm. wide; consequently, with these two jaws two places in the spectrum lying closer than 1 cm. cannot be obtained. A series of single strips, knife-edged on both their vertical surfaces and beveled at their ends, should be made up. These strips should vary in width, starting at 1 mm. and increasing by .5 mm. up to 1 cm. Each should be provided with a spring clip at the back narrower than the front width of the strip. When these are to be used, J_1 and J_2 are removed, and any desired one of these strips inserted in their places. Such a series, probably, will be adequate for the determination of the qualitative D. L. in animals.

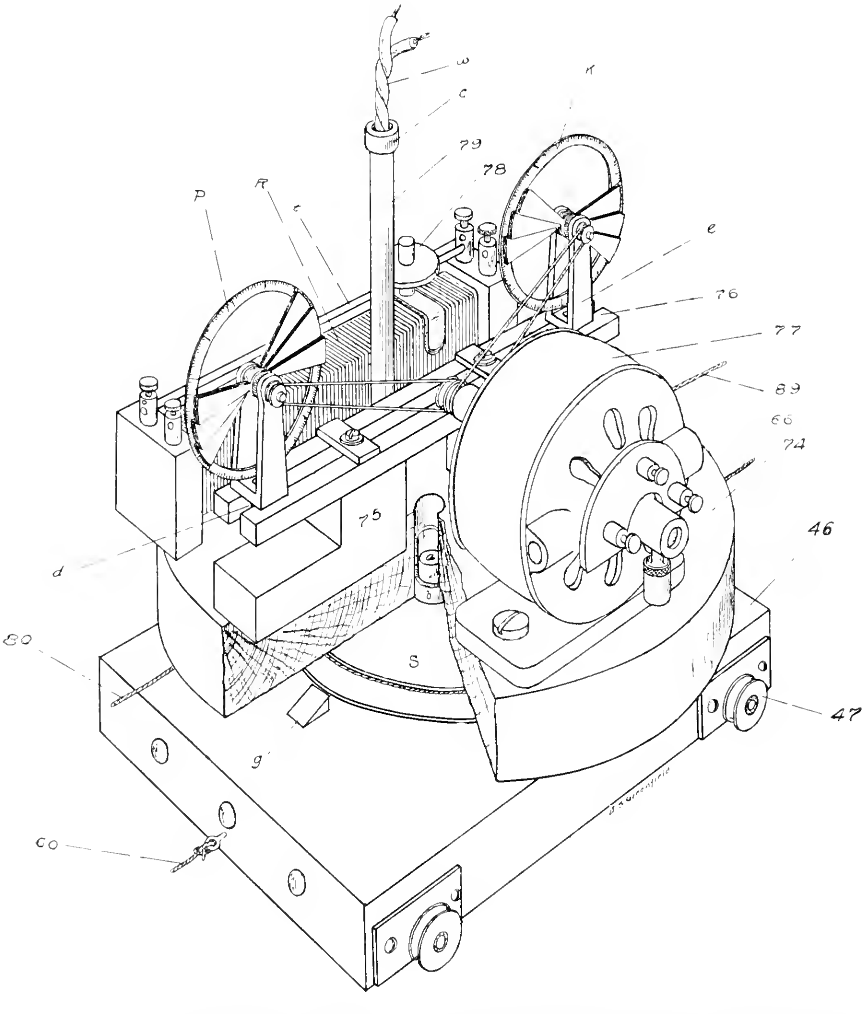

FIGURE 11—The episcotister table. The two rotating sectors are driven by the motor 77. The speed of the motor is controlled by the sliding resistance R. The whole apparatus is mounted upon a rotating table, 74, the rotation of which is controlled by a set of cords, in the hands of the experimenter, passing around the drum S. The position of the sectors with respect to the two beams is determined by the position of the carriage 46.

b. The episcotister table.—Fig. 11 is an enlarged drawing of the episcotister system shown upon the trestle work, E, of fig. 7. In the center of block 46 is fixed a vertical shaft or pivot, a, about which the circular table 74, with everything on it, is free to rotate. To the under surface of 74, and concentric with it, is fixed a wooden drum, S, 15.9 cm. in diameter. This carries a turn of gut cord, the ends of which are shown at 80 and 89. These cords are attached to H, fig. 7, and used to rotate the episcotister table. The method of winding the cord around this drum is shown separately in fig. 12.

The hole through the center of the table, 74, and the drum, S, is bushed with a brass tube, b, to prevent wear. In the illustration the bushing is partly cut away to show the pivot inside of it. Two L-shaped wooden blocks, one of which is shown at 75, support a metal track, 76, made of two ½″ brass bars, 30 cm. long, clamped to the wooden block ½″ apart. The episcotister frame **e** is locked to the stand by a clamp screw **d**. The other parts of the apparatus are as follows: K and P are two Zimmerman episcotisters 10 cm. in diameter. 77 is the motor already referred to on page 55. It is supplied with a special pulley containing two grooves ¼″ apart for receiving the belts from the two episcotisters. R is an ordinary sliding rheostat, with slides shown at 78. 79 is a ½″ brass tube, 12″ high, bushed at **c**, to receive the feed-wires, **w**. The ends of the cords attached to block 46 and to the carriage H of fig. 7 (to produce the lateral motion) are shown at 60 and at 66 on the opposite side. The working of this cord system has already been explained (p 54). At **g** is a small triangular wooden block, which prevents the cords encircling the drum S from slipping between the drum and the block 46. There are two others not shown in the figure. Finally, at 47, is shown one of the four ball-bearing pulleys, upon which block 46 travels.

In fig. 12 is shown the winding of the cord system and the mechanism for rotating the episcotister table. The disc shaded with the diagonal lines is the drum S spoken of in connection with fig. 11. The positions of the motor, M, and of the episcotisters, P. and K, are indicated. A, Fig. 12 shows how the cords (a single continuous cord is really used) are fastened to one point of the drum circumference before the free end of 89 is wrapped around it. B, fig. 12, shows that cord 89 is given one turn around the drum. The two ends of the cord are then forced to run over fixed pulleys and are joined as described on page 56 and made to run freely through a hole in the metal bar supplied with a clamp-screw, 87 in fig. 7. It must be remembered that block 46 is free to slide on its track from right to left. Suppose that block 46 is pushed to the left, and that the cord around the drum is locked at 87; fig. 12, C shows what will happen: first, note the position of the episcotisters in B, fig. 12, and compare this with C, fig. 12, where block 46 has been made to travel one-half its distance from right to left. It will be seen that the drum 74 has been forced into rotation by the unwinding of 89. At the same time, cord 80 has been made to wind up. Note that in C, fig. 12, motor M and the two episcotisters have moved one-fourth of a turn clockwise (in which position the episcotisters no longer interrupt the beams). In fig. 12, D, block 46 has reached its extreme left position. Each cord is now half wound up. The episcotisters are now reversed (as are the right-left relation of the two colors). In fig. 12, B, (corresponding to position shown in fig. 7) the green is on the right and is interrupted by episcotister K, whereas the red beam is interrupted by P. In fig. 12, D, the green beam is on the left and is still interrupted by K; whereas the red is on the right and is still interrupted by P. Referring again to fig. 12, B, suppose that the cords 80 and 89 are not fixed and are allowed to move freely through the clamp 87, fig. 7; as block 46 is made to travel as before to its extreme left position at fig. 12, D, the cords 80 and 89 will not wind and unwind as they did in the other case, but will slip easily over their pulleys. The table 74 will not rotate, and consequently the episcotisters will interchange with respect to the two beams. In this case at fig. 12, B, P will engage the green and K, the red.

As might be inferred from the above description and from that on p. 56, three possible ways of using the mechanism are open:

(a) The sectors may be turned until they take the position fig. 12, C, the cord being allowed to run freely through the clamp 87, fig. 7. The full intensity of the beams is available.

(b) The same sector can be made to interrupt a given beam regardless of the latter's left-right position (in order to effect this turn the sectors to the position B, fig. 12, and lock the cord at 87, fig. 7). This adjustment must be open to us when we are

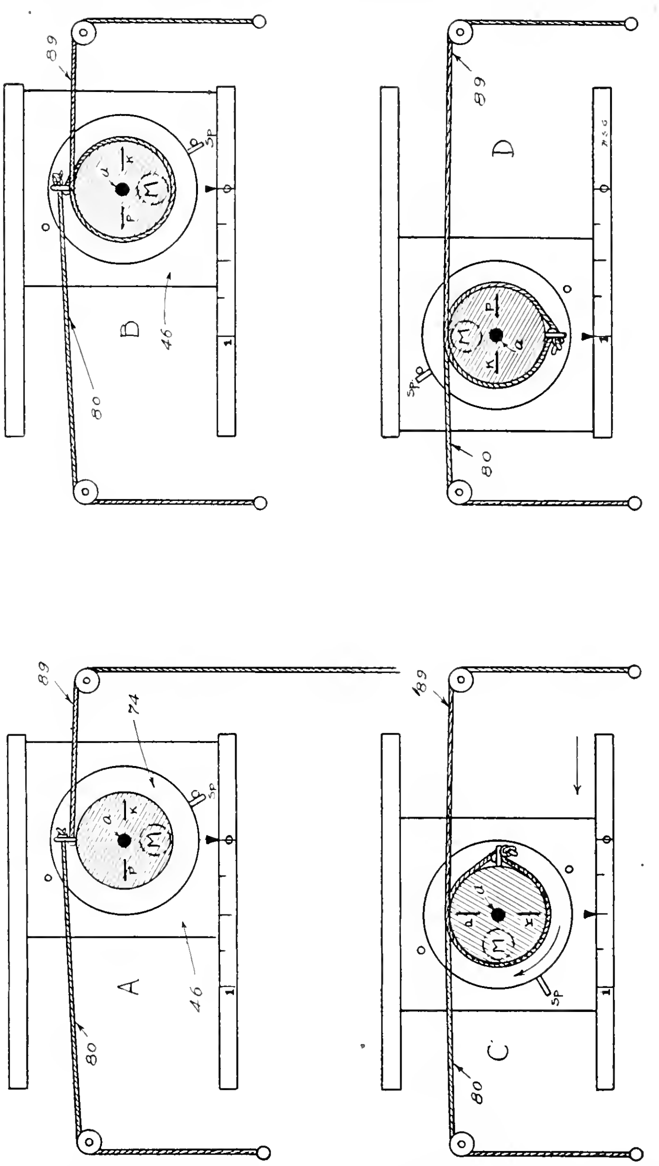

FIGURE 12—A schematic drawing of the mechanism for rotating the episcotister table. The rotating table of fig. 11 is marked here by the number 74. The shaded circular area represents the drum S of the previous figure. The motor is indicated by M, the sectors by P and K, the cord system by 80 and 89. A shows the method of attaching the cords; B, C and D show the different positions of the sectors.

working with a fixed and known difference in energy between the two beams. Where quantitative relations are to be thus maintained, special sectors, described on p. 76 must be used.

(c) The sectors can be made to interchange with respect to the two beams (turn sectors as before to position B, fig. 12, but do not lock cord at 87, fig. 7). This is desirable where abrupt changes in brightness are to be introduced. For this work the Zimmerman sectors are best. One of the sectors can be set with a wide angular opening, the other with a small opening. The intensity of the two beams is thus automatically changed with every change in the left-right position of the beams. Care must be taken in making this setting that both of the colors remain clearly supra-liminal for the animal when the sector with small angular opening respectively engages them.

4. Description and cost of parts of apparatus

a. Sources and their control.—Sunlight and heliostats. A good heliostat greatly increases the ease with which sunlight may be used. There is no cheap and satisfactory heliostat on the market. Nearly all of them are supplied with clockwork which is too weak to drive them steadily. They are usually made too light to withstand gusts of wind. Furthermore the mirrors attached to them are usually silvered on the back. This enormously decreases the intensity of the reflected beam and gives rise to a series of disturbing secondary images. The mirrors may be silvered on the anterior surfaces, but the silver film deteriorates rapidly.

The Fuess heliostat is a convenient one. It permits of use in any latitude and will reflect the beam in any direction. It is listed by Max Kohl (supplied through the Arthur H. Thomas Company) at $125. At the Johns Hopkins University Professor Anderson has modified the original castings of Professor Rowland, and has devised a massive heliostat supplied with two heavy speculum mirrors. These mirrors are ground and polished by Brashear to a surface equal to that of good plate glass, which is accurate enough for the requirements of most work on vision done in psychological laboratories. This heliostat can be supplied for about $150.

Arc lamp.—The automatic arc of Bausch and Lomb with adjustable rheostat of 25 amperes capacity is especially recommended as the standard source in all general high intensity work. This lamp, supplied by the Arthur H. Thomas Company, Philadelphia, complete for $102, is simple in its mechanism. The feed is purely magnetic. As the two carbons burn away they offer greater and greater resistance to the flow of current; finally a portion of the current is shunted through the feeding mechanism. The carbons are then fed toward each other until the resistance becomes so small that no further current passes through the feeding mechanism. The forward motion of the carbons, therefore, ceases before they are brought into actual contact. The lamp is always practically noiseless, with the exception of the "cluck" or series of "clucks" made by the feeding mechanism. A drop of from 1 to 3 amperes is sufficient to start the feednig device.

It was long ago shown by Abney that even a large decrease in amperage does not alter the intensity of the crater of the positive carbon. *It merely decreases the size of the crater.* Since the height of the slit used is less than the diameter of the image, it follows that the variation in the energy of the monochromatic bands is hardly detectable. Of course there are slight imperfections in the carbon, which occasionally produce a sudden flicker and slight shiftings of the positions of the carbons, but such disturbances are *momentary* and *negligible.* It is essential to have a *large crater.* This can be obtained only by the use of a high amperage. Twenty-five amperes is a necessity. A positive cored carbon (Elektra) 9-16″ in diameter and a cored negative carbon 7-16″ in diameter are very satisfactory. If other sizes of carbons are used, or if the amperage is low, there will be a shifting of the crater and a tendency for the two carbons to burn unevenly. Suitable carbons may be purchased with the lamp.

These lamps are very durable. One of them at the Johns Hopkins University has now been in operation two years and gives entire satisfaction. It burns for 1½ hours without change of carbons. It has burned daily for months without attention and during that time has never jammed the carbons nor in any other way interrupted an experiment.

If energy measurements are to be made, it is essential to have both an ammeter and a voltmeter in the circuit with the arc. The voltmeter should read 0–130 by 1-volt divisions.

(It is assumed that the current used will be D. C, ranging between 108 and 120 volts.) This voltmeter will show the general steadiness of the power-house or city circuit. The city current should be used at the time of day when it is most steady. The ammeter should read 0–25 amperes. These instruments need not be of expensive type. Jas. G. Biddle, Philadelphia, has satisfactory instruments, listed as the Keystone type C. voltmeters and ammeters. The cost is about $15 each for voltmeter and ammeter.

In using the arc with the Bausch and Lomb adjustable rheostat admitting the maximum of current it will be found that the amperage is at first rather high, but that as the lamp and resistance box gradually heat up the amperage drops to 23 or less. This increased resistance soon reaches a maximum, however, if the room is well ventilated. The arc will thereafter burn steadily within fixed limits of amperage.

It is advisable to take off the casing of the Bausch and Lomb lamp and to study the mechanism in action. It comes already adjusted but there is a small " vibrator " or interrupter at the bottom of the lamp which may need adjusting. This is the chief source of trouble in the lamp, but it is not serious. The small feed wires connected with the negative and positive carbon receptacles are too small as they come with the lamp, and are likely to burn out, especially if the carbons are not screwed in tightly. It is desirable to replace these with slightly larger wires if this mishap occurs. The lamp is supplied with both horizontal and vertical adjustments. The positive carbon is put in line with the optical axis of the system, and leveled with an ordinary spirit level.

The Nernst filament. The Nernst glower is the most satisfactory form of source where a spectrum of medium to low intensity can be used. It is the only source suitable for stimulus limen (R. L.) and stimulus difference (D. L.) work. A card containing 12 filaments, .8 amperes, 110 D. C., may be purchased from the Nernst Lamp Company, Pittsburg, Pennsylvania, for $3. In addition to the filaments a small " ballast " (resistance) must be burned in series with the filament. This is supplied for 50 cents. In doing quantitative work this filament should be burned in the circuit with a volt- and ammeter. The voltmeter just described is adequate but since the amperage is small, an ammeter reading 0–1 (or 0–5) should be used; this likewise can be purchased from Jas. G. Biddle, Philadelphia, for about $15. The Nernst filament is used by some experimenters simultaneously as source and slit. Others mount it immediately behind the slit (e.g., S, fig. 6). These two methods of using the Nernst are unsatisfactory for continued use, for several reasons which need not be entered upon here. The best method of mounting is that suggested on p. 47.

Slits.—The first slit in the optical system, S, fig. 6, is an ordinary cheap form: (No. 1251 in Max Kohl's catalog.) It is supplied through the Arthur H. Thomas Company, Philadelphia, for about $8. The slit as it comes from the factory is greater in height than is necessary for the present work. It is best to limit the height to about 2 mm. by the use of auxiliary metal strips at the top and bottom. These should be knife-edged in the usual way. The width of the slit is controlled by a micrometer screw.

The double slit-wall, fig. 10, is made from our own design by Wm. Gaertner, of Chicago, for about $45. If it is desired the parts supported by casting Y, fig. 9, can be furnished complete by the Johns Hopkins University. This includes the casting itself, the whole of the double slit mechanism, prisms, prism stands, lenses, lens holders, etc. The cost will be about $100.

b. Lenses.—Suitable lenses of large aperture and short focal length are very hard to obtain for the apparatus at a reasonable price. Many of the large photographic houses in Boston and New York deal in second-hand portrait lenses. In equipping the psychological laboratories of Harvard, Chicago, Illinois, and Johns Hopkins, very satisfactory lenses of this type have been purchased, at prices ranging anywhere between $5 and $35. It is not difficult to get portrait lenses of 3″–4″ aperture with long focal length, but these must be avoided if an intense spectrum is to be obtained.

To obtain satisfactory *condensers* is especially difficult. Probably the best and easiest solution of the problem is to get Bausch and Lomb to grind these lenses as single achromats. A single achromat of 3½″ aperture and 6″ focal length is recommended. The cost of this lens unmounted is $30. The two elements of the condenser should not be cemented, but mounted with an air-space between. Four such lenses have already been ground to our order. They are very satisfactory.

After this lens has been installed it should be carefully protected from a possible discharge of particles from the arc by a metal cap. The danger from the arc comes when it is first started and when the carbons have "frozen" and suddenly burn apart. After the arc has begun to burn steadily the cover can be removed. There is little or no danger of breakage from heat.

A compound portrait lens is best for the *collimator*. The Voitländer, if it can be obtained with short focus, is very satisfactory. There are several of these on the "second-hand" market. They should not be over 12″ in focus nor under 3″ clear aperture.

The *objective* should be of the compound type if possible. A large compound lens from a camera or stereopticon can be used. The clear aperture should be at least 3½″ in diameter and the focal distance not over 50 cm. Several Steinheils may be obtained which are accurate enough for all the work recommended in this report. They may be had of Robey-French and Company, Boston, or from Chas. G. Willoughby, 814 Broadway, New York.

It is well to test the lens before purchasing, by mounting it as a camera and allowing the image of a series of long, accurately ruled cross lines to fall on a ground glass plate. These lines should all appear in the image equally intense and undistorted. Many of the compound portrait lenses on the market give images which are not sharply defined. This "softness" in definition is an advantage in photography but it is a serious defect in an objective for optical work.

Several small achromatic projection lenses are needed—three behind the double slit, one for the box containing the Nernst filament (see p. 50) and one as a condenser when the Nernst is used in place of the arc. For these purposes we have used small field or opera glasses. Opera glasses costing $3 or $4 a pair will afford suitable lenses. They should be about 3¼″ to 4″ in focal length and should have an aperture of about 1″. They are to be entirely removed from their mountings and remounted as shown in fig. 9. The Wollensak Optical Company, Rochester, N. Y., will grind small single achromats to order at a very reasonable price. The small lens used as a condenser with the Nernst filament (p. 47) and the small projection lens referred to on p. 51 were furnished by them for $1 each. The lenses of the system need not cost over $100.

c. Prisms.—The *spectrometer*, or refracting, *prism* recommended may be had of O. L. Petitdidier, Lake Ave. and 53d St., Chicago, or of Hans Heele (Arthur H. Thomas Company, Philadelphia). Heele furnishes a dense flint 60° prism 80 mm. aperture (ref. ind. for D=1.70) for $60. (Extra dense flint, ref. ind. for D=1.78 for $68.) Petitdidier furnishes a very satisfactory prism 4″ x 4″ face for $50, another 3½″ x 3½″ for $30. He rarely carries these sizes in stock, but will make them to order.[1]

This prism should be mounted on a metal table 5″ in diameter (see p. 7 fig 7). It should be set in minimum deviation for some clearly marked line easy to obtain in sunlight or arc, e.g., the D line, and never thereafter moved. Care must be taken to level the prism very accurately after it has been installed. For this reason it is best to have the top of the prism table made in two parts after the manner described on p. 62.

Small *total reflection prisms* of flint or crown glass may be purchased of Queen and Company, Philadelphia; O. L. Petitdidier, Lake Avenue and 53d St., Chicago, or Bausch and Lomb, Rochester, N. Y. Queen and Company furnish them most cheaply and with all the accuracy required for the present work.

Two 9 mm. prisms are needed immediately behind the double slit. These may be had for $1.75 each. Two 19 mm. reversing prisms are required, $2.50 each; and two 25 mm. spacing prisms, $3 each.

A small compound double image prism, a sketch of which is shown on p. 49 is necessary for use in experiments on the liminal difference for intensity (D. L.). This may be had of Steeg und Reuter through the Arthur H. Thomas Company, Philadelphia. The cost of this prism is about $30.

All prisms should be cemented permanently to their respective tables. Several cements are on the market, but a most satisfactory cement can be made by taking dry shellac and pouring a small amount of 95% alcohol in with it, warming the mixture over the flame until a homogeneous, fairly thick paste is formed.

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[1] A prism with high refractive index is very likely to tarnish. Mr. Petitdidier recommends a prism with refractive index not greater than 1.66.

The metal surface should be warmed quite thoroughly and then spread quickly and evenly with the shellac. The prism should be warmed also and then firmly pressed down upon the metal surface. After drying (for about 2 hours) a satisfactory union is obtained.

d. Episcotisters; and motor iris diaphragm.—An episcotister supplied with movable sectors has its advantages and its disadvantages. Its chief advantage consists in the fact that it may be set so as to cause only a small loss of energy in the beam. It is made with a rim of metal graduated in degrees, which is attached to the rotating shaft by two fixed sectors of 21° each. The rest of the sectors are free to move concentrically on the shaft, where they can be clamped by a lock nut in any desired position. They can thus be made to close the whole 360° opening, or folded in behind the two fixed sectors in such a way that the angular opening reaches its maximum of 318°. They can be arranged thus to give about 88 per cent. of the full intensity of the beam.

Its chief disadvantage consists in the fact that there are so many sectors that an accurate adjustment of the angular opening cannot be made. In making threshold tests or tests of the DL for intensity and in accurately adjusting energy relations of any kind by the use of the selenium cell, the episcotister supplied with movable sectors is out of the question. It is, however, extremely valuable for qualitative work, where one desires quickly to present a color stimulus first with high, then with intermediate and finally with low intensity. Zimmerman, through the Arthur H. Thomas Company, Philadelphia, furnishes three sizes of adjustable episcotisters—10 cm. opening, 38 marks; 15 cm. opening, 50 marks; 20 cm. opening, 65 marks. The first two sizes are especially adapted to our work.

In order to make a satisfactory sector for use in all quantitative experiments one uses the frame work, shaft, pulleys, etc., of the one just described, but unscrews the rim with its two fixed sectors and takes off the free sectors. Two sectors are then prepared in the following way: Two discs of brass 10 cm. in diameter—or 15 cm., depending on the size of the Zimmerman episcotister—are drilled at the center to fit the shaft of the episcotister. The one of these discs taking the place of the rim and the two fixed sectors of the above, should be 1-16″ in thickness and the other should be 1-32″. Each of these discs should be laid off and cut out as follows: Two diameters are marked out at right angles to each other. Opposite quadrants of the four thus formed should be sawed out, leaving an outside rim of 5 mm. and an inside rim of 10 mm. at the axle. One of the quadrants should be graduated in degrees. This work should be done with great accuracy. The heavier of the two discs is then screwed into the bushing on the axle which formerly held the fixed disc of the episcotister. The thin disc is slipped on in place of all the movable sectors. It is clear that the two opposite open quadrants of the movable sector can be made to coincide either with the open or closed sectors of the fixed disc. In the one case is given the maximum opening of 180°, and in the other the minimum, 0°. The graduation on one of the quadrants shows one-half the total opening always.

When it is remembered that the energy of an interrupted beam of light is directly proportional to the angular opening of the rotating sectors, it is seen that when once the full energy of the beam has been determined by means of the selenium cell, the energy of the interrupted beam becomes known from the angular setting of the episcotister. It is possible thus to make liminal and differential threshold-tests with accuracy.

In making settings of the episcotister of less than 2° (i. e., of less than a reading of 1° on the scale), a graduated wedge should be used, permitting an opening as small as 1-100° to be made with accuracy. In making threshold tests this opening will have to be obtained by the use of an angular slit mechanism controlled by a micrometer screw. The opening can be set with an accuracy of 1-1000 mm.

Any small high speed motor may be used to drive the episcotisters. Motor No. 5700, 110 D. C., 1-20 H. P. of the C. H. Stoelting Company, Chicago, costing $15, is very satisfactory. The circular starting box and resistance usually supplied with it should not be used, but in its place should be substituted a sliding rheostat of suitable winding (75 ohms). James G. Biddle, Philadelphia, supplies a duty free "G. R." rheostat, type E. H., 75 ohms resistance, of excellent construction, for $5.36.

Slender circular leather belts, glued together and sandpapered until they are perfectly smooth running, should be used for driving the sectors. Lacking these, rubber bands may be used. The latter work well for a time, but soon deteriorate. It is well to keep a supply of them close at hand for emergency use.

Iris diaphragms [1] with maximal diameter of 2.5 cm., suitable for mounting upon the small projection lenses shown in fig. 9, may be obtained of Spindler and Hoyer through Arthur H. Thomas Company, Philadelphia, for 5 marks. They are not very accurate at best, and their use is recommended only as an additional means of control of intensity. Had we proof that the interruption of a beam of light by the rotating sector alters the intensity of light in the same ratio for the animals as it does for the human being—i. e., according to the law of mean squares—there would be no necessity for any other form of control of intensity. Lacking the actual proof, however, it seems best to have occasional recourse both to the iris diaphragm and to the smoked wedge.

c. Mirrors.—Speculum mirrors are far more satisfactory in this work than any other form. They are expensive, however, and difficult to obtain. The expense is due largely to the difficulty in manufacture. A model for the mold must first be made in wood, from which a metal casting is made. The casting is then accurately planed. The speculum metal is melted and poured into the mold. A constant stream of illuminating gas is made to enter the mold while the molten mass is being poured in. The gas ignites and consumes all the air present in the mold. The plates are removed from the mold and placed in a bed of burning coke for several hours, in order to anneal them properly. After cooling they are ready for grinding and polishing. In the work we are attempting to do there is no necessity for obtaining a planeity of surface greater than that offered by the best plate glass.

The three large mirrors 3″ x 5″ called for in this apparatus were cast by Mr. Childs, and ground by John A. Brashear of Pittsburg. The total cost of each mirror is about $15. Max

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[1] Since the openings in the double slit wall are in the foci of these lenses it follows that the size of the images falling upon the plaster of paris surfaces is not altered by the use of the diaphragm.

Kohl charges a much higher price—400 marks for the 4″ x 5″ size; 300 marks for the 3″ x 3″ size.

These mirrors with care are almost absolutely permanent; several speculum metal gratings made by Professor Rowland in 1890–95 show no signs of deteriorating. If through neglect the mirrors do become somewhat dull, they can be repolished by using a fine grade of prepared chalk, moistened in distilled water or alcohol. One applies the chalk and polishes with absorbent cotton kept wholly free from dust. If after long disuse the surface of the mirror appears stained, it can still oftentimes be brought into first class condition by the application of dilute C. P. ammonia. This also is applied with absorbent cotton. After using the ammonia the mirrors are cleansed thoroughly with distilled water, and then polished with prepared chalk as before. Finally if through neglect the surface has deteriorated beyond the point where the above simple remedies will restore them, they can always be repolished by Brashear at a fraction of their original cost.

Professor Anderson of Johns Hopkins has devised a method whereby mirrors of a permanent kind can be made by depositing various metals possessing high indices of reflection, directly upon plate-glass by an electrolytic process. These mirrors may now be obtained in gold, silver, nickel and platinum. They are far less expensive than speculum mirrors, and make a satisfactory substitute for them when expense has to be considered.

f. Instruments for measuring wave-length and intensity.—Selenium cell and auxiliary apparatus.—Professor A. H. Pfund has devised for us an exceedingly delicate method of measuring the energy of the various monochromatic bands *after being diffused by a ground glass or plaster of paris surface.* He gives the following brief description of the method: "In order to measure the energy carried by a beam of monochromatic rays, some bolometric device is usually chosen. When the amount of energy to be measured is so very minute, the sensitiveness of the best bolometer is found insufficient, and recourse must be taken to some other form of energy-measuring device. The wave-length interval over which the present work is to extend lies within the visible spectrum, and since it is precisely in this region that the selenium cell is so very sensitive, it was chosen above others to serve as a radiometric device.

"To determine whether or not an animal has color vision, it is essential, in testing the response of the animal to two differently colored beams, that the energy carried by these two beams be the same—i.e., that they differ in wave-length only.[1] This control is obtained by the use of a selenium cell whose color sensibility curve is known. For the details of the method used in determining such sensibility curves the reader is referred to the Physical Review, vol. 28, p. 324. Suffice it to say here that the sensibility curve is plotted between galvanometric deflections caused by changes in resistance of the selenium cell, and the wave-length of incident beam, the energy carried by each bundle of monochromatic rays being constant. Given the sensibility curve of a cell it is evident that we have the means at hand of determining the condition under which two bundles of monochromatic light carry the same energy.

"Selenium cells obtained from different makers do not necessarily have the same sensibility; hence it is necessary that each cell be calibrated as above indicated. Furthermore it is required to know in terms of C.G.S. units the energy carried by the light used in the excitation of the cell. This is necessary in order that the result obtained by any one investigator may be strictly comparable with those of any other investigator. Although the selenium cell connected in series with two or three dry batteries and the galvanometer may be used when the amount of energy to be measured is large, it is best to use the cell as a part of the simple potentiometer, thus placing all possible degrees of sensitiveness at the immediate disposal of the investigator. The following plan is suggested for the standardization of this work:

"A central bureau is to be decided upon, where the calibration of all instruments is to be carried out. The color sensibility curve for all cells is to be carried out in the wave-length interval 450–800, and for the same absolute intensity of light. Lower intensities than that at which the cell is calibrated are obtainable through the use of a rotating sector. Due to the fact that the selenium cells, galvanometer, batteries and resistances will not

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[1] This is only one of the reasons for an energy control. We desire oftentimes to present the two beams when they differ very markedly in energy, and for the sake of reproducibility of conditions it is essential to know the energy of the beams at all times.

be identical in all laboratories, and further to the fact that all the above instruments are affected in their behavior by temperature changes, it is necessary to provide for some method of standardization which will make it possible to employ the cell always under the conditions which obtain while the cell is being calibrated. This method is briefly as follows: While the sensibility of a given cell is being determined, it is noted that under the influence of green light ($\lambda=500\mu\mu$) a deflection of 60 mm. is obtained. The cell is then exposed to the total radiation of the standard 8 c.p. incandescent lamp, which is removed to such a distance that the deflection produced is also 60 mm. Next, the cell is exposed to another similar lamp, burning as before at an accurately measured voltage, and this lamp is also removed to such a distance as that at which a deflection of 60 mm. is obtained. This second lamp accompanies the selenium cell. When it becomes desirable to use the cell again it is connected with the galvanometer and potentiometer and is exposed to the incandescent lamp which is burning at the same voltage and at the same distance from the cell as at the time of standardization. If then the galvanometer does not record a deflection of 60 mm. its sensibility is varied until such a deflection is obtained. However true it may be that the manipulation of the selenium cell is a trifle complicated, it is to be noted that this objection is more than off-set by the tremendous sensibility placed at our disposal."

The apparatus for measuring energy consists of the following parts: (1) A selenium cell of 2,000,000 ohms resistance, supplied by J. W. Giltay, Delft, Holland, through Arthur H. Thomas Company, Philadelphia, for \$20. (2) A Leeds and Northrup type H wall galvanometer with a low resistance coil (31 ohms), supplied with telescope and scale, costing about \$45. (3) Three Leeds and Northrup resistance boxes (1–10,000 ohms) for altering the sensibility of the galvanometer and for use with the selenium cell, costing about \$24 each; these, with the galvanometer, can be had of the Leeds and Northrup Company, Philadelphia. (4) Four storage batteries, open glass cell chloride accumulator, with CT type of element, 4″ x 5″, supplied by Jas. G. Biddle, Philadelphia, at about \$2.50 each.

Professor Pfund has consented to standardize a few of the selenium cells. If it is desired, the whole apparatus can be purchased through the Johns Hopkins University. It will be sent out after being standardized, with a chart and full directions for installation.

Spectrophotometers.—While the measure of energy in the bands of monochromatic light seems to be the most desirable form of control, since it is absolutely independent of the sensitivity of the human eye, the apparatus for obtaining it, as we have seen above, is expensive, and the technique is somewhat difficult. It seems worth while, accordingly, to mention at least another standard method of control—that of spectrophotometry. This method, as is well known, measures the intensity of a variable monochromatic beam in terms of the intensity of a monochromatic beam of the same wave-length coming from a standard source. There are many complex forms of spectrophotometers on the market, such as the Lummer-Brodhun, costing about $500, the Brace, costing $375, Glan's, costing $125, but all these are more complicated than is necessary for our work.

After some experimentation we suggest the use of Nutting's pocket spectrophotometer. This is a compact little instrument, which gives an accuracy within 2-3 per cent. of the larger instruments. It is inexpensive ($31) and easy to use. It is made by R. Fuess, and may be purchased through the Arthur H. Thomas Company, Philadelphia.

The instrument needs a small tungsten lamp of known candle power attached to it at a fixed distance from the slit, e. g., 10 cm., for the purpose of giving a reference or standard spectrum. The instrument should be mounted in a metal arm running at right angles to it for convenience in clamping it to an upright. This arm is graduated in mm. and carries the standard lamp. The white light from this lamp enters the instrument through a window in the side, meets there a small total reflection prism, and is reflected through the slit parallel to the axis of the instrument; passing through the usual lenses, direct vision prism and Nichol prism (the polarizer), it is refracted, polarized and finally focussed on the vertical slit in front of the eyepiece. The width of this slit is adjustable. The variable monochromatic beam enters at the end of the instrument, passes through the first Nichol prism (the "analyzer"), thence through the lenses, the second Nichol, etc., as above. In the eyepiece one spectrum appears vertically above the other. The slit in front of the eyepiece is then adjusted so as to admit the whole of the variable beam. Immediately below it with no line of demarcation one finds a band of monochromatic light of exactly the same wave-length, coming from the *standard* source. The latter in this work is adjusted in intensity so that the standard beam is always fainter than the comparison. The comparison beam is then decreased in intensity by the use of the analyzing Nichol until the two are of the same brightness. The angle of the analyzer is then read, which gives after proper translation the intensity of the variable beam in terms of the standard.[1]

This method, while in general use, is subject to all the variations present in the photometry of white light. A standardized procedure, accordingly, should be adopted. Numerous determinations should be made and with a dark-adapted eye. Since they do not have to be made frequently, it seems desirable to allow at least 15-20 minutes for adaptation to darkness before taking readings.

The light chosen as a standard should be a well seasoned miniature tungsten with approximately straight filament (the bulb should be marked with fiducial lines and the lamp should be burned in a position constant with relation to the instrument) of about 1½ c. p. at 2 volts pressure. It should be burned in series with a rheostat and one two-volt storage battery. A volt meter reading 0–6 in 1-25 volt divisions should be placed in the circuit. Switchboard type C voltmeter, supplied by Jas. G. Biddle, Philadelphia, for $15, will suffice, but a precision voltmeter of the well known Westinghouse type is better.

Flicker photometer.—In making color tests upon animals, the student of behavior is not especially interested in obtaining color stimuli which offer "equality of brightness" to the human eye. This relation may or may not have bearing upon the animal work. It is always interesting, however, to test the animal under such conditions. The flicker photometer presents probably the most uniform way of obtaining between disparate colors a relation which is considered by some to be that of equality. For a thorough experimental treatment of this

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[1] For further description of the instrument, see P. G. Nutting, Bull. Bureau of Standards, 1906, vol. 2, p. 317.

subject, the reader may be referred to the work of Ives, which is to appear shortly in the Physical Review.

Spectrometers.—There are many simple instruments upon the market which will give the wave-length of the bands used with sufficient accuracy for the present work. A pocket form of instrument supplied with a scale is the most convenient. The relation of the scale divisions to the distinct lines in the solar spectrum is then determined, and the "curve" of the instrument drawn on millimeter cross section paper.

The Browning pocket spectroscope is supplied by Max Kohl for 82 marks. Hans Heele also furnishes a pocket spectroscope with scale for the same price (purchase with Amici prism of high dispersion). Either of these instruments may be imported through the Arthur H. Thomas Company, Philadelphia.

We suggested on p. 63 that the scale of the double slit be calibrated directly in terms of wave-lengths. Once this has been accurately done there is no further need of a spectrometer. It is well, however, to have one at hand for use in making occasional tests.

g. Experiment box.—On account of the great differences in the structure, form, and instinctive capacity of animals which are likely to be used as subjects in these tests, no fixed type of experiment box can be recommended for use with the color apparatus. That shown in fig. 4 suggests a simple type of construction.

One of the chief difficulties in the way of using spectral light in dark-room work is the peculiarity which the shorter wave-lengths exhibit in illuminating the interior of the black experiment box. Even the darkest of our black paints reflects the green rays sufficiently to show the outlines of the floor, the partition, and the walls of the experiment box. The red rays, on the other hand, are completely absorbed by some black paints. This means that under the ordinary conditions of our tests a secondary criterion is afforded the animal. On the basis of the criterion, it soon learns to *avoid* the more highly illuminated compartment, if its food is given with the color of longer wave-length, or to *seek* it if its food is given with the color of the shorter wave-length. Two animals, a white rat and a rabbit, under experimental observation soon learned to make 100 per cent. of correct choices, on the basis of the difference in illumination of the two compartments.

This defect in the method of presenting chromatic stimuli is not peculiar to spectral light. Any transmission method offers the same difficulty. So far as we know this defect has not hitherto been called to the attention of experimenters. The difference in illumination after 10–15 minutes of darkness adaptation is so marked that one must notice it. The phenomenon does not depend upon the difference in energy (or " brightness ") of the two colors. It is apparent even when the green is but one-twentieth the energy of the red. It is still more apparent when the two colors have been judged " equal in brightness " by direct comparison. It is due chiefly to the fact that black paints offer a surface of reflection for rays of the green-blue-violet regions of the spectrum.

After long experimentation we have found two ways of wholly eliminating it. The first method calls for the abandonment of tests with complete darkness adaptation. One mounts a 40 watt tungsten lamp in a light-tight metal cylinder, in the front end of which is fitted a graduated iris diaphragm with a disc of ground glass behind it. The diaphragm can thus be opened and closed to regulate the intensity of the light. Since the light is perfectly diffused by the ground glass, the size of the illuminated field does not appreciably change when the diaphragm is opened or closed. This light is mounted centrally over the experiment box at a height of 1.5 meters. Care must be taken that the white light offered by this source does not enter the cabinet (p. 57) and fall on the plaster of paris surfaces. With this illuminating device the two food compartments may be so highly illuminated that the relatively slight difference in illumination, arising from the source discussed above, is completely eliminated. Entirely apart from its uses in this connection, the device gives us the means of studying the formation of associations under standard conditions of light adaptation.

The second method consists (a) in mounting a series of diaphragms in front of the windows in the experiment box which admit the colors; (b) in making the floor of the experiment box non-reflecting, by means of a metal grill; (c) in fastening dead-black velvet to the sides of the box and to both sides of the partition. These three precautions totally eliminate all difference in the behavior of the long and short wave-lengths, for the very simple reason that all the reflecting surfaces where light immediately falls have been removed.

(a). The diaphragms are made from 1-32″ sheet brass. Eight pieces 4″ x 7″ are cut out, and in the center of each a rectangular opening 2″ x 4″ is milled and knife-edged. Four such diaphragms should be mounted together and placed in front of each of the two windows in the experiment box. They should be mounted as follows: The four 4″ x 7″ sheets are clamped together and drilled at the four corners with a $\frac{1}{4}$″ hole; four $\frac{1}{4}$″ brass rods are cut, 6$\frac{5}{8}$″ long and are tapped and supplied with hexagonal nuts $\frac{1}{4}$″ thick. The four diaphragms are slipped on these rods, and are separated from one another by means of collars 2″ long, made from brass tubing, the inside diameter of which is $\frac{1}{4}$″. The set of diaphragms is acid-blackened. This method of mounting the diaphragms enables one to dispense with a supporting floor, which would offer a reflecting surface. The diaphragms when assembled should be mounted in front of the two windows in a bearing which offers universal adjustment, for ease in centering with respect to light. (As a precautionary measure it is well to cover each of the diaphragms with dead black velvet. The velvet should not be placed nearer than $\frac{1}{4}$″ to the edges of the knife edged rectangular opening.)

(b). The non-reflecting floor grill is made to serve both as a punishment device (if desired) and as a means of absorbing light. It is made as follows: (The size given is one fitting the floor of an experiment box made for small mammals. This box is similar to the one shown in fig. 4. The grill fits snugly the whole of compartment B.) Three $\frac{1}{4}$″ brass rods 20$\frac{1}{2}$″ long are tapped at their ends and supplied with nuts $\frac{1}{4}$″ thick. The whole rod is bushed with wood-fiber tubing, the outside diameter of which is $\frac{3}{8}$″. Forty strips of brass 1-32″ thick, 1″ wide and 20″ long, are then drilled at the center and at the two ends with a 7-16″ hole, so as to admit the three bushed rods with a good deal of play. The strips are all acid blackened and slipped on the rods one at a time. They are inclined at an angle of 60°. A fiber bushing $\frac{1}{2}$″ long, sawed at an angle of 60° is slipped on each of the rods between each of the metal strips. Before blackening, the strips should be carefully smoothed on their upper surface. This grill when properly acid blackened reflects no light. At first sight objection may be raised to it for the reason that it slows the progress of the animal. This is a distinct gain rather than otherwise. It is distinctly more difficult for the animal to make a hurried dash to the food boxes. It forces leisure for choice. Since there are no sharp points the animals are not discommoded by it, and rapidly become accustomed to making the proper steps. The cover for the box should be made in a similar way, only in this case the metal strips need not be insulated. Furthermore, the strips may be separated from one another by a distance of 2″ or more. If small animals like the rat or mouse are used, a woven wire cover may be placed above the cover just described. After the animal has had a few days' experience in the box, the remaining tests may be made without the use of the cover.

(c). Ordinary high grade dead black *velveteen* may be used for lining the walls and partition of the experiment box. The addition of the velvet lining is merely a precautionary measure since the diaphragms effectually prevent all lateral reflection.

When the experiment box is used with the color apparatus, one other matter should be considered. It will be remembered that the experiment box has to be shifted 25 cm. each time the relative position of the two colors is reversed. It is just possible that such a movement of the experiment box might give the animal a secondary criterion for making a choice. In order completely to eliminate such a possibility it is well to make compartment A, fig. 4, entirely separate from B. Compartment A, containing the animal, may then be removed and the apparatus adjusted for a new test before A and B are joined.

VI. CONCLUSIONS AND SUMMARY OF RECOMMENDATIONS

The purpose of this investigation has finally turned out to be the devising of apparatus and modes of procedure by which highly accurate determinations may be made (a) of the limen (threshold) light and color stimuli for an animal; (b) of the limits of sensibility with respect to wave-length and intensity; (c) of the difference limen for light and for chromatic stimuli; (d) of the stimulating values of different chromatic stimuli (curve of luminosity for the eye of a given animal should thus be obtained); (e) of the chief characteristics of adaptation; (f) of visual defects in animals.

It is our conviction that the methods which are herein recommended will enable us to discover, by the comparative method, facts which are of fundamental importance for visual theory.

We desire to offer the following recommendations concerning methods of studying the various aspects of vision which have been considered in this report.

Light perception.—That the standardized light apparatus, as herein described or in improved form, be employed for accurate determination of the capacity of organisms to respond to light. In connection with the use of this apparatus we deem it important that tungsten lamps be used as sources of stimuli and as photometric and radiometric standards; that the light box be provided with movable screens which shall minimize the reflection within the light box; that the standard plates be accurately cut and kept in perfect condition; that differences in the visibility of portions of the two symmetrical halves of the experiment box, resulting from different intensities of the two stimuli or from differences in the surfaces of the parts of the box be excluded, as far as possible, by means of such devices as are suggested on page 85; that experiments be conducted in ordinary illumination whenever possible; that the experimenter to the extent of his ability strive to render the apparatus automatic in its operation so that he shall be able to avoid disturbing the reacting animal; that intensive painstaking observations with one or a very few individuals be sought in preference to extensive and superficially made observations on a large number of individuals; that a thorough investigation of the *light* vision of an animal preface and prepare the way for any investigation of its *color* vision; that the intensity of lamps used as sources be accurately determined to begin with and at stated intervals by means of reliable standards and measuring devices, such for example as the standardized tungsten lamp and the Lummer-Brodhun contrast photometer; that radiometric measurements be made with a radiomicrometer or a selenium cell; that stimulus areas be photometered by comparing them (balancing them against) a precisely similar standard area, 5 or 6 cm. circle, one meter distant, which in turn is illuminated by the standard source (tungsten). This standard source is to be mounted upon a movable carriage. It is further recommended that in arranging the apparatus for making the determination the Lummer-Brodhun screen be fixed midway between stimulus area and standard area, and that the coarse adjustment (necessary to bring the intensity within the range of the photometer bar) be made by using a rotating sector (See p. 76) in the path of the light from the standard source, and that the fine adjustment be made by moving the standard lamp towards or away from the standard area until a balance is obtained in the Lummer-Brodhun screen. When on the other hand it is desired to set the stimulus lamps so as to give a known illumination value upon the stimulus area the standard lamp is set at the desired distance from the standard area and the stimulus lamp adjusted until the desired balance is obtained in the photometer. Every precaution must be taken to guard the screen from extraneous reflected light. It is recommended that this be done by the introduction of screens as described by C. H. Sharp (Measurement of light intensity, "Lectures on illuminating engineering," vol. 1, p. 411).

Size perception.—The recommendations under light perception apply here also. In addition, it is desirable that the standard plates be chosen so that discrimination shall at first be fairly easy; that after the ability to choose correctly on the basis of size has appeared check tests be devised which shall exclude possible peculiarities in the plates or in the illumination of the box; that differences in the illumination of the two halves of the experiment box, resulting from differences in the size of the stimulus areas be carefully controlled so that the animal shall not acquire a habit of attempting to discriminate on that basis; that the photometric values of each size stimulus be determined by balancing it against the light transmitted by a circle of standard area (6 cm. diameter, 28,2743 sq. cm. area) in fixed relation to standard source; that energy measurements be made with radiomicrometer or selenium cell, as in the case of light perception.

Form perception.—In addition to the above recommendations we would suggest the desirability of making certain that discrimination is dependent upon form alone; that plates of same area and plates whose opening may be inscribed within the standard 6 cm. circle be used in varied relations; that the relative ease of discrimination by form and size be determined in preliminary tests.

Distance perception.—It has not been possible for us to provide a method of testing this factor of visual discrimination with our standardized apparatus without troublesome and expensive complications. We, therefore, have left this aspect of vision for examination by means of devices which may be introduced in connection with our light and color apparatus. It is our plan to arrange mechanical devices by means of which the distance of the two stimulus areas from the animal may be altered by a few centimeters without avoidable changes in the other conditions. The testing of apparent distance as a factor in discrimination is especially important because of the distance-effects of colors.

Color perception.—The method of applying chromatic stimuli should be determined by (a) the manner in which the stimulus is obtained (reflection, transmission, or dispersion method) and (b) the characteristics of the animal. The first task of the investigator is to decide which of the three methods of obtaining stimuli will best serve his purposes. Having selected one of the three general methods, he should perfect an experiment box to use in connection with the standard light or color apparatus (the *light* apparatus may perfectly well be used in tests for color vision with either reflected or transmitted light from papers, cloths, glasses, etc.)

Our chief recommendations concerning the use of the color apparatus are these: That for high intensity work either the sun or an automatic open arc lamp, and for low intensity work a Nernst glower, be used as a source; that compound achromatic lenses be used for condenser, collimator, objective, and single achromats for small projector; that the double slit be calibrated for wave-lengths; that accurately cut and calibrated rotating sectors be used for the control of the intensity of the two beams, but that iris diaphragms be used instead, for supplementary check tests; that extreme pains be taken to prevent dependence upon secondary criteria, such as differences in illumination, differences in size, form, or apparent distance of stimulus areas; that in addition to making accurate photometrical and radiometrical measurements of the stimuli, the experimenter vary the conditions of the tests in all convenient ways in order to make certain of the kind of discrimination with which he is dealing.

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CONTENTS.

I. INTRODUCTION.

The study of the death feint of Belostoma flumineum and Nepa apiculata was undertaken at the suggestion of Prof. S. J. Holmes, whose own researches on this instinct have added new interest to this line of work. The principal points which we have attempted to bring out in this paper are:

(1) The duration of successive death feints.
(2) The effect of dryness and moisture on the duration of the death feint.
(3) The effect of temperature on the duration of the death feint.
(4) The effect of light on the duration of the death feint.
(5) The effect of mutilation on the death feint.
(6) The origin and development of this instinct.
(7) The psychic aspect of the death feint.

II GENERAL CHARACTERISTICS OF THE DEATH FEINT.

1. *Death-feigning posture compared with naturally dead specimens:* It struck Darwin (4, p. 364) that it would be a rather strange coincidence if insects, when feigning death, should exactly simulate the attitude of really dead specimens. He writes, " I carefully noted the simulated positions of seventeen different kinds of insects (including an Iulus, Spider, and Oniscus) belonging to the most distinct genera, both poor and first-rate shammers; afterwards I procured naturally dead specimens of some of these insects, others I killed with camphor by an easy, slow death; the result was that in no one instance was the attitude exactly the same, and in several instances the attitude of the feigners and of the really dead were as unlike as they possibly could be." However, according to Kirby and Spence (16, p. 448) "the common dung-chafer (*Geotrupes stercorarius*) when touched, or in fear, sets out its legs as stiff as if they were made of iron-wire—which is their posture when dead—and remaining perfectly motionless, thus deceives the rooks which prey upon them."

Although the death-feigning postures of Belostoma are very characteristic, the simulated positions are quite different from those of naturally dead specimens. A glance at figures 1 and 2, Plate I, p. 47, of the death-feigning postures of Belostoma when compared with figures 4 and 5 of those naturally dead shows a marked difference in the position of the limbs. In the dead specimens as well as in individuals which are dying, the abdomen often droops considerably as shown in figure 6. In Nepa it becomes at times impossible to distinguish with the eye alone, a death-feigning specimen from one that is really dead. As a test, a number of dead Nepas were placed in a dish containing feigning specimens and an entomologist, who was familiar with the habits of these insects, was asked to separate the dead from those feigning. This experiment was repeated several times, but in each case several mistakes were made in separating the specimens into the two classes.

2. *How to elicit the death feint*: To bring about the death feint in Belostoma is usually a very simple affair. The creature often assumes this immovable condition when raked or scooped out of the water. When picked out of the water from an aquarium it often becomes motionless. Sometimes, however, the insect will not feign when taken out of the water, but will kick about vigorously in an endeavor to free itself. Such a specimen may usually be put into the death feint by a method which we employed throughout most of our experiments. The individual was held by the lateral margin of the thorax, ventral surface upward, between the thumb and forefinger of the left hand and then the thumb of the right hand was repeatedly placed in contact with the abdomen immediately behind the last pair of legs, while the fore-finger of the same hand was placed in contact with the wings. Immediately the insect passed into the death feint and the limbs always assumed a very characteristic position (fig. 2).

To cause Nepa to feign death, either in the water or out of it, is not a difficult task. When the bug is in the water, a light touch with a pencil or other object upon the back will usually throw it into the death feint. The same effect may often be produced by taking the hemipteron out of the water with a pair of forceps, grasping it by the body, breathing tube or any of the legs. If this method fails, the death feint may usually be elicited by dropping the insect upon a table from a small height. Even while feeding, Nepa may be put into the death feint, the insect often retaining possession of, and keeping the styliform mandibles and maxillae sunk into the prey.

3. *Death-feigning postures:* When Belostoma is handled in the manner just described, it usually assumes a definite and constant attitude while in the death feint. When the thumb of the right hand is placed in contact with the abdomen behind the last pair of legs, instantly every femur is projected upward (the insect being held ventral surface uppermost) at almost right angles to the long axis of the body. The claw-like tibia and tarsus of the front pair of raptorial limbs is held tightly within the groove of the femur, while either the tibiae or the tarsi of the middle or the hind pair of legs may be crossed. Figure 2 shows the position of the limbs from a lateral view. Although all Belostomas when handled in the manner just described, can be induced to assume this death-feigning posture under normal conditions, yet they often assume a different attitude when taken out of the water.

If one stops to examine a number of feigning Belostomas which have been raked or scooped out of the water or taken out of an aquarium in the palm of the hand, one usually finds that the legs are folded against the ventral surface of the body as shown in figure 1. A femur of the raptorial limbs, with the claw-like tibia and tarsus within the groove, is held close to either side of the head. The tibiae of the posterior pairs of legs are drawn beneath the body and held close to their respective femora so that but little more than the femoro-tibial joints are visible from a dorsal view (fig. 3).

There is no characteristic position which Nepa assumes while simulating death, the attitude taken depending mainly upon the position of the legs just previous to the death feint. Thus, while in some cases the middle and hind pairs of legs may be extended straight out laterally, in others, again, they may be held backward below the body. All sorts of intermediate positions of the posterior pairs of legs may be assumed. The front pair of legs, however, are usually stretched forward or the tibia and tarsus of each leg may be bent back fitting into the groove of the femur. If the insect, either while in the water or out of it, is rolled over and over laterally, the legs are forced to assume a characteristic position; the front pair are stretched forward with the tibia and tarsus either extended or bent back upon the femur, while the middle and hind pairs of legs are held backward below the abdomen, the middle pair being held just within the hind ones. While in this position, the posterior pairs of legs are bent at the tibio-femoral joint, the middle pair but slightly, the hind pair considerably more, so that its tibiae are usually crossed.

4. *The condition of the muscular system while in the death feint:* Verworn (27) has called attention to the extreme muscular tension under which various vertebrated animals labor while in the so-called hypnotic state. Holmes (14, p. 183) found that young terns, inhabiting the island of Penikese, do not show this tetanic contraction of the muscles while in the death feint. He writes, "you may pull them about, stretch out their legs, necks, or wings and place them in the most awkward positions, and they will remain as limp and motionless as if really dead." Other birds, however, labor under a muscular strain while feigning death or while in the so-called hypnotic state. Wrangle (4, p. 363) gives the most curious case of apparently true simulation of death of the geese which migrate to the Tundras to molt, and which are then quite incapable of flight. He says that they feigned death so well "with their legs and necks stretched out quite stiff, that I passed them by, thinking they were dead." Verworn (27, p. 29) in his experiments upon the so-called hypnotism of the hen finds, that "Auch beim Huhn ist ferner ein sehr deutlicher, individuell aber verschieden starker Tonus der an der betreffender Bewegung betheiligten Muskeln zu bemerken."

A similar condition of muscular rigidity is quite common among the invertebrated animals. Concerning some amphipods and isopods, Holmes (12, p. 203) writes, "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." In certain spiders that feign death, Robertson (23, pp. 412 and 417) describes the "sham-death" as a "complete tetanus." The young of Ranatra quadridentata, which are only five days old, Holmes (13, p. 161) claims "could be picked up by one of the slender legs and held out without causing a bend in any of the joints, thus showing that the muscles were in a state of extreme contraction."

In feigning Belostomas the muscles are also in a state of "extreme tetanus." If one attempts to pull the tibia of any leg away from the femur while the insect is feigning death, it becomes evident that the muscles of the limbs must be in a state of extreme contraction; but if, on the other hand, this is done when the bug is not feigning death, the tibia offers almost no resistance.

Nepa, while feigning death, may be taken by any tibia or femur and held in a position so that the weight of the entire body is borne by the extensor muscles of a single segment of but one leg, and yet this position will be maintained until the weight of the body causes the muscles to relax, when the body descends slowly. Again, when any attempt is made to bend a leg while the insect is simulating death, it is found that the muscles are in an extreme state of contraction. Nepa, while in this state of tetanus, may be placed in a great variety of unnatural positions, and still these will be maintained for some time. When a Nepa, that is not feigning death, is experimented upon as above, it will be found that the muscles are not set and no unnatural positions will be maintained for any length of time.

If one compares the attitude of a Belostoma which has just been caused to feign by the usual method (fig. 2) with an individual which was feigning on its back for a considerable time, it will be noticed that in the latter, the posterior pairs of legs have usually spread apart considerably while the front pair droop more or less towards the head. This movement of the limbs is so slow that it is imperceptible and must be accounted for by the gradual relaxation of the muscles.

Preyer[1] in his work on the guinea pig observed that, "Während des Zustandes der Bewegungslosigkeit stellt sich bei einzelnen Thieren nach einigen Minuten oft ein Zittern aller Extremitäten ein, das ziemlich stark werden kann und häufig mit ein Aufstehversuch endet. Ueberhaupt werden nicht selten von den Thieren Aufstehversuche gemacht, die aber oft, ohne zum Ziele zu führen, im Keime stecken bleiben. Die Thiere sind dann gleich darauf wieder vollkommen ruhig."

We also have observed a twitching or a quivering of the limbs in some Belostomas while they were lying on their back in a death feint. The beak may grope around and the styliform mandibles and maxillae may be protruded and retracted in a threatening manner; or the feigning individual may move the

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[1] Quoted from Verworn's (27, p. 6) paper.

claw-like tibia and tarsus of the raptorial limbs or unfold the swimming legs and then sink back into its quiescent state. After a few seconds or minutes or even a quarter of an hour or more, the specimen may suddenly right itself and endeavor to escape by fleeing very rapidly.

5. *Termination of the death feint:* The termination of the death feint is sometimes preceded by an outward indication in some animals. Holmes (8, p. 192) in describing the awakening in one of the large sand-fleas, Talorchestia longicornis, writes as follows: "Waking up, however, is not instantaneous, but is preceded by certain symptoms which may readily be observed if the creature is closely watched. There is first a nervous twitch here and there, then a slight unbending of the antennae and a straightening of the legs and body—all of which indicate a slight relaxation of the muscular tension under which the animal labors—and finally a sudden spring and attempt to escape." Fabre (6, p. 15) gives a somewhat different account in the beetle, *Scarites gigas, Fab.* "Les tarses tremblotent, ceux d'avant les premiers; les palpes et les antennes lentement oscillent, c'est le prélude du réveil. Les pattes maintenant gesticulent."

While Belostoma does not give any marked outward signs previous to coming out of the death feint, Nepa usually behaves somewhat differently. Although in some instances Nepa, when feigning upon its back, will come out of the death feint suddenly, right itself and run away, all within a few seconds, ordinarily it gives us some warning as to when it is coming out of the feint. The first noticeable movement is usually a twitching of the tarsi, or tarsi and tibiae together of the middle and hind legs, after which these legs are extended slowly and stiffly away from the body. A very peculiar phenomenon may now take place; the middle and hind legs may move about very stiffly and mechanically, as if they were being worked with strings that were jerked at intervals. Sooner or later this movement ceases and the insect endeavors to right itself, often falling back while trying to do so. The shock effect of falling back may be sufficient to throw the bug into a feint again, but if this does not occur, the hemipteron will finally right itself. Now again the shock effect of falling over on its ventral surface may be sufficient to cause the specimen to drop back into the death feint. When once righted, the insect, if it does not feign again, slowly draws its legs into a walking position. After remaining quiet in this attitude for a short time, another peculiar phenomenon may take place. One set of legs are slowly extended, the insect pulls itself suddenly forward and stops for a short time; now the other set of legs are extended, the insect pulls itself suddenly forward and stops. In this way Nepa may move forward in jerks several times, but finally these movements cease and the insect runs rapidly away. It is only when it runs rapidly away that Nepa is entirely out of the death feint.

Preyer[1] observed in the guinea pig that loud noises, sudden visual impressions, a breath of air, or a contact stimulus causes the animal to right itself. Belostoma also can be brought out of the death feint by blowing a breath of air against it. Seizing one of the legs with a pair of forceps frequently produces the same result. A common house-fly or another Belostoma crawling upon the feigning specimens may sometimes cause an instantaneous righting reaction.

A specimen is often aroused from its immovable state without any apparent external stimulation. It may feign only a short time and before giving any evidence of a gradual relaxation of the leg muscles, it may spread its legs, brace the tip of the abdomen against the substratum and with the aid of its swimming legs make vigorous efforts to right itself. Whether the contracted leg muscles of Belostoma relax suddenly and a new strong contraction sets in, bringing about the righting reaction, or whether a new energetic contraction is superimposed upon the first, we had no way of determining. Verworn (27, p. 25), however, has determined from rather difficult experiments which he performed on the guinea pig, "dass der Muskel, welcher sich während der bewegungslosen Rückenlage des Thieres in tonischer Contraction befindet, bei jedem Aufstehversuch plötzlich einen starken Contractionszuwachs erfährt und nicht eine Hemmung, wie etwa bei den bekannten Versuchen von Heidenhain und Bubnoff."

6. *Apparent insensibility to pain while in the death feint:* One of the most remarkable peculiarities of the death feint in some Arthropods is the fact that they can be severely mutilated or dismembered, or even roasted alive without showing any appar-

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[1] Trans. from Verworn's (27, p. 6) paper.

ent symptom of pain. Concerning a little timber-boring beetle, Anobium pertinax, De Geer (5, p. 229) claims that "you may maim them, pull them limb from limb, roast them alive over a slow fire, but you will not gain your end; not a joint will they move, nor show by the least symptom that they suffer pain. A similar apathy is shown by some species of saw-flies (Serrifera), which when alarmed conceal their antennae under their body, place their legs close to it, and remain without motion even when transfixed by a pin. Spiders also simulate death by folding up their legs, falling from their station, and remaining motionless; and when in this situation they may be pierced and torn to pieces without their exhibiting the slightest symptom of pain."

We repeated one of De Geer's experiments on Belostoma, but in not a single instance could a specimen be roasted to death without its first coming out of the death feint and making violent efforts to escape. Severe mutilations were also performed with Belostoma. If one of the limbs be snipped in two with a pair of fine scissors, the bug may not respond at all, or the limbs may twitch or quiver, or the insect may right itself and scramble eagerly to get away. One or two repetitions of this experiment with those specimens which did not come out of the death feint immediately after the cut was made, was sufficient to bring them out. We often noticed with these mutilated specimens when they were put back into the death feint in order that we might again repeat the brutal experiment, that the beak would grope around, the styliform mouth-parts protrude and retract, and a white liquid be discharged and collect at the base of the beak.[1]

The behavior of Nepa, when mutilated or dismembered, is entirely different from that of Belostoma. Several Nepas, which were feigning death, were placed upon their backs, and with a pair of fine scissors the tibia of each leg was cut in two with a sharp, quick cut. Not even a quiver was noticed. Each femur was then cut in two and yet the insect did not give any apparent sign of feeling. The tip of the abdomen of each specimen was now snipped off and still no movement was to be seen. Finally

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[1] Locy (17, pp. 355–6) has found what he calls the "cephalic glands" which open externally by means of short ducts on each side of the head between the eyes in the genera Lethocerus, Belostoma and Ranatra. "When these insects are irritated, a secretion is freely thrown out around the base of the beak, which produces death very quickly when introduced on a needle point into the body of an insect."

the insects were cut through the middle of the prothorax and both parts remained quiet, the posterior part, however, losing the rigidity of the muscles almost immediately. A number of individuals, which were feigning death, were placed upon a hot stove, but all without a single exception came out of the feint immediately. Placing them upon the surface film of water even as low as 40° C. gave the same results. A number of specimens were laid upon a stove at a temperature of 21° C., and then the temperature was gradually increased, but in not a single instance could an individual be roasted to death without its first coming out of the death feint and making violent efforts to escape.

III. DURATION OF SUCCESSIVE DEATH FEINTS.

7. *Duration of the first five successive death feints:* Fabre (6, pp. 15 and 16) put a beetle, Scarites gigas, Fab. into five successive death feints and found that, "Les cinq épreuves consécutives, de la première à la dernière, ont duré respectivement 17 minutes, puis 20, 25, 33 et 50 minutes. Ils nous disent qu'en général le Scarite prolonge davantage sa pose inerte à mesure que l'épreuve se répète." We performed a similar experiment with a half dozen Belostomas which were taken from water at 21° C., and caused to feign five times at the temperature of the atmosphere at 21° to 23° C. Each specimen was placed with its back upon a solid substratum and as soon as it came out of the feint, it was immediately put back into its inert state again, care being taken to give each individual about the same amount of handling and to keep conditions as nearly uniform as possible. The temperature of the room varied within two degrees throughout the experiment. The following figures show the duration of the first five successive feints in minutes:

TABLE I.

TIME OF THE FIRST FIVE SUCCESSIVE DEATH FEINTS OF SIX BELOSTOMAS.

	A	B	C	D	E	F	Averages
	1	11	3	13	3.5	10.5	11.5
	4.5	27	23.5	27.5	26	38.5	13.4
	28.5	15	16	24	20	37	15.5
	14	12	11.5	7.5	21	7	18.3
	9.5	2	23.5	19.5	22	14	18.5
							21.4
Average	11.5	13.4	15.5	18.3	18.5	21.4	
							16.4 Total average

Our results as seen from Table I are entirely different from those of Fabre. There is a wide variability in the duration of the first five feints in the different individuals under uniform conditions. A glance horizontally across the columns shows a considerable amount of variation in the time of corresponding feints in the specimens, and a glance down any column shows that the duration of successive death feints in each individual also varies, while even the averages of the first five feints shows a variability.

8. *How long can successive death feints be continued?* Fabre (6, p. 16) found that the Carabid, Scarites gigas, Fab. could not be induced to feign indefinitely. "Tôt ou tard, ahuri par mes tracasseries, les Scarite se refuse à faire le mort. A peine mis sur le dos après un choc, il se retourne et fuit, comme s'il jugeait désormais inutile un stratagème de si peu de succès." Holmes (12, p. 204) put ten Ranatras into successive death feints from "9 A. M. and continued without interruption until 5 P. M., when the last specimen refused to feign longer." He found that the duration of the death feint diminishes with successive trials. We performed a somewhat similar experiment with ten Belostomas. They were taken from water at 19° C., and laid upon their backs while feigning death, at the temperature of the atmosphere at 21 to 22° C. As soon as a specimen had righted itself, it was immediately put back into the inert position again; the conditions were kept as nearly uniform as possible, no sunlight being allowed to shine upon the insects. The following table shows the time in minutes of each feint; ellipses indicate that the bug assumed the usual death feigning posture but when the insect was placed upon its back it immediately righted itself:

TABLE II.

Time in Minutes of the First Series of Successive Death Feints in Ten Belostomas.

A	B	C	D	E	F	G	H	I	J
6.5	58.5	48.5	.5	6.	2.5	10.	7.	1.	10.
64.5	52.	22.5	5.5	10.	21.5	34.	54.5	15.	45.
92.	18.	25.	50.	37.5	29.	19.	41.5	40.5	19.5
25.5	29.5	16.	51.	5.5	14.5	18.5	27.5	39.5	12.5
15.5	32.5	13.	3.	16.	9.	19.5	14.5	25.5	11.5
14.5	16.	16.	2.	16.	10.5	9.	15.	34.	26.
21.	17.	27.	3.	29.5	8.	8.	13.	46.5	22.
13.5	13.5	24.5	3.5	6.5	6.	10.5	11.	25.	14.5
1.	18.5	28.5	4.	6.	5.	17.5	39.	16.5	14.5
2.	3.	13.5	3.5	24.	4.5	12.	7.	16.5	5.
.5	17.5	14.5	2.5	27.	4.5	12.	6.	5.5	1.
4.5	2.5	11.	3.	11.	4.	9.	5.	4.5	....
5.	10.5	6.	2.5	10.	5.	3.	7.	5.5	1.
6.5	17.5	10.5	2.5	12.	5.	8.	3.5	6.5	....
4.5	10.	10.5	1.	3.5	3.	7.	5.5	9.	....
4.	4.	12.	2.5	13.5	5.5	9.	3.5	4.	....
.5	2.5	19.5	1.5	5.	2.	9.	7.5	4.	....
2.	3.5	5.5	1.5	8.5	1.	3.	2.	4.	....
15.5	.5	12.	2.	6.5	3.	5.	3.	1.	
3.5	2.5	4.	2.5	3.5	1.5	4.	17.	2.	182.5
14.5	1.	9.5	1.5	7.5	2.	8.	8.	2.	
2.5	3.	6.	2.5	12.	2.	1.	10.5	.5	
6.5	3.5	7.5	2.	4.	3.	1.5	6.5		
7.5	7.5	6.	2.5	9.	1.5	4.5	3.5	308.5	
7.5	3.	4.5	2.5	4.	.5	1.	5.		
2.	4.	5.	.5	1.	3.	3.5	6.5		
2.	2.	8.5	1.	3.	2.	6.5	1.		
.5	3.	9.	2.	3.	.5	1.	2.5		
.5	3.	5.	1.	2.	1.5	....	1.5		
.5	.5	10.	1.5	3.	1.5	....	3.		
2.5	.5	7.	1.5	3.	2.5	.5	4.		
4.	.5	9.5	1.	2.	.5	....			
6.5	.5	5.5	1.5	4.	.5	.5	342.		
4.5	2.	4.5	.5	4.	....	....			
4.	1.	4.5	1.	2.5	.5	....			
2.	.5	5.	....	1.5	....				
1.5	1.	4.5	....	2.5	.5	255.			
1.5	1.5	6.	.5	2.5	....				
.5	.5	5.5	.5	5.	.5				
.5	1.	3.	.5	3.	....				
.5	3.	3.	....	.5					
.5	1.	4.	....	1.5	167.5				
1.	.5	3.	1.	.5					
2.	1.	2.	....	.5					
.5	2.	.5	....	1.					
1.	.5	3.	....						
1.	.5	3.5	....	340.					
.5	1.								
.5	.5	485.	172.5						
.5	2.								
....									
	381.								
382.									

A glance down any of the columns of figures shows that the duration of successive death feints diminishes with repeated trials.

The above experiment was repeated with ten different Belostomas taken from water at 15° C., and exposed to the temperature of the atmosphere at 22° C. The total number of minutes and the number of times each specimen could be induced to feign in both of these experiments is shown in the following table:

TABLE III.

Number of Successive Death Feints.		Total Number of Minutes Each Specimen Could be Induced to Feign Death.	
Experiment I.	Experiment II.	Experiment I.	Experiment II.
47	77	485	474
51	72	382	317.5
50	70	381	317
31	40	342	295
45	40	340	289
22	25	308.5	262.5
35	36	255	201
18	31	182.5	199.5
47	35	172.5	197
40	24	167.5	147.5
Average 38.6	45	5 hours	4.5 hours

While experiment I was being carried on, a similar series of experiments were started at 8 A. M. with two Belostomas that had attained their full growth by moulting during the night. With these specimens, the duration of the death feint also diminished with successive trials. It was found, however, that the total average time that these two bugs could be induced to feign was only one hour, whereas in experiments I and II the total average time was five and four and one-half hours respectively. This difference may be attributed, in part at least, to the weakness following the tedious task of moulting which these two specimens had recently undergone, and also to the effect of dryness upon the organisms.

As soon as the ten Belostomas, which were used in experiment I, refused to feign, they were thrown into an aquarium. After remaining in the water for a few minutes, they could again be induced to feign death, and were put through successive feints until they refused to feign longer, when they were thrown into the aquarium a second time. This was repeated until finally the insects absolutely refused to feign. The total average time which the ten Belostomas feigned throughout all the series of successive death feints was eight hours; the total average time of the first series of successive death feints was five hours, thus making an increase of three hours that the specimens could be induced to feign by placing them in water for a short time whenever they refused to assume the inert state.

Towards the end of this series of experiments, the tetanic condition of the leg muscles became weaker and of shorter duration. When one of these specimens was taken from the aquarium and put into the usual death-feigning posture, it would maintain this position only for a short time; the legs would sprawl apart and often the insect would make no attempt to right itself. Consequently it often became exceedingly difficult to say with certainty just when the death feint ended. When thrown into the aquarium, the bug would swim about rather listlessly. One would naturally be inclined to believe that these weaker responses were due to fatigue, but that this is not entirely the case will be shown later. After these series of experiments were discontinued, the ten Belostomas were kept over night in the aquarium and the next morning we were surprised to find that most of the individuals had died.

The previous experiments on how long successive death feints can be continued suggested a number of problems: (1) the cause of the weaker reaction toward the end of this series of experiments, if it is not entirely due to fatigue; (2) the reason for the marked diminution in time of the death feints with successive trials; (3) the cause of the cessation of the feint in each series of successive death feints, if it is not wholly due to fatigue; and (4) the probable explanation of the death of most of the ten Belostomas.

A similar series of experiments were carried on with ten Nepas. Every specimen was made to feign by taking it out of the water with a pair of forceps, dropping it upon a moist blotter from a small height and turning it over and over laterally three or four times. The insects were now laid upon a table upon their ventral surface, but it was found that it became impossible at times to determine positively when the death feint ended . Although the bugs would assume a walking attitude after they had given the first signs of coming out of the death feint, yet they would often remain in this quiet state for hours at a time with their muscles perfectly lax. On account of the impossibility of being certain just when the death feint ceases in every case, it was decided to consider the time when the muscles of the limbs became relaxed as the termination of the feints, although in reality, the durations of the feints in each case were somewhat longer. As soon as the muscles of the legs became relaxed, the time was recorded, the individual being then induced to feign death again. This was repeated until the aquatic bugs would feign no longer. The experiment was begun at 8 A. M. and at 2.30 P. M. the last specimen refused to feign. Here as with Belostoma, it was found that the durations of the death feints decrease the oftener the insects are made to repeat the performance.

When the last three Nepas refused to feign, they were dipped into water, which was at the temperature of the room, and then they could be readily put into the feint again. In this way, by dipping the bugs into the water whenever they refused to feign, we succeeded in making them feign until four o'clock, when the experiment was discontinued. Undoubtedly they would have feigned longer had we continued the experiment.

IV. THE EFFECT OF DRYNESS AND MOISTURE ON THE DURATION OF THE DEATH FEINT.

9. *The effect of dryness on the death feint:* In order to throw some light on the problems suggested in connection with the previous experiments with Belostoma, a number of experiments were performed to determine the effect of dryness upon the duration of the death feint. Fifteen Belostomas were taken out of the water at 19° C. and exposed for one and a half hours to the temperature of the atmosphere at 21° to 22° C. so that their bodies might dry. It may be of interest to note here, that two specimens at the end of this time made eager efforts to escape by flying against the sides of the dish in which they were confined. The following figures indicate the averages of the first five successive death feints of each insect: .9, .9, 1.5, 1.7, 4.3, 4.5, 4.5, 7.2, 7.3, 7.8, 8.3, 10.2, 12.4, 12.5 and 18.2 minutes. The average of these averages, or the total average, is 6.8 minutes.

In the experiment under table II, the difference in temperature of the water and the atmosphere was identical with the present experiment. The total average of the first five successive death feints of the former, however, was 24.9 minutes, while in the latter it is but 6.8 minutes. It is evident, therefore, that the drying of the body of Belostoma causes a marked diminution of the death feint.

In another experiment, eight Belostomas were placed into a glass jar lined with blotting paper, and were there exposed to the atmosphere at 21° to 22° C. Twelve hours later all the specimens were caused to feign three successive times, and it was found that every single death feint was less than five minutes. Sixteen hours after being confined in the glass jar, three individuals had died and one could not be induced to assume the usual death-feigning posture. The four remaining insects were put into three successive death feints of which the total average was one and one-half minutes. Twenty hours after being exposed to their dry surroundings, three of the remaining bugs had died; the other two were too weak to assume the usual death-feigning posture and these died two hours later.

If the behavior of the eight specimens in the previous experiment is compared with that of the ten Belostomas used in the experiments in determining, how long successive death feints can be continued, it will be noticed that both lots show a weaker reaction towards the end of the experiments. In all probability, this weaker response in the latter cannot be wholly attributed to fatigue, but must, in part at least, be due to the effects of dryness upon the organisms. It is evident further that dryness causes a marked diminution in the duration of the death feint. The decrease with successive trials in the duration of the feint and also the cessation of the death feint must be attributed in part to the effects of dryness rather than entirely to fatigue. In all probability it was also the effect of dryness which caused the death of the ten Belastomas after they had feigned eight hours on an average in the above experiments.

10. *The effect of moisture on the death feint:* The object of the following experiment was to determine what effect moisture has upon the duration of the death feint. Twenty Belostomas were taken out of water at 18° C. and caused to feign death at the normal temperature of the room with their backs resting upon some wet blotting paper that had been soaked in the same water from which the individuals had just been taken. Imme-

diately after the insect came out of each feint, it was stroked with a camel's hair brush and put back into the immovable position again. It was found that as the blotting paper lost a considerable amount of moisture and the bugs became dry on the ventral surface, it was not long before the hemiptera usually came out of the death feint. The following figures indicate the averages of the first three successive death feints in each specimen: 10, 12, 23, 25, 26, 30.5, 31, 34.5, 42.5, 45, 46, 58, 59, 59.5, 65, 66.5, 68.5, 69.5, 71 and 104 minutes. The average of these averages, or the total average, is 47.3 minutes. One would not hesitate to conclude from this experiment that the duration of the death feint is increased under these conditions.

From the experiments upon the effect of dryness and moisture on the duration of the death feint, one is strongly inclined to believe that the death feint is increased by a large amount of watery vapor in the atmosphere and decreased in a dryer atmosphere.

11. *The effect of placing the death-feigning animal in water:* The death feint in some aquatic invertebrated animals can often be terminated by placing them in water. Holmes (13, p. 162) finds that "in Ranatras of five days old or less the death feint often persists for a time after they are placed in water." In the mature Ranatra (13, p. 162), however, "the moment the insect is placed in the water the death feint entirely disappears."

The death feint of Belostomas often ends suddenly when the insects are thrown into water; frequently, however, the bugs bob up to the surface of the water and continue to feign there. Those specimens, feigning on the surface of the liquid medium, also showed a wide variability in the duration of the death feint, as was the case with those which feigned upon a solid substratum. While some individuals came out of their inert state almost immediately, others would remain motionless at the surface film for a few seconds and then begin to swim about very actively, while still others feigned for a much longer time. Occasionally, those insects, which feigned for some time at the surface of the water, first gave an outward sign before coming out of the feint. The proboscis groped about in the water and the legs were gradually sprawled apart. The hemipteron would remain with its legs in this position from a few minutes to a considerable length of time. Next, one would sometimes notice the swimming legs make a few weak strokes. Probably the aquatic bug is still under the influence of the death feint. A little later Belostoma scurries to the bottom of the aquarium.

In order to have as slight a shock effect as possible, a dozen Belostomas, which had been kept in water at 19° C., were picked out of the water, caused to feign death and then carefully transferred to the surface film of the same water. The temperature of the room was kept at 21° to 22° C. The following figures show the duration of the first death feint in the twelve specimens, the dashes indicating that the bug came out of the feint almost immediately after coming in contact with the water or feigned less than half a minute: —, —, —, .5, .5, .5, 1, 1, 1.5, 3.5, 9.5 and 23 minutes.

The previous experiment was repeated with seven Belostomas under similar conditions, but each specimen was caused to feign five successive times. The averages were: 3.3, 4.6, 11.5, 12.7, 14.5, 16.7 and 18 minutes; the total average was 11.6 minutes.

In the experiment under table II, the difference in temperature of the water and the atmosphere was identical with these conditions in the present experiment. The total average of the first five successive death feints of the former, however, was 24.9 minutes, while in the latter it was 11.6 minutes. It is evident, thus, that the effect of placing Belostoma on the surface film of the water diminishes the duration of the death feint.

It occurred to us now that Belostoma would probably feign below the surface of the water. A toothpick was fastened horizontally by one end about an inch below the surface of the water, while at the other or free end the feigning insect was placed so that this end of the toothpick passed between the middle and hind pairs of legs. The experiment, however, had its faults, for as soon as the extreme muscular contraction of the limbs relaxed somewhat, the legs gradually spread apart and the bug rose to the surface film. This experiment was repeated with the same individual again and again. As in the preceding experiments, there was a considerable variability in the duration of the feint in those specimens which could be induced to feign under these conditions. Although there were some bugs which would feign below the surface of the water for a short time, we finally succeeded in getting one to feign 6.5 minutes, another 11, a third 12, and a fourth 13.5 minutes, the last continuing to feign four minutes longer, upon the surface film. In some individuals thus experimented upon, we observed that when they arose to the surface film and came out of the death feint, they would take in a fresh supply of air almost immediately. It is evident, thus, that the duration of the death feint diminishes when Belostoma is caused to feign below the surface of the water .

While Nepa will also feign death in water, it does so only for a short time. In one experiment, nine specimens were taken out of water, which was at a temperature of 17° C., and after being put into the death feint in the usual manner, were again placed into the same water. In every instance they continued to feign, but only for a short time varying from forty seconds to somewhat less than four minutes. The following figures are the durations of the death feints in seconds of the nine specimens: 40, 55, 60, 60, 65, 90, 170, 180 and 215.

In a second experiment nine Nepas were made to feign without taking them out of the water, which was at a temperature of 17° C., by merely touching them upon their backs two or three times with a pencil. In every instance care was taken to keep the insect entirely submerged. The durations of the death feint in this case were: 50, 60, 70, 90, 90, 115, 130, 180 and 180 seconds.

In both of these experiments, the first sign of Nepa coming out of the death feint was a movement of the breathing tube. The legs were then moved and, if the aquatic bug was on its back, righting took place, after which the abdomen with its breathing tube was raised so that the latter penetrated the surface film. Some specimens were made to feign again and again before they were permitted to reach the surface film with their breathing tube, but soon all efforts to put these insects into the death feint, without first permitting them to reach the surface of the water with their breathing tube, failed. If these individuals were allowed to take in air, however, they could very readily be put into the death feint again.

V. THE EFFECT OF TEMPERATURE ON THE DURATION OF THE DEATH FEINT.

12. *The effect of a high temperature on the duration of the death feint:* The duration of the death feint diminishes if Belostoma and Nepa are caused to feign in a high temperature. In one experiment five Belostomas were taken out of water at 25° C.

and caused to feign death at the temperature of the atmosphere at 31° to 32° C. The average of the first six successive death feints of each individual were: 6.3, 7.1, 7.6, 9.1, and 11.5 minutes, the total average being 8.3 minutes.

With Nepa, two separate experiments were performed, in each of which two lots of specimens of eight or ten were made to feign, one at a high temperature and the other at a temperature considerably lower. In both of these experiments, all of th- water-bugs were first kept for three or four hours in the teme perature at which they were afterwards put into the inert state. The averages of the first death feints under these conditions were:

TABLE IV.

Experiment 1.

Nepas kept at	34° to 35° C.,	4 minutes.
" " "	28° " 29° "	11.8 "

Experiment 2.

Nepas kept at	25° C.,	13.7 minutes.
" " "	16° to 17°C.,	27.6 "

13. *The effect of a low temperature on the duration of the death feint:* A considerable amount of difficulty was experienced in determining the effect of a low temperature upon the duration of the death feint in Belostoma. A number of experiments were performed in which the transition in temperature from the water to the atmosphere was not very great, thus avoiding a sudden shock effect; these experiments were also carried on at a time of the year, in which the aquatic bugs had been surrounded with a low temperature in their natural environment, the specimens in the first three experiments, table V, being taken after a thin coating of ice had formed over the water. In all of the experiments, six or more Belostomas were caused to feign at least five successive times. The following table shows the transition in temperature from the water to the atmosphere, and the total average of the death feints of all the specimens in each experiment:

TABLE V.

Water	4° C.	Atmosphere	—1° to 0° C.	Total average	.5	minutes.
"	3° "	"	4° " 5° "	" "	1.3	"
"	4° "	"	6° " 7° "	" "	.8	"
"	8° "	"	9° " 10° "	" "	4.6	"
"	9° "	"	10° " 12° "	" "	2.	"
"	10° "	"	12° " 13° "	" "	5.4	"
"	14° "	"	15° " 16° "	" "	29.08	"

It is evident from these experiments that the duration of the death feint diminished when the insect is taken from water at a low temperature and exposed to a temperature of the atmosphere lower than 12° C. This result differs from Fabre's (6, pp. 23–4) work on the Buprestid, Capnodis tenebrionis, Lin. and Holme's (12, pp. 207–8) investigation on Ranatra, for both of these naturalists find that cold increases the duration of the death feint to a very marked degree.

It occurred to us that the warm stimulus of one's fingers probably had some effect upon the specimens and a number of the experiments under table V were repeated, care being exercised not to touch the insects with our fingers but to seize them with a pair of forceps and cause them to feign by stroking them with a camel's hair brush. But we noticed no marked change upon the duration of the death feint.

It is worthy of mention that in those experiments in which the temperature of the water was 10° C. or lower, many Belostomas could only be induced to assume that death-feigning attitude in which the legs are folded against the ventral surface of the body (fig. 1). Probably this condition was due, in great measure, to the numbness produced by the cold. Belostomas, however, were often raked or scooped out of the water in the autumn or taken out of an aquarium when the temperature of the water was considerably higher than in these experiments and yet the bugs often assumed this death-feigning posture; these insects, however, could always be induced to assume the other characteristic death-feigning attitude (fig. 2).

When Nepas, on the other hand, are exposed to a low temperature, the insects remain in the death feint considerably longer than when they are made to feign in a higher temperature (table IV). Two experiments were performed, in each of which care was taken to expose each lot of Nepas for three or four hours to the temperature at which they were afterwards made to feign. The averages of the first death feint in ten specimens in the two experiments were as follows:

Experiment I.

Nepas kept at 13° C., 21.9 minutes.

Experiment II.

Nepas kept at 9° to 10° C., 33.1 minutes.

This result agrees with Fabre's (6, pp. 23-4) work on the Buprestid, Capnoides tenebrionis Lin. and Holmes's (12, pp. 207-8) investigation on Ranatra.

14. *The effect of a sudden change in temperature upon the duration of the death feint:* The duration of the death feint decreases when Belostoma is taken from water at a high temperature and exposed to a low temperature of the atmosphere. In one experiment six Belostomas were taken from water at 21° C. and caused to feign upon a blanket at the temperature of the atmosphere at 9° C. The averages of the first ten successive death feints of each individual were: .3, .7, .8, 1, 1, and 1.7 minutes; the total average was .9 minutes. This experiment was repeated with a half dozen different Belostomas taken from water at 23° C. and exposed to the temperature of the atmosphere at 12° to 13° C. with somewhat similar results.

With Nepa it was found that previous exposure to a high temperature of the water and a transition to an atmosphere considerably lower in temperature, decreases the duration of the death feint. In the first set of experiments, eighteen specimens, that had been kept in water at a temperature of 22° to 23° C. for six hours, were caused to feign at a temperature of the atmosphere at 11° to 12° C., while eighteen different individuals, that had been kept in water at 11° to 12° C. for twelve hours, were also made to feign at the same temperature of the atmosphere. The averages of the first death feint in each experiment were as follows:

Nepas exposed to 11° to 12° C. throughout experiment, average 19.6 minutes.
Nepas kept in water at 22° to 23° C. for six hours, then caused to feign at a temperature of the atmosphere at 11° to 12° C., average 6.9 minutes.

In the second set of experiments, one lot of Nepas, that had been kept in water at 23° C. for three hours, was caused to feign at the temperature of the atmosphere at 12° to 13° C., while another lot, that had been kept in water at 12° to 13° C. was also made to feign at the same temperature of the atmosphere. The averages of the first death feint in each experiment were as follows:

Nepas exposed to 12° to 13° C. throughout experiment, average 22.6 minutes.
Nepas kept in water at 23° C. for three hours, then caused to feign at a temperature of the atmosphere at 12° to 13° C., average 7.6 minutes.

The following question naturally suggested itself: Does the transition from water at a low temperature to a higher temperature of the atmosphere have any effect upon the duration of the death feint? Thirty-five Belostomas were taken from water at 3° C. and exposed to the temperature of the atmosphere at 21° to 22° C. Many specimens absolutely refused to feign when taken out of this cold water, while others would remain in the inert state only a few minutes at the most. Those individuals which did feign, always assumed that death-feigning posture in which the legs are folded against the ventral surface of the body (fig. 1); but later, as the insects overcame their numbness, they could be induced to assume the characteristic death-feigning attitude (fig. 2) and then they feigned for a considerable time.

VI. THE EFFECT OF LIGHT ON THE DURATION OF THE DEATH FEINT.

15. *The effect of sunlight on the death feint:* Fabre (6, pp. 21-23), experimenting upon the effect of sunlight on the death feint in two species of beetles writes, "Aussitôt, sous les rayons directs du soleil, le Scarite se retourne et déguerpit," and " En quelques secondes de ce bein chaud et lumineux, l'insecte," (a Buprestid) "entr' ouvre les élytres, dont il fait levier, et se retourne prompt à prendre l'essor si ma main ne le happe à l'instant."

With Belostomas the duration of the death feint is also decreased when the feigning insects are exposed to sunlight. Five specimens were taken from water at 20° C. and caused to feign in sunlight at a temperature of 36° to 37° C. The following figures show the time, in minutes, of the first death feint in each individual: .5, 3.5, 3.5, 5.5, and 5.5, the average time being 3.7 minutes.

In working with direct sunlight, however, one cannot say whether the duration of the death feint was diminished through the direct effect of light upon the organism, or whether this effect was due to the heat rays, or a combination of the two. To overcome these difficulties an artificial light was used.

16. *The effect of an artificial light upon the duration of the death feint:* In the following experiment, a sixteen candle power incandescent electric lamp was used, the lamp being attached to a flexible cord of wire, which was fastened at one end to the ceiling, so that the lamp could be swayed back and forth over

the insects like a pendulum. A shade was used to reflect as much light down upon the specimens as possible. The heat rays were intercepted by placing a flat dish containing an inch and a half of pure water between the electric lamp and the bugs. This work was carried on in a darkened room, so that the insects experimented with were exposed to light only from this lamp.

Holmes (12, p. 208) finds that Ranatra comes out of the death feint more quickly under a bright light than under a much dimmer light, a result which we also obtained with Belostoma and Nepa. In one set of experiments, six of twelve Belostomas were put into the death feint and then exposed to the light of a stationary sixteen candle-power electric lamp, while at the same time, the remaining six were caused to feign in a much dimmer light in another part of the room. None of the insects had been exposed to the light of the incandescent lamp previous to the time that they were put into their first feint. The results were as follows: averages of three successive death feints in six Belostomas kept under a stationary sixteen candle-power incandescent electric lamp 4.5, 10, 13.5, 21, 21 and 26 minutes, the total average being 16 minutes; averages of three successive death feints in six Belostomas kept under a much dimmer light 27.5, 28.1, 28.5, 28.5, 29 and 30 minutes, the total average being 28.6 minutes. The difference between these two total averages is 12.6 minutes, from which one would not hesitate to conclude that the awakening occurs more quickly under a bright light.

Nepa also feigns death longer, as a rule, in a dim light than in bright light, provided the insects have been previously exposed for some time to that intensity of light in which they are afterwards made to feign. In the two following experiments, two lots of specimens were exposed for three hours to the light of a sixteen candle-power incandescent electric lamp about twelve inches away, while two other lots were being kept in a much dimmer light for the same period of time. They were all then made to feign in the usual manner with as nearly the same amount of handling as possible and transferred to practically the same intensity of light to which they had been exposed. In these experiments there was no shock effect due to change in temperature, for the water in which the insects were kept was at the temperature of the atmosphere. The average of the first death feint in ten specimens kept at 18° C. under bright light was 8.7 minutes, while in a dim light and at the same temperature the average was 13 minutes; in the second experiment, the specimens were kept at 14°–16° C. and now the averages were 13 minutes under a bright light and 20.4 minutes under a dim light.

That previous subjection to darkness, and a sudden transfer of the insects from this into a bright light has an effect upon the duration of the death feint of Nepa may be seen from the following experiments. Three lots of specimens were exposed for three hours to the light of a thirty-two candle-power incandescent electric lamp about eighteen inches away, while three other lots were kept in almost total darkness for the same period of time. All were then made to feign in the same intensity of light to which the first three lots had been exposed. The averages of the first death feint in ten specimens used in each experiment are as follows:

	Kept in bright light throughout experiment.		Kept in darkness, then transferred to bright light.	
Temperature of atmosphere	18° C.	14.8 minutes.	18° C.	9 minutes.
" " "	18° "	16 "	18° "	6.2 "
" " "	16° "	10.8 "	16° "	4.7 "

Belostoma and Nepa are aroused from their death feint more quickly under a swaying light than under a stationary one. Twenty Belostomas were taken from water at 17° C. and caused to feign under a stationary light of a sixteen candle-power incandescent electric lamp, the temperature of the atmosphere being 23° C. Each individual was, on an average, about six inches below the light. The time of the first death feint of each specimen under these conditions was as follows: 3, 3, 3, 4, 5, 5, 5.5, 6.5, 7, 7, 11, 12, 14.5, 17, 17.5, 19, 20, 20.5, 23 and 28 minutes, the average being 11.5 minutes. The sixteen candle-power electric lamp was now slowly swayed back and forth at the rate of about one complete oscillation per second above fifteen different Belostomas lying on their backs in a death-feint, the temperature conditions being identical with those in the previous experiment. The following figures indicate the time of the first death feint: .5, 1, 1, 1, 1, 1.5, 2, 3, 4, 6, 6, 8, 11, 14.5 and 22 minutes, the average being 5.5 minutes.

A glance at tables I and II shows that the first death feint under normal conditions is usually shorter than the next three or four successive feints. For this reason, the two preceding experiments were repeated; each specimen was taken from water at 18° C. and caused to feign five successive times at the temperature of the atmosphere at 21° to 22° C. The averages of the first five successive death feints in ten Belostomas kept under the stationary lamp was as follows: 6, 7.2, 11, 14.8, 16.2, 16.4, 22.9, 24.8, 25.2 and 25.5 minutes, the total average being 17 minutes. The averages of the first five successive death feints in eighteen specimens kept under the swaying electric lamp was: 2, 4.3, 5.7, 6.2, 7.7, 8.8, 9.8, 9.9, 12.8, 14, 14.4, 14.4, 14.6, 15.5, 15.7, 17.2, 21.2 and 23.2 minutes, the total average being 12 minutes. The difference in the total averages of the first set of experiments is 6 minutes and of the second set of experiments, 5 minutes. Evidently Belostomas are aroused from their death feint more quickly under a swaying light than if it is kept stationary and this is true whether the average of the first death feints or the first five successive feints of a large number of specimens are taken.

In similar experiments with Nepa, all the insects were first exposed for three hours to the light of a stationary lamp about eighteen inches away. Ten Nepas were used in each experiment. The averages of the first death feints are as follows:

Temperature of atmosphere 18° to 19° C.

Under stationary light.	Under moving light.
12.8 minutes.	7.3 minutes.
15.9 "	10.9 "

17. *Reactions to light previous to and after coming out of the death feint:* Nepa, when feigning death while lying on its ventral surface under a moving light, soon responds to the movements of the lamp by corresponding head-movements. Thus, if the light is moved back and forth over the specimen laterally, the head is turned each time so that both eyes receive some illumination. If the lamp is moved over the long axis of the body, the head again responds, lowering while the light is being placed in front of the individual and tilting upward when in back of it. If the light is moved in a circle, the head also rotates in a circle. These head movements are at first slight, and either the side to side or the up and down movements will be given

first, depending upon the direction in which the lamp is moved with reference to the body of the insect. Soon, however, the movements increase in vigor, the animal performing the movements with machine-like regularity and precision. These head movements may be given without any other apparent movements of the body or limbs. If the light is continually moved over the long axis of the body, the insect, when it comes out of the death feint, usually turns at right angles to the path that the light is swaying in and runs away. If, while the aquatic bug is running away, the light is again moved back and forth over the long axis of the body, the insect changes its direction almost immediately by turning ninety degrees as before, and continues on its new path. In this way Nepa may be forced to change the direction in which it is moving again and again. If the light is kept stationary, on the other hand, in the center of a circle of feigning Nepas lying on their ventral surface, some facing the light and others turned away from it, in almost every instance will the former turn about and run directly away from it, while the latter will, when they come out of the death feint, run away without turning. Oftentimes when the bugs are thus running away from the light, they can be brought to a standstill by suddenly placing the light directly before them. With the aid of a light alone, the animal can be forced to go in any direction, and even in a circle by holding the light to one side and a little in front of the creature. From these experiments it is seen that Nepa is decidedly negatively phototactic to the light of a thirty-two or sixteen candle-power incandescent light immediately after the aquatic hemipteron comes out of its feint.

With Belostoma, however, but few specimens give the lateral and vertical head movements alone in response to the light rays previous to coming out of the death feint. By moving the electric lamp back and forth laterally over the body of some individuals, the head is turned so that its dorsal surface is at right angles to the direction of the light rays, as in Nepa; but if the light is swayed lengthwise over the body, vertical movements of the head and prothorax combined are given. When the light is passing from the posterior to the anterior region of the insect, the head accompanied by the prothorax is lowered; if the light is now passed backward, the head and prothorax are tilted upward. Most of the bugs, however, do not give these reactions before coming out of the feint.

A large number of insects experimented upon with the electric light in this manner, gave no reactions previous to coming out of the death feint, but simply righted themselves and usually endeavored to escape by fleeing away from the light. One noticeable peculiarity of some of the fleeing individuals was the swaying movements of the body, combined with the hurried movements of escape. When these fleeing specimens were allowed to run at large on the floor, many ran in a large circle, the body being tilted toward the light. It was found that sooner or later most of these specimens would finally return to the light. Some bugs, however, would simply right themselves after coming out of the feint and remain motionless for a time, but later they would follow the light, while still others would right themselves and follow the light immediately.

VII. THE EFFECT OF MUTILATION ON THE DEATH FEINT.

18. *The effect of decapitation on the death feint:* Preyer and Verworn have both worked on the effect of decapitation on the so-called hypnotism of vertebrated animals. Preyer[1] decapitated a hen and two cocks and believes that his results, "stehen im Einklang mit der Annahme, das auch geköpfte Thiere durch starke tactile Reize kataplegisch werden können." Verworn (27, pp. 57–8) repeated the experiments of Preyer and concludes, "Immerhin möchte ich die Möglichkeit nicht bestreiten. Aber wie dem auch sei, auf keinen Fall würde aus diesem Umstand der Schluss gezogen werden dürfen, dass beim intacten Thiere die Ursachen für den Eintritt der Bewegungslosigkeit in abnormen Körperlagen ihre Localisation im Rückenmark hätten, - - - - ."

Robertson (23, p. 417) concludes that among the invertebrated animals "the 'sham-death' reflex is carried out without the aid of the abdominal nerves, and in the active species [Epeira (producta?) and Amaurobius sp.?] can be performed in an altered manner by the thoracic ganglia alone, or even by the ganglia of the posterior or two anterior segments of the thorax alone. - - - - With the supra- and sub-oesophageal ganglia removed the reaction is still carried out in the active species, but it is now weaker, has a longer latent period (in Epeira sp. at least,

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[1] Quoted from Verworn's (27, p. 56) paper.

and probably in Amaurobius sp.) and it is a rhythmically interrupted tetanus." Holmes (12, p. 211) in his work on Ranatra concludes that "it is abundantly evident that the removal of the supra-oesophageal ganglion causes a marked diminution of the duration of the death feint."

19. *General features of the nervous systems of Belostoma flumineum and Nepa apiculata:* The nervous system of Belostoma flumineum and Nepa apiculata is somewhat similar to that which we (19) have described and figured for Ranatra. The supra-oesophageal ganglion is situated in the upper posterior part of the head and is closely connected with the infra-oesophageal ganglion by the circum-oesophageal commissures. Near the anterior margin of the prothorax lie the fused infra-oesophageal and first thoracic ganglia (fig. 7, in). Packard (20, p. 226) also describes a fusion of the sub-oesophageal ganglion with the first thoracic, in Acanthia, Nepa and Notonecta. As in Ranatra, the rest of the ganglionic system of Belostoma and Nepa consists of a large ganglion situated mostly within the mesothorax but extending backward also into the metathorax.

20. *Shock effect of decapitation:* In snipping off the head of Belostoma or Nepa, only the brain is removed. A quick, sharp, clean cut was made with a pair of fine scissors in all of the following mutilation experiments. When the head was removed from feigning Belostomas lying on their backs, the insects, with but few exceptions, came out of their inert state immediately. Of the small number that maintained the immovable state, some would keep the usual death-feigning posture for a few seconds while others would do so for a somewhat longer time.

As a general rule, most of the decapitated Belostomas showed a marked shock effect. They would usually move all their legs vigorously after the head was severed from the body, but did not often succeed in righting themselves. Some were placed on their backs in a glass dish with the bottom either covered with water or moist blotting paper and yet most of these failed to right themselves for days; others, however, would assume the normal righted position very readily. When the cover of the glass dish was raised, the decapitated individuals lying on their backs would often respond by moving their legs.

In one set of experiments, six Belostomas were beheaded and placed upon their backs in direct sunlight at a temperature of

36° C. Although these bugs became very active, only one succeeded in righting itself and this individual assumed the normal position repeatedly when placed on its back. In another set of experiments, the head of six specimens was severed from the body and the body was then exposed to the hot sunshine at a temperature of 41° C.; in this case only two of the hemiptera succeeded in turning over into the walking position.

When placed right side up in their normal walking position shortly after the operation, some of the headless bugs would attempt to walk backward with the abdomen dragging along the substratum and with the anterior portion of the body held high up in the air. The posterior two pairs of legs would draw the body back a short distance and then the decapitated insect would topple forward, sometimes to one side and then again to the other. The front legs would play no part in this sort of locomotion. Occasionally the front legs, which were covered with blood that had oozed from the wound, would be rubbed together; sometimes these legs would attempt to rub the former head region, as if an irritation had been set up by the removal of the head.

Thirty Nepas were decapitated while they were feigning death, and about half remained in the same inert position, while the other half came out of the feint immediately. Those specimens, that did not apparently come out of the death feint immediately, lost the rigidity of the muscles the instant the cut was made. While some of the decapitated individuals would try to right themselves, others would lie quietly upon their backs, only now and then moving one or more legs. Frequently the legs would quiver violently, however. Of those headless insects that tried to right themselves, there were some that succeeded in a perfectly normal manner, some that did so only after many trials, while other failed entirely and then lay motionless. Oftentimes the latter could be induced to right themselves by stimulating them with a camel's hair brush. Most of the decapitated bugs that did right themselves, walked about in an apparently normal manner, although there were others that stood upon their posterior pairs of legs with the front pair stretched upward as far as possible. This peculiar attitude was undoubtedly due to the shock effect of the operation.

21. *Reflex acts:* When the end of the abdomen of the more active, decapitated Belostomas was pinched gently between a

pair of forceps, violent efforts were made to rub off the source of stimulation with the tibia and tarsus of either one or both hind legs. On pinching the posterior end of the body more to the right side, the right leg made an eager effort to rub the stimulated region, when more to the left side, the left leg was used. Sometimes, however, both legs were used to rub the end of the abdomen both on the dorsal and ventral surfaces.

The swimming reflex can often be elicited with headless Belostomas by simply throwing them into water. In one set of experiments, sixteen individuals were decapitated while they were lying on their backs in the inert condition. When the cut was made, all of the bugs came out of the immovable state; immediately after the operation, most of the insects could be induced to assume the usual death-feigning posture, but they maintained this condition for less than one minute. After they were exposed to the atmosphere for half an hour, so as to enable their wounds to heal somewhat, the insects were all thrown into the water in which they had been swimming just before the head was severed from the body, when it was found that thirteen of the sixteen specimens swam about actively and in an apparently normal manner.

A beautiful example of a reflex act was observed in Belostoma and Nepa. If decapitated Nepas, that had their front legs extended, were touched lightly with a needle on the groove of the femur or the inner surface of the tibia or tarsus, the tibia and tarsus would invariably quickly close upon the femur. If the leg was touched lightly on the outer, upper or lower surface, the reaction was usually not given. Within three minutes this reaction was given one hundred times, the needle being applied alternately to the femur of each front leg and withdrawn from the insect's grasp. As soon as the needle is withdrawn, the tarsus and tibia are usually extended again. Although this reaction is given by normal Nepas, it is not so invariably obtained with these, owing probably to the inhibitory action of the brain.

Nepas, when stimulated upon the ventral surface of the abdomen about five minutes after decapitation took place, would assume the rigid state of the legs, a condition which is so characteristic of the death feint of normal individuals, but they would maintain this state only for a few seconds. After the lapse of five hours, some of the specimens, when stimulated, would extend the legs out stiffly as before, but this rigid state would again be maintained only for a few seconds. This experiment was repeated at intervals of five and ten hours with always similar results until the insect became too weak to respond. Decapitated Nepas were kept alive for seven days in a dish with just enough water in it to keep the bottom moist.

Hundreds of Belostomas were decapitated to determine the effect on the death feint. With the removal of the supra-oesophageal ganglia, there is a marked variability in the behavior of the specimens. It was absolutely impossible to force some of the headless individuals to assume the usual death-feigning attitude. Robertson (23, p. 417) also found that in the sluggish species of spider "(Celaenia excavata), the 'sham-death' posture cannot be induced without the head ganglia * * * ." Most of the bugs, however, from which the head has been severed, could be induced to assume the usual death-feigning attitude through the method usually employed to bring about the inert state, but that marked firmness and stiffness of the limbs, so characteristic of the intact insects, was very weak and of only short duration and often even entirely absent. Often this muscular rigidity could only be brought about by gently stroking the abdomen with a camel's hair brush, but as soon as this was discontinued, the legs would sprawl apart and become flaccid. With every stroke of the camel's hair brush over the body of a specimen whose legs were held in the characteristic death-feigning attitude, there would be a marked muscular contraction of the legs, but the instant the stroking ended, the legs would spread apart and show evidence of limpness. If the tibiae of the posterior pair of legs of a specimen in the same attitude were raised with a tooth-pick, the tarsi would bend down as if the stimulation threw the muscles in a state of contraction. It appears, seemingly, that the contact stimulus sets up a reflex which brings about a weak contraction of the leg muscles, rather than that the tetantic condition was brought about through a death feint. It may be possible, however, that these reactions are connected with a death feint of very short duration, due as Holmes (12, p. 211) believes, "to the heightened irritability which normally follows when the inhibiting influence of the supra-oesophageal ganglia is not exerted." Again, the very much weaker response may possibly find its explanation in the loss of blood which had oozed out from the wound after decapitation had taken place.

22. *Reactions of Belostoma and Nepa with the body severed between the prothorax and mesothorax:* In cutting the body of Belostoma or Nepa between the prothorax and mesothorax, neither the fused infra-oesophageal and first thoracic ganglia, nor the large ganglion, which innervates the posterior pairs of legs and the abdomen, are injured. In Belostoma, the wound of the part anterior to the cut is exceedingly large, whereas in the posterior portion it is rather small.

When the body of feigning Belostomas was severed between the first two thoracic segments, both parts usually remained in the death-feigning attitude, whereas decapitation, as a general rule, brought the water bugs out of the death feint. If the part posterior to the cut (mesothorax, metathorax and abdomen intact) is thrown into water, it may make a few feeble strokes in an attempt at swimming, but not in a single instance did such a part swim about actively as was often the case with decapitated specimens.

In one set of experiments ten Belostomas, while they were feigning death, were cut in two between the prothorax and mesothorax. After the cut was made, both parts of the body of two specimens came out of the death feint immediately; the two parts of the remaining specimens, however, maintained the death-feigning posture, some not even giving as much as a quiver when the body was severed. The following table shows the time in minutes that each part remained in the death-feigning attitude:

TABLE V.

Duration of the Death-Feigning Posture in Eight Belostomas After the Body was Severed Between the Prothorax and Mesothorax; Temperature of Atmosphere 21° C.; of Water in Which Belostomas Were Kept 19.5° C.

	Head and Prothorax Intact.			Mesothorax, Metathorax and Abdomen Intact.	
A	1	minutes	A	9	minutes
B	1.5	“	B	14	“
C	3	“	C	4	“
D	3	“	D	3.5	“
E	5	“	E	18.5	“
F	7	“	F	5.5	“
G	13	“	G	14	“
H	17	“	H	25	“
Average	6.3	“	Average	11.6	“

Immediately after coming out of the death feint, the parts posterior to the cut were thrown into the water in which the specimens had been swimming just before the body was severed. They were then taken from the water and handled in the usual manner to bring about the death feint. Two of the ten water-bugs could be induced to assume the characteristic death-feigning posture, but only one showed any signs of a muscular contraction of the legs when stroked with a camel's hair brush. Twenty hours after the operation, the severed posterior portions of the body of the ten Belostomas were again treated as before, with somewhat similar results.

It is evident from the previous experiment, that the severed posterior portion of the body remained in the death-feigning posture often for a considerable length of time after the cut was made; but that this was often due to a shock effect in some individuals may be seen from the following observations. After the body of a particular specimen was severed between the first and second thoracic segments, the part posterior to the cut righted itself and assumed a very awkward position. The posterior pairs of legs were extended stiffly forward, there being no bending in the femoro-tibial joints. The anterior part of the body was raised high into the air, while the posterior portion touched the substratum. Unquestionably it was the shock effect which produced the rigidity of the leg muscles in this mutilated individual. With some specimens when the cut was made, the legs would not merely quiver, but would move up and down repeatedly and then become rigid again. Here again there is a renewed tetantic condition brought on, in all probability, through a shock effect.

Holmes (12, p. 213), in his work with Ranatra, cut a feigning specimen in two across the prothorax and found that "the posterior portion of this specimen continued to retain its rigidity for some time after it was cut off, - - - - . 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."

Fifteen Nepas were cut through the posterior region of the prothorax and in nearly all cases the anterior portion continued to feign death; the posterior part, however, either lost the rigidity of the legs immediately or remained perfectly quiet for an indefinite period, in which case, it was impossible to say with certainty just when the leg muscles became relaxed. The severed anterior portion continued to feign from two to eleven minutes and could readily be made to repeat the performance. The posterior part, when stimulated, would react like the decapitated specimens by stiffening out the legs, the rigidity, however, being lost soon after. In no case did the posterior part even attempt to right itself; the anterior portion, on the other hand, would right itself very readily and pull itself forward with the front legs, frequently falling over forward upon its back while moving in this manner, but soon righting itself again and continuing on its course.

If, instead of cutting Nepa in two, the nerve cord is cut in the same region as before through a small slit made on the ventral surface of the body, the insect will live somewhat longer. The part anterior to the cut may then be put in the death feint, while the muscles of the posterior pairs of legs are perfectly lax.

23. *Reactions of Nepa with the body cut across the metathorax behind the last ganglion:* In one experiment ten Nepas, while in the death feint, were cut in two across the metathorax just in front of the hind legs. In this operation the insects were cut close behind the last ganglion, which is situated towards the anterior end of the metathorax. In nearly every instance did the anterior portion continue to feign, remaining in the same inert position for a period varying from two to nineteen minutes, the temperature of the room being 18.5° to 19° C. The posterior part, which contains no ganglion, remained perfectly quiet with the hind legs very lax and did not respond to any stimulus, even when a red hot needle was applied to the ventral surface of the abdomen.

From these mutilation experiments on Nepa, it is evident that the severed part of the body retaining the brain will feign death for a considerable length of time, the legs, when the body is turned over and over laterally, assuming the characteristic position taken by intact specimens that have been put into the death feint in this way. The severed posterior part of the body or the part lacking the brain will, if it contains a ganglion, extend the legs out stiffly when the body is stimulated, but the rigidity of the muscles will be maintained only for a short time.

24. *The effect of light on the severed parts of the body:* The severed parts of five Belostomas, which had been cut in two

between the prothorax and mesothorax, were exposed to a swaying sixteen-candle power electric lamp. The part containing the head usually came out of the death feint more quickly than the posterior portion and showed marked responses to the light, while the latter would not react to it at all. As in the intact individuals, but few of the anterior parts, when placed dorsal side upward upon a table, gave the lateral and vertical head movements in response to changes in the position of the light previous to coming out of the death feint. After coming out of the death feint, the anterior portion endeavored to follow the light, the raptorial claw-like tibiae and tarsi catching hold of the table and dragging the head and prothorax along.

Five Nepas, while in a death feint, were cut across the metathorax behind the last ganglion and without exception every anterior portion continued to feign death. A light was then passed back and forth over these anterior parts and soon they gave the head reflexes apparently as well as normal Nepas. After coming out of the feint, these anterior parts were decidedly negatively phototactic, walking away from the light as well as possible, often falling over forward upon their back, but soon righting themselves again and continuing on their path away from the light.

VIII. THE ORIGIN AND DEVELOPMENT OF THE DEATH FEINT.

Various theories of the origin and development of the death feint have been advanced, but it is by no means evident that the development has been the same in all cases. Preyer (24) ascribes the shamming dead of insects to the exclusive influence of "kataplexy," or mesmeric sleep. Romanes (24, p. 309) believes with Preyer that "the shamming dead of insects is a phenomenon in which the principles of hypnotism are probably concerned. But if so, I regard these principles only as furnishing the materials out of which natural selection has constructed this particular instinct. Therefore, whether or not these principles are really concerned in the phenomenon, is only a side question; the important consideration for us is, that the instinct, whether or not developed from materials supplied by kataplexy, must certainly have been developed by natural selection."

Holmes (8, p. 195), who studied death feigning in terrestrial Amphipoda with the end of ascertaining, if possible, how their peculiar instinct may have arisen, concludes that "the death-feigning instinct of Talorchestia longicornis is an instinct, which, - - - -, has its root in the thigmotactic responses common among other amphipods."

It is a matter of common observation, that various aquatic insects belonging to different orders manifest the instinct of feigning death when taken out of the water. The instinct crops out among some of the nymphs of the orders Plecoptera, Ephemerida and Odonata, and again among the Neuroptera, as in the larva of Corydalis and the adults of Sialis. The death feint also occurs among some of the larvae of the aquatic Coleoptera and is developed to an unusual degree in some of the families of the aquatic Hemiptera. Traces of the death feint are found in some of the adults of the families Corisidae and Notonectidae, but it is in the family Nepidae that this instinct reaches its highest development among the adults of this group. Again, in the family Belostomidae, which includes Belostoma flumineum, the form with which we have been working, this instinct is exhibited to a marked degree, while in the closely related forms, Lethocerus americanus and Benacus griseus, also members of this family, this phenomenon can sometimes be induced with the proper manipulations.

It is agreed generally that all aquatic insects descended from terrestrial forms. It is evident that adaptations for an aquatic existence must have arisen independently amongst insects a number of times, for the families of insects that lead an aquatic life are often only distantly related and belong to different orders. If the instinct of feigning death was not handed down through inheritance from the various terrestrial ancestors to the aquatic representatives that exhibit this phenomenon, it must have arisen independently during their aquatic existence.

Holmes (13, p. 163) gives the following interpretation of the death feint in Ranatra: " In fact Ranatra very seldom leaves the water of its own accord on account of any sort of inducement, and one is therefore strongly inclined to believe that the death feint which is manifested only when the insect is in the air is rather an incidental result of certain physiological peculiarities of the organism than an instinct which has been built up by natural selection for the benefit of the species."

Is there any reason for believing that the instinct of feigning death could have been developed during the aquatic existence among other Arthropods that are not insects? Andrews (1, p. 172) in his work upon the breeding habits of the crayfish, Cambarus affinis, observed that during sexual union the female feigns death while in the water. "During the whole process of union, the male is in a state of excitement while the female is quite the reverse as far as could be judged. The action of the male in turning and adjusting the female is greatly assisted by the state of passivity simulating death that overtakes her soon after being seized by the male. This inertia of the female extends even to the respiratory movements, which seem absent in strong contrast to the condition in the male." Andrews (1, p. 179) furthermore found that the female crayfish shortly after egg-laying lies motionless upon her back with the limbs stiffly extended and seems dead unless the strongly bent abdomen suggests muscular contraction. Holmes (9, p. 288–292) noticed in a number of amphipods that the female, as soon as it is seized by the male, curls up, her thoracic legs are drawn up and the abdomen is held strongly flexed; the whole body in short assumes as compact a form as possible. The female, while being carried about, keeps remarkably impassive. "Males which were mutilated so that they could not resist seizure were carried about as if they were members of the other sex. The mutilated males were more active than the females are under the same conditions, and did not assume the bodily attitude, * * * ." In Cyclops, Holmes (10, p. 315) again finds that "the females tend to remain quiet in a condition somewhat resembling the death feint while being seized by the males." Among these Crustacea, the death feint of the females in the water may possibly be a sexual modification which has been secondarily acquired.

Among the aquatic Hemiptera, the death feint may have arisen out of positively thigmotactic propensities which are manifested to such a marked degree by various members of the families Belostomidae and Nepidae. In a previous paper,[1] attention has already been called to the fact that Belostoma and Nepa as well as other closely related aquatic Hemiptera cluster together to form groups whenever possible, which is probably a manifestation of their positively thigmotatic response. Belos-

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[1] Journ. N. Y. Ent. Soc. XIX., No. 2, pp. 99–108.

toma will crawl, whenever possible, beneath aquatic plants or other objects and will then often assume that death-feigning attitude in which the legs are folded against the ventral surface of the body (fig. 1). Specimens, which had cuddled within thick masses of Elodea or Ceratophyllum, often required a considerable amount of shaking to bring them out of their inert state. Nepa can be caused to feign while in water by a mere contact stimulus.

One would be inclined to believe that successive death feints in the water would interfere with the respiration of those insects which come to the surface to breathe, and one would naturally expect, as our results show in the case of Belostoma and Nepa, that there be a marked decrease in the duration of the death feint when these insects are caused to feign in the water. As already mentioned, Nepas were made to feign again and again before they were permitted to reach the surface film with their breathing tube, but all efforts to put these insects into the death feint, without allowing them first to reach the surface of the water with the breathing tube failed. If these specimens were permitted to take in air, however, they could very readily be put into the death feint again.

IX. THE PSYCHIC ASPECT OF THE DEATH FEINT.

There is a lack of evidence obtained through experimental methods to show that the higher vertebrated animals feign death as a result of conscious reflection in order to deceive their enemies. Verworn has observed that many of the higher animals are keenly aware of visual, auditory and olfactory stimulations while they are in the so-called hypnotic state. In the case of the hen, he (27, p. 44) writes, "Dagegen habe ich mich bei Hühnern ganz deutlich davon überzeugen können, dass sie durch schwache Wendungen des Halses und Kopfes meine Bewegungen verfolgten, besonders, wenn ich hinter sie trat, so dass sie, um deutlicher zu sehen, den Kopf immer nach der Seite meiner Bewegung etwas umdrehen mussten. - - - - Es ist also zweifellos, das die Thiere alle Vorgänge, die in ihren Gesichtskreis fallen, mit grosser Aufmerksamkeit verfolgen und dass der Gesichtssinn durchaus in wachen Zustande ist." According to Holmes (14, pp. 184–5) death-feigning, "is doubtless associated in birds and especially mammals with a tolerably acute consciousness of the situation. It involves a more or less deliberate intention to profit by the deception, yet at the same time it is probably not a result of conscious reflection. There can be little doubt that a fox which slowly opens its eyes and warily looks around is acting with an intelligent appreciation of his predicament, but it is not to be inferred that he could have reasoned out his course of action did not an innate proclivity in that direction form a part of his instinctive make-up."

While it is possible that among the higher animals which sometimes feign death, there may be an attempt to deceive their enemies, it is probable that among the lower animals there is no room for such a supposition. The death feint in the Arthropods is simply a non-intelligent instinctive act. Fabre (6, pp. 17–18), in his experiments with a Carabid beetle, determined that his presence had no effect upon the duration of the death feint. "Elle affirme, de façon expresse, que l'attitude mortuaire n'est pas une supercherie de l'insecte en danger. Ici rien n'intimide l'animal. Autour de liu tout est silence, isolemênt, repose. S'il persiste dans son immobilité, ce ne saurait être maintenant pour duper un ennemi. A n'en pas douter, autre chose est en jeu."

Herrera,[1] believing as other naturalists that the simulation of death is a voluntary act, endeavored to ascertain if the animal possessed a notion of time, or knew the duration of the time of its feint. From his work on a small insect, Thaptor oblongus, he concludes that the duration of the death feint does not depend upon external conditions, but upon the volition of the animal.

Holmes (12) and Robertson (23) have shown that the death feint of some insects and spiders is not entirely dependent on the brain. It is evident from our work that external conditions do play an important rôle in the duration of the death feint.

IX. SUMMARY.

The principal points that we have attempted to bring out in this paper are:

1. Belostoma flumineum assumes two characteristic death-feigning attitudes, both of which are quite different from those

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[1] Memorias de la Sociedad cientifica Antonia Alzato, Mexico, 3–4 (1892). Paper not accessible; translated from Mancini's (18) paper.

of naturally dead specimens. There is no characteristic position which Nepa assumes while simulating death, the attitude taken depending mainly upon the position of the legs just previous to the death feint. In Nepa it is sometimes impossible to distinguish with the eye alone, a death-feigning specimen from one that is really dead.

2. While in the death feint, these aquatic bugs labor under an extreme muscular tension. A feigning Nepa may be taken by any tibia or femur and held in a position so that the weight of the entire body is born by the extensor muscle of a single segment of but one leg.

3. One of the most remarkable peculiarities of the death feint in Nepa is the fact that it can be severely mutilated or dismembered without showing any apparent symptom of pain. In Belostoma, however, severe mutilations can not be performed without the specimen coming out of the death feint and making violent efforts to escape.

4. The first problem which we attempted to solve was to determine how long successive death feints could be continued. After one lot of Belostomas were put into thirty-eight death feints on an average, they refused to feign. These specimens could again be induced to feign death after placing them in water a few minutes. This was repeated again and again until finally the insects refused to feign longer, even after being immersed in water. The average time that all of the Belostomas feigned throughout all the series of successive death feints was eight hours. The average duration of the first series of successive death feints was five hours, thus making an increase of three hours which the specimens feigned after being immersed in water whenever they refused to assume the inert state. Similar results were obtained with Nepa.

5. The previous experiment suggested a number of problems: (1) Why the reactions towards the end of this experiment should be weaker; (2) why the duration of the death feint diminishes with successive trials, and (3) the cause of the cessation of the feint in each series of successive death feints. From our experiments on the effect of dryness on the death feint, the explanation of these problems cannot wholly be attributed to fatigue, but must be ascribed, in part at least, to the drying of the body when exposed to the atmosphere.

6. Dryness decreases and moisture increases the duration of the death feint in Belostoma.

7. The duration of the death feint diminishes when Belostoma is placed upon the surface film or below the surface of the water.

8. The duration of the death feint diminishes when Belostoma and Nepa are exposed to a high temperature of the atmosphere. The death feint decreases in Belostoma, but increases in Nepa when these insects are caused to feign at a low temperature of the atmosphere. In Belostoma, the death feint diminishes when the transition occurs from water at a low temperature to the temperature of the atmosphere lower than 12° C. The duration of the death feint decreases when Belostoma and Nepa are taken from water at a high temperature and exposed to a low temperature of the atmosphere.

9. The death feint diminishes when Belostoma is exposed to sunlight. In order to determine the direct effect of light alone on the death feint, an artificial light was used. It was found that Belostoma and Nepa are aroused more quickly under a bright than under a much dimmer light, and under a swaying light than under a stationary light. Previous subjection to darkness, and a sudden transfer into a bright light decreases the duration of the death feint in Nepa considerably.

10. Decapitation of a feigning Belostoma usually brings the water-bug out of the death feint. Although the majority of specimens with the supra-oesophageal ganglion removed could be induced to assume the death-feigning posture, still that extreme muscular tension under which the intact insect labors while in the death feint was very much weakened and of short duration and often even entirely absent. With those decapitated Belostomas that assumed the death-feigning attitude, a weakened tetanic condition of the muscles could be induced by gently stroking the abdomen with a camel's hair brush, but the instant the stroking ended the legs would sprawl apart and become lax. One is inclined to believe that the death-feigning attitude is induced by the usual method of handling the insect while eliciting the death feint and that the weak contraction of the leg muscles is a reflex in response to a contact stimulus, rather than that the tetanic condition was brought about through a death feint. It may be possible, however, that there is a marked diminution of the death feint due "to the heightened irritability which

normally follows when the inhibiting influence of the supra-oesophageal ganglion is no longer exerted;" and the very much weaker response may possibly be due to the loss of blood which had oozed out from the wound after decapitation had taken place.

With Nepa, decapitation always resulted in the immediate loss of the muscular rigidity. While the legs of some of these decapitated specimens would become rigid when the insects were stimulated with a camel's hair brush, still this condition, like that in Belostoma, was only of short duration.

11. When the body of Belostoma is cut in two between the prothorax and mesothorax, both parts usually continued to feign death. The part posterior to the cut often remained in the death-feigning attitude for a considerable length of time after the operation. After the severed posterior portions come out of the inert condition, many cannot be induced to assume the usual death-feigning attitude; others will assume the death-feigning position, and when the abdomen is stroked with a camel's hair brush, the legs show evidence of a weak tetanic condition of but short duration which may in a very small per cent. of cases be maintained longer than one-half minute. It seems probable, that in some individuals at least, the shock effect may perhaps cause a renewed tetanic condition of the leg muscles, which condition may last for a considerable length of time after the cut was made. With the exception of the behavior shown immediately after severing the body, the reactions of the severed posterior portion of the body of Belostoma is somewhat similar to that of the decapitated individual.

If the body of Nepa is severed between the first two thoracic segments, the part anterior to the cut will react very similar to the intact specimen, while the posterior portion behaves like decapitated individuals.

12. When Nepa is cut across the metathorax behind the last ganglion, the severed posterior part does not respond to any sort of a stimulus; the anterior portion, on the other hand, again reacts similar to the intact bugs.

We are indebted to Prof. S. J. Holmes for many valuable suggestions in this work and for the constant use of literature borrowed from his library.

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EXPLANATION OF PLATE I.

Fig. 1. Ventral view of a feigning Belostoma flumineum with the legs folded against the ventral surface of the body.

Fig. 2. Side view of a feigning Belostoma with the legs held in the usual characteristic death-feigning attitude.

Fig. 3. Dorsal view of a Belostoma, feigning with the legs folded against the ventral surface of the body; in this view but little more than the femero-tibial joints are visible.

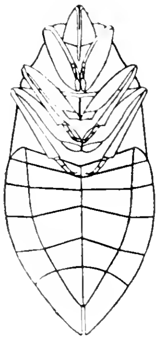
Figs. 4 and 5. Ventral views of Belostomas that have died a natural death, showing that no definite nor constant positions of the legs are assumed.

Fig. 6. A dying Belostoma showing the drooping of the abdomen. *s*, strap-like appendages which are retractile and usually withdrawn from sight in the living specimen.

Fig. 7. General features of the nervous system of Belostoma. *in*, infraoesophageal and first thoracic ganglia fused.

PLATE I

1



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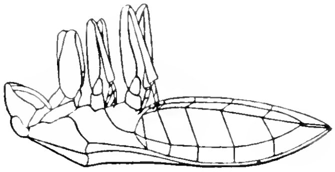

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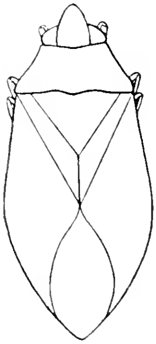

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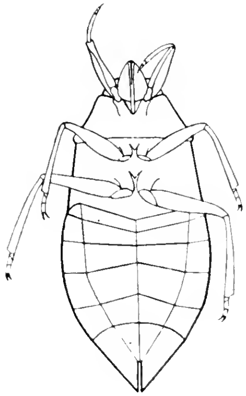

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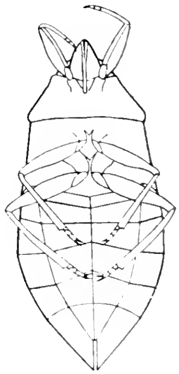

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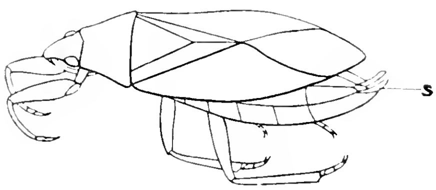

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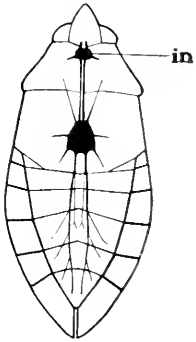

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In Preparation

The Biology of Physa. By Jean Dawson.

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Volume 1, Number 4, 1911 Serial Number 4

Edited by JOHN B. WATSON
The Johns Hopkins University

The Biology of Physa

JEAN DAWSON

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The Biology of Physa

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Department of Biology, Normal Training School, Cleveland, Ohio

TEN FIGURES

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CONTENTS

THE BIOLOGY OF PHYSA.

The present work is an attempt to study one of the lower animals, the common pond snail, in the field and laboratory by both observational and experimental methods. The work is divided into the following parts all of which are interdependent: I. The relation of *Physa* to its natural environment, II. Mucus and Mucous Threads, III. Food and food activities, IV. Respiration of *Physa*, and V. Some psychic phenomena of *Physa*.

The work was begun at the University of Michigan and was completed at Clark University. Grateful acknowledgments are due to the following people for assistance: Professor Jacob Reighard for general supervision of the work, Dr. Charles C. Adams for supervision and for liberal aid in the preparation of part I, "The relation of *Physa* to its natural environment," Professors H. S. Jennings and C. F. Hodge for invaluable suggestions in the final preparation of the manuscript, and Mr. Bryant Walker for the identification of the snails.

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V. General Summary and Discussion.

I. Introduction.

The following ecological study of the snail, *Physa*, was made principally in the region of Ann Arbor, Michigan. A large number of streams and bodies of water were examined and the following species were studied: *Physa gyrina* Say, *Physa gyrina hildrethiana* Lea, *Physa anatina* Lea, *Physa ancillaria* Say, *Physa heterostropha* Say, *Physa elliptica* Lea, *Physa sayii* Tap. and *Physa integra* Hald. Wherever living snails were found, special attention was given to the conditions in order to analyse the stimuli to which they continually react.

II. Local Distribution.

No attempt was made to determine the distribution of *Physa* in a geographical sense. Their occurrence in local bodies of water is all that was sought.

The dispersal of snails in bodies of water which have currents and waves is relatively simple when one considers that not only the parent snail itself, but its eggs, attached in masses to weeds and other floating bodies, may be easily transported. Thus the distribution in many lakes, and in river systems, may be readily understood, but the manner of dispersal in certain small isolated bodies of water, by such agents as man, animals and floods alone is in many cases not entirely clear. Further search shows that frequently an explanation may be found in a study of the origin and history of the small bodies of water themselves. A study of the physical processes which influence lakes and rivers shows that these systems are undergoing continual changes, some of which lead to the formation of small bodies of water which become cut off and isolated from the parent body, or in other cases the lakes themselves may gradually grow smaller and smaller until they become ponds.

In some cases before these ponds cease to be identified with the parent waters, they may contain much animal life in common which subsequently either dies or lives on in more or less abundance, as the resulting environment decrees. While we may account for the presence or absence of the snail in different waters by these means yet they do not give us a clue as to why the animal is found in one part of a given body of water rather than in another.

Preference for a definite habitat is one of the most important phenomena in the local distribution of an animal. This definite tendency was continually met with in the field work on *Physa*. It is well illustrated by the occurrence of the snail in a certain tamarack swamp whose invertebrate life was studied in detail. This swamp, which lies south of Kavanaugh Lake in Washtenaw county, Mich., is a lake basin, formerly of greater extent, and is surrounded by morainic hills. Only a relatively small portion of its 300 acres is covered with tamarack trees. There are two small ponds in one section of the swamp, which have several streamlets and one large ditch draining into them. A large ditch drains both, as there is still a slight connection between them.

Numerous ditches and streamlets occur in the swamp and serve to lower the water level so that standing water is found only in the deeper holes and small pockets, which occur in less than one-half of the entire swamp area. This swamp is a good locality for the study of local distribution because it has many conditions common throughout its extent. It has a surface substratum of peat, and since flooding took place during spring freshets before the ditches were dug and also since that time, the question of opportunity for dispersal may be eliminated. If *Physa* is not found in certain spots in the swamp where there is water the year round, it is probable that this is not because it was unable to reach these places. The accompanying diagram, Fig. 1, shows the standing water in the swamp. The places where *Physa* is found are dotted and its relative abundance is shown by the number of dots.

A glance at the diagram will show that *Physa* is abundant in some waters and absent in others. The question therefore is, Why this kind of distribution and what conditions determine it?

Before giving in detail the observations made upon *Physa* in the different bodies of water, I wish to set forth briefly the main objects and methods of the work. They are two, as follows:

1. To determine the combination of conditions which make the normal abode of *Physa*.
2. After obtaining these combinations, to determine the causes which modify them.

The first named object involves the following steps:

(a) A study of the gross environment (lake and river systems) to determine the general conditions under which *Physa* lives.

(b) An analysis of the conditions prevailing in each locality occupied by the snails in order to determine the elements making up the habitats.

(c) A comparative study of the habitats and the determination of the most favorable conditions for snails.

It is evident that in comparing one habitat with another, there must be some standard of comparison. I have therefore taken in each body of water the habitat that yields the greatest number of snails, and have called this the "optimum" for that water, and have compared it with the other habitats having a less number of snails. In general the relative suitability of a snail habitat may be estimated by the number found flourishing in it. In a body of water where the agents of dispersal are constantly at work, one can have but little doubt that the snail and its eggs will be thoroughly dispersed throughout its extent. Whenever snails occur in very favorable conditions they multiply and flourish in great numbers. Less favorable conditions produce of necessity a fewer number of snails; and in some places these conditions are so unfavorable that the snails perish, and thus fail to propagate their race. It is largely due to the fact that a single body of water offers such a variety of conditions, that we usually find a discontinuous distribution of snail life in it.

The second object may be more fully indicated as follows: After once establishing the elements making up a *Physa* habitat, it is desirable to study the causes which are continually modifying these conditions and producing changes which make for or against the optimum conditions for the snail. These changes are caused by both natural and artificial means. The natural changes affecting the given elements in a stated place may be well predicted within a certain limit, but the artificial ones are more difficult to anticipate.

III. The Brook-Creek-River System as a Habitat.

The relation which the snail bears to the river system may be better understood, perhaps, if the river habitats are studied in the order of succession found in passing from the headwaters down stream. By this method the description of the conditions is greatly simplified and emphasis may be placed upon the relative influence of the dominant forces which change the environment. No effort is made to describe any given river from its source to its outlet, but rather to discuss in general the various situations in which *Physa* occurs in the definite order which the snail presents in going from the source toward the mouth of a river.

1. *Springs and Brooks.* Active springs and small brooks resulting from them do not seem to be promising waters for *Physa*. They throw light upon the problem at hand only through the absence of *Physa* in them. I have examined many hillside springs and brooks about Ann Arbor as well as those in other parts of the state, and I have seen *Physa* in such waters but once. This was in a box sunk in the ground on the banks of Chelsea Pond near Chelsea, Mich. Here, apparently feeding upon algae, was found *Physa gyrina hildrethiana* Lea.

a. *Brooks.* The absence of snails from springs and from such brooks as do not become creeks is probably due to their isolation. The absence of *Physa* from springs is well illustrated by one which was found flowing down the side of a steep clay bluff of Lake Michigan at Frankfort. The water flows from an upper stratum of the bluff, but is lost before reaching the lake. In no case was *Physa* found in such waters and indeed it is difficult to see how snails could be carried there. The absence of the snail from brooks is illustrated by those flowing down the morainic hills of Crystal Lake near Frankfort, Mich. One of these rushes down a steep hillside fully 90 feet above the level of the lake and on account of the swiftness of the current, there is little opportunity for the snail to become dispersed into these waters from the pools and shallow waters of the lake below.

b. *Brook-ditches as Habitats.* With the tiny brook may be placed the brook-ditch. By a brook-ditch is meant a stream that has had its bed artificially lowered. Its course is fairly straight and its banks steep, presenting uniform conditions on both sides of the stream. The ditch depends largely upon surface drainage for water and in consequence varies greatly in depth and swiftness of current during the year.

Kavanaugh swamp has many of these ditches presenting habitats that vary widely, as a glance at the preceding diagram, Fig. 1, will show. Brook X follows the road which runs north and south on the east side of the swamp and represents the optimum for that region, Fig. 2. It rises on the border of the moraine, seen in the distance, and flows north to where it joins the large ditch draining the lake. The bottom of the ditch is covered with soft, decaying debris, over which algae and *Chara* grow in thick masses. Above these water plants, flows water from two to three inches in depth, with some current in the spring and during heavy rains, but rather sluggishly at other times. The snails live upon this mass of plants which is growing over a bed of organic debris. This habitat was very well stocked with *Physa gyrina* in the spring months, but during the dry fall it was examined again, and the snails had greatly decreased in number. Many were found dead.

Another brook-ditch arises on the north edge of the swamp and flows toward the south to empty into the lake ditch just described. This presents conditions almost like the optimum except that there is very little water over the plants and the current is always feeble. *Physa gyrina* is not abundant in this habitat except near the mouth where it empties into the swiftly flowing lake ditch. (Fig. 2.)

The remaining ditches of this swamp contain a less number of snails on the average than does the optimum and present somewhat different features which are as follows: There is usually less than one-half the number of plants and the current is perhaps twice as strong as that found in the optimum habitat. Instead of decaying vegetation there is a clean substratum of peat. The temperature of the water varies in different parts of the brook-ditch, due perhaps to springs bubbling up through the peat; at least water is seen to bubble from the ground and is two or three degrees colder than the surrounding water. The snails gather in greater numbers in the warmer pools; and there is practically no shade.

2. *Creeks*. No attempt is made to describe as a whole the creeks examined, and, in general, account is taken only of such portions of their waters as contain *Physa*. Comparison is also made with other regions of very similar appearance, but which lack *Physa* in order to learn if possible what disturbing element or elements have modified the normal environment. *Physa*

has a general but not a uniform occurrence in the creeks examined. To this statement the objection may be raised that the snail may be found in these habitats at one season but not at another, or during one year and not another, so that a description of the present habitats leads to nothing. Moreover it may be said that natural and artificial changes are going on continually and the snail is bound to become dispersed or destroyed, as the old habitats disappear and new ones arise through these modifying agencies. However, the question which I wish to discuss is primarily whether there is a combination of like physical elements which are met with in every flourishing normal habitat and if so in what way these elements are changed by natural causation.

a. *Creek Bed Habitat.* For convenience, I shall describe the optimum creek habitat first, and follow with those of less importance.

The small creek in question lies northeast of Ann Arbor along the Toledo & Ann Arbor R. R. track, on the edge of the city. It rises a few miles north of the city and flows into the Huron river near the City Park. This creek meanders for a distance through its flood plain, cutting from the concave and building up on the convex side. At times it carries a load of silt or deposits it in some quiet pool, and again sorts gravel and stones and leaves them in heaps in its bed. In Fig. 3, is shown a load of stone deposited and it is here that the optimum *Physa* habitat occurs in this stream. The bank on the left side of the picture is very gently sloping while that on the right side is somewhat steep. The stones cover the bottom at this point and the water flows quite rapidly over them. No large water plants grow above or below this immediate spot, but *Cladophora* grows in abundance upon the submerged stones, in felt-like masses. The *Cladophora* shows a well marked correlation in size and abundance to the velocity of the stream. Wherever the current strikes with full force upon the stones, the plants are short, but on the sheltered sides they grow more heavy and abundant. The stones are placed in such relation to each other that one or more of the faces of each is protected. Many of them are so placed that they also protect the bottom of the creek which lies between them. The current strikes the first stone squarely and breaks over its top and in turn strikes the successive stones in its path in a similar manner. The protection given by these stones to the stream bottom depends upon the size of the stones and the distance between them.

Feeding upon the *Cladophora* and crawling upon the gravel on the bottom of this creek are myriads of *Physa gyrina;* hundreds of these snails can be picked up in the space of a few feet. At first sight they seem to be crawling without regard to the swift current, but upon closer examination they are found to be living on the sheltered sides of the stones and on the sheltered creek bottom. In general the number of snails corresponds with the density of the growth of the plant on the stones. The thickly massed *Cladophora* is crowded with snails, while the shorter and less crowded plants have correspondingly fewer snails.

The conditions of this habitat are: (a) a gently sloping shore and shallow water throughout (a slope of about 1 inch to the foot); (b) running water, well aerated and having no decaying vegetable debris; (c) protection from the current by stones; (d) a growth of *Cladophora*, which furnishes abundant food; (e) no growth of large pond weeds such as *Chara* and *Ceratophyllum;* (f) full sunlight; (g) a stable substratum.

Above this optimum habitat, and opposite to the two trees on the bank in Fig. 3, is a place that is somewhat similar to the optimum just described but which differs from it, in that its banks are steeper and its bed narrower. In consequence the water is deeper and the current swifter. A small number of snails are found feeding upon *Cladophora*, on the more protected sides of the stones, but more are living on the long grass which trails into the water from the creek banks. Other instances of the snail living in the creek bed, and apparently braving the current, are found in this region of the creek. For instance, where an old shoe or tin can lies near the shore in the shallow water specimens of *Physa gyrina* are found living on their protected sides.

Considerable time was spent in examining this creek in detail, but it did not furnish another favorable creek bed habitat. For the greater part of its length, the creek has cut a wide, deep bed in which it flows less swiftly than at the optimum previously described. In a few cases, however, it presents areas whose physical condition greatly resembles the optimum, but upon closer examination it was found that there were additional factors, which in all probability caused their barrenness. The following illustrations will serve to show these influences: On the north side of Detroit avenue, Ann Arbor, Mich., where the creek crosses the street, the stream presents conditions almost exactly like those of the optimum; there is the shallow water with stones and *Cladophora* showing the same relation to each other and the current, but there are no snails to take advantage of their shelter and food. The presence of a flock of ducks which frequent this section of the creek may perhaps explain the absence of the snails at this place. The problem of snail enemies is one to which no special study was given, but it was observed that where fish, ducks, and crayfish abound in the creek, snails are either absent or very few in number.

In Fig. 4 is represented another place in the creek bottom where one would naturally look for snails, but here it is seen upon closer inspection that a layer of silt covers the stones and bed. There are no pond weeds growing here except a few opposite the basket, shown on the right bank in Fig. 4. These are in a little pool of quiet water, where the only *Physa* in this region are found. The stones are covered with a thick, soft mass of silt, which at a glance resembles *Cladophora*, but upon examination proves to be a fine, muddy deposit. None of this deposit is found beyond a deep pool in the creek which lies in the stream between Fig. 4 and Fig. 3. The location of the pool may be seen in Fig. 3 near the fence. The bottom of this pool is covered with a deposit of silt and it is concluded that the mud which the stream was carrying above this point had settled when the flowing water entered the deeper quiet pool. A small amount of algae grows about its edges and upon it are living a few adult *Physa*. It was not determined why *Physa* is not found in the region shown in Fig. 4, unless it is on account of the absence of food, or perhaps it is more probable that the snail has been unable to gain a foothold in the current of water; however, it might also be due to the mode of respiration of the snail. A pulmonate snail like *Physa* whose lung is full of air has a specific gravity much less than the water so the only way it can descend into the water is by adhering to the substratum by means of its foot. In consequence of its lightness the snail exerts a pull upon the substratum, which, if it is not very coherent, yields and the snail is buoyed to the surface of the water. If this happens in a creek with a swift current, the animal is carried down the stream on the surface of the water, or if it expels the air from its lung, as it often does when unexpectedly pushed upward, it sinks to the bottom of the creek bed and is rolled along by the current. An examination of the diagram of Kavanaugh swamp, Fig. 1, will show the lower part of Creek F and the large ditches leading into, and the one leading out of the lake are practically devoid of *Physa gyrina*. In all three the water is flowing swiftly (faster than in the other streams of the swamp) over coarse peat which is so unstable that it does not offer a sufficiently firm substratum for the snails to maintain a foothold.

b. *Shallow Eddies as a Habitat.* In the background of Fig. 5, the stream may be seen to spread out; where the banks on both sides are low, into a shallow eddy-pool, near the middle of which the stream divides into two unequal parts. The larger, swifter part flows to the right in the picture, while the gently flowing water of the left division passes around through the pool to meet and be carried on by the swifter stream as it flows again into the deeper channel. In the relatively quiet waters a quantity of algae grows and furnishes food for the abundant snail population of the pool. On the sides of the creek is found an occasional small quiet pool containing *Physa* here and there, except where the fish are abundant or where a great many pond weeds grow. A large shallow pool, well grown over with *Chara* and *Ceratophyllum*, was found in the creek east of Lima Center, Mich., and contained a moderate number of *Physa anatina* Lea.

Physa is found in creeks in five other habitats which deserve mention for reasons other than the number of snails found in them. They are as follows:

1. Where a stream is not building up its convex bank too rapidly a small number of *Physa* are found in company with some pond weeds. The creek on the west side of Lima Center, Mich., is an example of this sort.

2. In deep pools (where fish and other enemies are not too abundant), the long grasses bend over into the moving water and to them cling small *Physa*. The noticeable fact about

this is that the snails are all young. This condition is found in a creek which drains Steere's Swamp, in Honey Creek, about five miles west of Ann Arbor, and also in the Railroad Creek.

3. Occasionally in the bottom of Honey Creek there are found small banks of *Elodea* over which flow, about twelve or eighteen inches of quite rapid water. Upon these banks live a small number of small young *Physa gyrina hildrethiana*.

4. In the background of Fig. 3 is a portion of a deserted creek channel, and where this joins the present stream bed, there is back water from the creek for a distance of 8 to 10 feet. Here *Chara* and *Spirogyra* grow in abundance. The water stands five to eight inches above the water weeds where it joins the creek, but a few rods back there is less and less water until the weeds project through its surface. Snails are found in this habitat in numbers except where there is but little water above the mass of weeds.

5. A creek on the west side of Lima Center furnishes a good example of an ox-bow pool habitat, Fig. 6. This habitat is becoming captured by water weeds. Solid masses of weeds grow in patches here and there, and in these masses no snails are found, but in the less obstructed portions *Physa gyrina*, *Physa anatina* Lea, and *Lymnaea palustris* are found in about equal abundance.

3. *River as a Habitat.* The Huron, the largest stream at Ann Arbor, was studied in detail. It is relatively small, being about 150 feet in width and two to six feet in depth above the dam at Ann Arbor. Its flood plain is bounded on both sides for miles along its course by high hills. Above Ypsilanti the river meanders from side to side forming bayous and ox-bow ponds. It is actively cutting and carries a load of silt. The boulders and heaps of coarse gravel deposited here and there in its bed tell of greater work during the spring freshets when it floods its banks and flows swiftly at twice its normal width. In waters like this, *Physa* must be well dispersed, yet the only place I found it living or dead was among some water weeds in the slack water above a dam. These snails were all young and were living upon the weeds and not upon the bottom. The following are examples of habitats found in waters cut off from the river.

1. The Huron river above Ypsilanti offers an example of a

deserted river bed habitat, but it is in a late stage of filling and contains many water weeds and few *Physa*.

2. At Geddes, Michigan, the Huron river has overflowed several acres of flat country, much of which remains under water the year around, a general view of which is shown in Fig. 7. This "overflow" was examined for *Physa*, but the snail was found only in the small ponds which had little or no direct communication with the river. Here *Physa* were crawling upon a mass of *Ceratophyllum* covered by about a foot of water. The peculiar feature of this habitat is that the snails are not restricted to a few inches around the margin of the pond, but extend six feet or more out from shore. They evidently use the water plants as a substratum as they are not found beneath them. The result is as though the snail lived in a very shallow pond of but a few inches in depth. With the exception of a few such rather isolated ponds this overflow is practically barren of snails. Few water weeds grow anywhere where the water is directly connected with the river and everything indicates the presence of the muddy load of the river.

3. West of the mill race at Ann Arbor, in the spring flood of the river some pools were left which became completely captured by *Chara*, *Ceratophyllum*, and *Elodea*. Very few *Physa* are found in them and these are very small and young.

4. *Discussion of the River System as a Habitat.* The river system does not offer very favorable conditions to *Physa* in spite of the fact that the little Railroad Creek east of Ann Arbor has very favorable conditions in some parts. The conclusion is reached, however, that such a combination of conditions as is seen in this particular habitat is very rare. The apparently favorable physical conditions found in streams are frequently seen but usually they are found in combination with others which tend to exclude *Physa* from the locality. The physical conditions found in the optimum itself are subject to change, which will undoubtedly sooner or later (judging from the places already cited having like conditions), cause a scarcity of *Physa* in the region that is now so very favorable for them. Thus the removal of the stones from the creek bed would cause this region to offer no shelter from the current and it would become like the region above and immediately

below this part of the creek, devoid of snails. The stones might be removed by man or by the stream and redeposited farther down its course during the spring floods. The deep pool lying above the optimum habitat, Fig. 3, might also become filled up so that the silt could no longer be deposited in its quiet depths and in consequence the silt from up stream would be carried past such a habitat. When such a deposition of silt occurs over a region it will then show similar physical conditions to those found in Fig. 4. Just what would be the result of a silt deposit upon the habitat where *Cladophora* has so strong a foothold would be difficult to say. It does not seem probable that under ordinary circumstances the stream would be carrying enough silt to kill the plant, but during the heavy rains the stream might carry a load sufficient to scour the stones and thus dislodge or kill the plant. This might furnish a possible explanation of why *Cladophora* is found in the region of Fig. 3, and not in that shown in Fig. 4.

It is interesting to note in connection with this so-called creek-bed optimum that Baker (1901 p. 660) cites conditions very similar in the Genesee river.

"Below the dam, which is now broken and very much out of repair, the river flows rapidly over a rocky bed, in many places the water being so shallow that persons can wade across. The right bank is very rocky, more so than the left, and forms little sheltered bays here and there, in which *Goniobasis* and *Physa* live by thousands, the former making a veritable pavement in some places."

He goes on further to say that near the railroad bridge where the water becomes deeper, the number of *Physa* decreases in number and that in deeper water still they disappear altogether. He cites another place in the river as follows: "The walls are very steep and stony, the river having cut away the soft shale, leaving great projecting ledges. *Physa*, *Planorbis* and *Lymnaea* are here notably abundant, living on ledges of rocks where the water is a few inches deep."

As was mentioned above, *Physa* was not found in the Huron river either in the vicinity of Ann Arbor or Ypsilanti except a few young ones found living upon water weeds in slack water. It was thought, perhaps, that this scarcity of snails is due to insufficient protection from current, especially during high water, but this alone does not seem to account for their scarcity in shallow protected water such as is found in the overflow at Geddes and the bayous above Ypsilanti. There is no perceptible current in either of these places and still there are found comparatively few water weeds and very few snails. In the bayous and in the backwater or "overflow" where there is direct communication with the river waters, there is a considerable deposit of silt which may probably account for their absence. It is only in the waters that are separated from the river that *Physa* flourishes. It is evident that as the bayou is cut off from the river by the deposition of material across its mouth that its waters will be less and less influenced by the inflow and silt from the river. As the bayou becomes separated from the river, it will take on more and more of the characters of an ox-bow pond (conditions similar to those of Fig. 6) and like it will furnish favorable conditions for *Physa*. When, however, complete isolation takes place, then the conditions are essentially like those of a pond.

Enemies. Cases have been cited above where fish and ducks were thought to prey upon *Physa*. It would seem that an animal that is as fertile as this snail, would in a comparatively short time, be very abundant in all available places in the creeks and rivers unless destroyed by enemies. The following observations upon the enemies of snails bear upon this point: Baker (1895) says: "Ducks, geese, swans and many other kinds of wild fowl are very fond of snails, and I have never failed to find the remains of them in their crops." Again he says: "Various species of fish feed upon snails as a regular diet. After feeding in one spot they repair in schools to some particular spot often many miles distant from the feeding ground where they digest the animals and eject the shells through the mouth or fœces." Tryon (1882) remarks: "The frog and water lizard eat the fresh water snails." . . . . "The species of *Perthostoma*, an American aquatic hemipterous insect, eat large quantities of *Lymnaea*, *Physa* and *Planorbis*, which they hold with the fore-legs by folding between the thighs and tibiae; even the larva of this insect, shortly after escaping from the egg, will seize and devour one of these mollusks with as much ease as if schooled in the process a long time." Needham (1901, p. 405) records the following for Little Clear Creek: "Snails were found in the stomachs of frog and fish, and are known to be the food of horsefly larvae (*Tabanidae*). There are certainly snails enough in the creek to justify the extraordinary abundance of horseflies in this vicinity." Forbes (1888 p. 482) says: "The delicate pond snails (*Succinea*, *Lymnaea*, and *Physa*) were taken chiefly by the smaller mollusk-eating fishes,—a few of them also by the catfishes and the suckers." *Chrysemys marginata* eats *Physa* greedily and there is little doubt that the water birds are formidable enemies.

Attention should be called to the places in the river system where young snails alone were found. It will be recalled that they are found living upon submerged water weeds in the bottom of the creek, long grasses that trailed into the deeper waters of the streams, and upon weeds in slack water in the Huron river. It is thought, perhaps, that either the eggs of the snail or the snail that afterwards laid the eggs, may have been caught in these plants while being transported down stream. It may be, that if they escape their enemies and are not swept away by the current they may live on in this region of the stream, where the conditions are favorable. Judging from the conditions under which the colonies of adult *Physa* are living, it does not seem probable that the present habitat of these young snails will prove at all lasting.

Summing up the conditions that are common to all the most favorable *Physa* habitats of the river system proper we have the following: Shallow, well aerated water; a firm substratum of rocks or weeds, full sunlight; relatively few enemies, the presence of some water plants, such as *Cladophora* or *Ceratophyllum*, and a protection from a strong current.

IV. Lake-Pond-Swamp Series.

1. *Lakes.* Owing to the large number of lakes in the immediate vicinity of Ann Arbor, a much more comprehensive study of them was made than was possible with the river system. These lakes are all of glacial origin, varying greatly in size, shape and in their different stages of extinction. In the present study of lakes it was early learned that *Physa* is found only in the littoral zone, and in consequence the factors which affect shores and shore margins alone will find place. *Physa* was also sought in the shallow marginal waters, beach pools and open

sedge formations of lakes and a study made of the conditions under which it was found living.

No *Physa*, either living or dead, are found in the shallow water along the shores of Lake Michigan at Frankfort, Mich. No visible plant or animal life is found in this shallow disturbed water, and the pebbles and stones are worn smooth by the waves which unceasingly break upon the shore. It is evident that *Physa* could not live in such conditions, as it occurs only in protected places. The lake in the vicinity of Frankfort is bounded by high clay bluffs which the waves are actively cutting; consequently there is a narrow, severely wave swept beach in time of storms. On such a beach there is no chance for the formation of pools or swamps which might harbor *Physa*.

Crystal Lake at Frankfort is cut off from Lake Michigan by a neck of land about one-fourth of a mile wide. This lake is about nine miles long and three miles wide, and is surrounded by high morainic hills. Living *Physa* were sought in vain in the shallow waters along its shores, but some bleached and weather-beaten shells of *Physa ancillaria* Say and *P. heterostropha* Say together with the shells of some other genera of fresh-water mollusks were frequently found scattered in the shallow water, and upon the dry sand of the shore. A diligent search in these waters proved them to be as barren of visible plant and animal life as was the same zone in Lake Michigan. The pebbles are worn and smooth and bespeak the power of the waves that break upon the shore.

a. *The Beach Pool as a Habitat.* The beach of this lake is wider than that of Lake Michigan, just described, and this is due to its water level having been lowered several years ago, by an outlet cut to Lake Michigan through Betsie River. Upon this wide beach are found depressions in the sand filled with ground water and water dashed up from the lake when the sea is high, yet they are far enough from the water's edge to be out of danger from too strong wave action. These pools were well populated with living *Physa ancillaria* Say, *P. heterostropha* Say and other genera of snails. The dead and bleached shells found in the shallow water of the lake and on the dry sand were probably washed from these beach pools in time of severe storm and died upon the sand or were killed by being tossed about by the waves.

The following conditions prevail in this habitat: Shallow water, from five to eight inches deep; full sunlight; a small amount of algae, but enough for food; clear sandy substratum; no vegetable debris; fresh water supply without severe wave action; and an absence of enemies, so far as observed.

Another class of beach pool habitats is furnished by small sedge-filled shores of small bodies of water, such as is found in the pond in Snow's swamp at Kavanaugh Lake. Some pressure was brought to bear upon the spongy shore, causing a depression which the water from the lake quickly filled. Reference to the preceding diagram, Fig. 1, will show the presence of *Physa gyrina* in such a habitat.

b. *Physa Habitat Behind an Ice-Rampart.* Kavanaugh Lake lies in Washtenaw County, Mich., about 22 miles west of Ann Arbor. It is about one mile long and one-fourth of a mile wide and is surrounded by sandy morainic hills, except on the south side which is separated from a tamarack swamp by a low ridge. The lake has a clear sandy bottom and its beach is narrow on the east and north sides. Here the waves are cutting and the shore presents about the same conditions as are found in the lakes above described. The south and west sides, however, furnish two *Physa* habitats which are of interest. The first of these is found on the south side behind an ice-rampart, Fig. 8. This rampart was formed by the pushing or crowding of the ice on the shore during the winter.[1] It extends nearly three-fourths of the distance across the end of the lake and is about 10 to 15 feet in width. It opens to the east and has two gaps in it through which the water from the lake passes freely at all times. During a storm the waves break over the full length of the rampart and the waters flow back into the lake through the gaps and at the open end.

The protected waters behind this rampart furnish a good habitat for *Physa gyrina hildrethiana.* The snails are found in the shallow waters behind the protecting bar. Neither the snails nor the water plants are evenly distributed in these waters. Few plants or snails are found living exposed to the waves that break through the gaps in the rampart, undoubtedly the wave action is too severe. The snails are found in greatest abundance on the shallow shore on both sides of the gaps. This was espe-

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[1] cf. Buckley, Ice Ramparts (1900).

cially noticed in the waters near the free or east end of the rampart. It is in the least disturbed waters, however, that the water plants are growing plentifully, and in some places are fast capturing the waters. *Chara* is found growing luxuriantly in these quiet waters while not a trace of it can be seen along the unprotected shores. It is found, however, growing in considerable abundance in the deeper, quieter waters of the lake.

In this habitat the following conditions prevail: Protection by the rampart from severe wave action; exchange of water with the lake; nearly full sunlight; little or no vegetable debris; clear gravelly substratum; on the average, a medium amount of water plants; shallow water with a gently sloping shore; and no enemies so far as observed.

c. *Open Sedge Formation as a Habitat.* Another habitat occurs on the more protected shores of Kavanaugh Lake. The filling in of this lake and Snow's pond by the natural invasion of sedges, goes on apparently in two somewhat different ways, which are of importance on account of their influence upon the snail's environment. The sedges on the west shore of Kavanaugh Lake are rapidly pushing from the shore into shallow water and, since they grow in isolated clumps there is as yet no severe struggle for the possession of territory. As long as sedges grow in the shallow water this method of sedge invasion is seen, but when the deeper waters are reached, their outward march is checked and then the open space between the clumps begins to fill in with the sedges until fairly solid ground results. Meanwhile the march into the deeper waters of the lake goes on very slowly. Every inch of ground is contested by the mass of sedges growing at the water's edge, as may be seen in the waters of Snow's pond and Doyle's Lake lying one mile east of it. Approaching Kavanaugh Lake from the west moraine, one first reaches the so-called bottom land which not many years ago formed a part of the open lake, but is now solid ground. Upon approaching nearer to the lake upon this newly reclaimed land, it is seen that the water becomes deeper and deeper and the sedges farther and farther apart. One can walk out over the water for a rod or more by stepping from one bunch of sedge to another. The shallow water near shore furnishes a fairly good habitat for *Physa gyrina* and perhaps would be very much more thickly peopled with snails were it not for the fact that this is the region of the lake in which the fish spawn. The water is clear and the substratum is of a fine texture, due to the formation of peat, so that it is not unusual to see the snails crawling upon the submerged roots and stems of the sedges instead of on the more unstable substratum.

The conditions making up this habitat are as follows: Fairly shallow water; unshaded, except by tall sedges; few water weeds (algae and *Riccia*); protected from wave action; fairly free exchange of water from the lake; very oozy substratum and probably numerous enemies.

d. *Habitats Behind Spit and Bar Formations.* Crooked Lake is about one mile west of Kavanaugh Lake and resembles it in size and general setting in that it has the same type of surrounding morainic hills, and gravelly bottom and shores. The chief point of difference between the two lakes is in their shape and in the consequent forces at work modifying their contours. Crooked Lake, in general outline, is not alone crooked, as its name rightly implies, but possesses also many minor irregularities which form small bayous which are being cut off from the main waters by various stages of spit and bar formation.[2] In fact, the general tendency of the lake seems to be that of rounding out its ragged outline. Bars are being formed both by currents and wave; erosion is going on on the north and west shores, and debris is being carried and built into spits and bars upon the south and eastern portions of the lake. The currents fail to conform to the curve of the shore and leap from point to point of land, thus cutting across the small bays. By the deposition from currents at their free ends spits are being extended and this growth goes on until each spit completely cuts off a portion of the lake and allows it to live out the shorter life of a pond or pool. The past work of the lake is shown by several small lagoons which have been cut off from the lake by bars and which now form part of the beach.

The following changes are taking place in the lake which are certain in the future to alter the present shores, and in consequence affect the life in its waters:

1. The north and west shores are being cut away and in consequence will become steeper while the south and east shores are being built out into the water.

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[2] cf. Gilbert, The Topographic Features of Lake Shores (1885).

2. On the south and narrower portion of the lake, bars are being built parallel to the shore.
3. The southwest shore is filling in by an invasion of the sedges.
4. Spits are closing off small bays on the east shore.
5. Bars just beginning to be formed tangential to the shore in several places on the east side of the lake, are marked by a growth of bulrushes.
6. Partially formed bars are gradually elongating and will soon reach the opposite point of the shore.
7. A spit is being formed from a small island in the center of the lake to the shore which will connect the island with the mainland.

Physa was sought in the open shore water, behind the different spit and bar formations, and in the waters that were wholly cut off from the lake. A very characteristic distribution of the snail was found in the different habitats which varied with the dominance of certain physical elements occurring there. The optimum habitat (Fig. 9) was found behind a spit some 20 to 30 feet off shore, which ran tangential to the southeastern shore of the lake. The spit is being built on its free end and in the near future will join the opposite shore. The snails are not at all evenly distributed even in this narrow strip of water, although it is so nearly enclosed by the spit. *Physa heterostropha* Say, and *Lymnaea desidiosa* Say are found by hundreds in this optimum habitat, for a distance of about 15 feet along the shore and about four to six feet back from the water's edge. In Fig. 9 this locality is shown opposite to the small white square near the center of the foreground. This clearly defined area is situated far enough back from the open end of the spit to be beyond the reach of severe wave action, and yet near enough to allow a free exchange of well aerated lake water. In point of numbers it supports a remarkable snail life. Loose soil has washed into this habitat from the neighboring ploughed field in such quantities as to fill in the shelving shore and to kill the plant life except for a moderate growth of *Chara* and algae. Numbers of both *Physa heterostropha* and *L. desidiosa* are crawling in this habitat in waters some of which are so shallow that the snails are not wholly immersed.

The number of snails behind this spit diminished from this thickly peopled optimum in the following manner: The number of snails decreased quite abruptly at the open end of the spit to the right of the optimum (Fig. 9), and also on the side toward the deeper water, but at a more gradual rate at the closed end of the spit. This gradual decrease of snails is accompanied by an increase of water plants and decaying debris which at this point have lodged in the quiet and undisturbed waters behind the spit. The amount of this debris has been greatly increased by the fallen leaves of willows and button bushes which border this part of the water.

The distribution of snails near the open end of the bar where protection from the current and well aerated water are at once secured, accords with the distribution of snails behind the ice-rampart formed at Kavanaugh Lake, as above described. The bar habitat has but one gap while the ice-rampart has several corresponding to the one of the spit through which the water from the lake has free access.

Analysis of the elements making up the optimum spit and the bar habitat: Gently sloping shore; an unusual amount of shallow water from the lake; protection from the severe sweep of the waves; comparatively few water weeds; unshaded; very little decaying debris; and no fish or other enemies so far as observed.

The conditions elsewhere in this lake are as follows: In waters wholly cut off by bars from the lake and where many water plants and deciduous leaves make the waters foul, there is little or no snail life found. Thus in one spit-formed pool the water is so laden with deciduous leaves that they had buried all the water plants except a small amount of *Hypnum*. This spit is curved and was doubtless formed by alternating currents which turn its point landward, making a hook. It has still a small opening to the south and before the bushes invaded the bar and shore it apparently furnished a favorable *Physa* habitat but as it stands today no snails are to be found in its foul waters. Another example of this sort is found on the south side of the lake where several approximately parallel bars have formed, one beyond the other, and where but little fresh water from the lake has access. The same conditions prevail that are found in all the waters that are cut off and have become filled with vegetation and decaying debris; they are devoid of snails. A moderate number of *Physa* are found in some of the small bays that have a supply of lake water which backs up into them in times of high water or storm. This number is no doubt greatly lessened by the amount of decaying leaves which fall into the water from the bushes and trees which skirt the lake shore. Along the east shore where a spit is just beginning to be built, a few snails and some dwarfed *Chara* may be seen. The shallow water on unprotected shores presents conditions very much like the waters of the same kind at Kavanaugh and Crystal Lakes, and is equally barren of life.

Passing over in review the spit and bar-formed habitats of Crooked Lake it is found that the waters are either so sheltered that they have become foul with decaying debris, or that the spits are too young to offer sufficient protection from wave-action. There is but one habitat which lies between these two extremes and offers both protection from waves and well aerated water and that is the optimum above described.

e. *Open Shores of Small Lakes as a Habitat.* This habitat occurs in the smaller, comparatively shallow lakes, which by their natural setting have a greater or less amount of shore which is protected from the sweep of the wind and waves and which offers a foothold to *Physa.* Long Lake, Benzie County, Mich., and the south shore of the Third Sister Lake, near Ann Arbor, furnish examples of this sort of habitat.

2. *Discussion of the Lake as a Habitat.* In general still water offers much more favorable conditions for *Physa* than does that of flowing water. Not only do the shallow marginal waters of the lake harbor the snail whenever protection from too violent wave action occurs, but in many cases the shores themselves offer very favorable conditions for it, (Gleason 1905 pp. 60-62). This observation agrees with that of Wetherby (1881 p. 158) who says: "First we may consider the circumpolar distribution of *Lymnaeidae.* These molluscs are essentially *lacustrine*, for while they are distributed into rivers and smaller streams to some extent, their station of fullest development is in lakes the world over."

Once knowing the conditions under which the snail lives in these lake waters it is well to consider the forces which are at work modifying these conditions and the resulting effect upon the future of *Physa* in these localities. It is not probable that the snails can ever find sufficient protection from the severe wave action of such lakes as Michigan and Superior as to enable them to live in large numbers in the lake waters proper. Although the beach of Lake Michigan at Frankfort offers no foothold for *Physa* there is no reason to doubt that in other regions of the lake there are pools and swamps in which the snail can live, similar to those found upon Crystal Lake beach. These pools are very likely to occur at a definite distance from the water's edge since they must depend almost entirely upon extra high waves, springs and rain for a water supply, but at the same time must be out of the reach of the severe sweep of the waves. Thus they will, through the future history of the lake, follow down the beach as its waters diminish in volume, always tending to keep at a certain definite distance from its edge.

Ruthven (1905, p. 24) cites beach pool habitats of very similar nature but very different origin in his study of a Lake Superior beach. "There are numerous pools on this beach, in the angular spaces formed by the removal, presumably by ice, of portions of rocks between the joint planes. These pools are, as a rule, above the reach of the highest waves, so that during the summer they are not flooded by the cold water of the lake. Their temperature is thus higher than the lake water. In several readings taken Aug. 6, 7 and 8, the temperature of the water in these pools varied from 60° F. to 68°, which was 10° higher than the lake water as it broke on the lower beach. The vegetation in these pools is very scanty, consisting chiefly of algae which line the sides. The small number of species is probably due to their isolation, shallowness (6-18 inches), and to their smooth sides which make it difficult for the plants to gain a foothold."

The snails found in these pools were *Physa ancillaria*, *Lymnaea desidiosa*, *Planorbis parvus* and occasionally *Lymnaea decollata*. It is clear that if these habitats do not receive their water supply from the lake, except in the time of severe storm, their duration is likely to be relatively short. Since these pools are entirely unshaded they are certain to become dry in seasons of drought and the snails will perish. But on the other hand, there will doubtless be found other pools lower down the beach as the waters of the lake diminish, and they like the pools in the sand above mentioned, will follow the lake in its life history always keeping a definite distance from its waters. This kind of habitat will cease when the character of the beach changes by erosion, sinking, or elevation.

The inmarch of sedges into the water on the protected sides of the lakes will probably always afford more or less of a harbor for *Physa.* It cannot afford very favorable conditions however, for there are two factors involved that cannot but affect snail life, namely: decaying debris and enemies. It will be remembered that it is under such conditions that peat beds are being formed through the decay of sedges, and also that such regions are the breeding grounds for fishes and frogs.

It has been shown that *Physa* does not find favorable conditions in the waters of large lakes, that spits and bars form beach pools and make life possible in the waters of medium sized lakes and that it is only when the smaller lakes or ponds are reached that *Physa* is found generally distributed in the shallow waters of the open shores. In the series of lakes studied the snail is found to have a very discontinuous distribution in the larger lakes and this becomes more or less continuous in shallow or marginal waters of the small lakes. Cases may be found where small lakes may have the snails completely girdling the shallow waters of its shores.

We have seen that the various habitats in lakes are also subject to changes as are those of the river. The snail lives under certain conditions and follows these conditions wherever they may lead. This is strikingly illustrated in the distribution of snail life behind the ice-rampart of Kavanaugh Lake and the spit and bar of the east shore of Crooked Lake. In all probability the snails followed the formation of this spit from year to year always keeping a definite distance back from the open end and away from the quieter debris laden water at its base. When such a spit reaches the opposite shore and the waters behind it are cut off entirely from those of the lake, snail life will rapidly die out in such a pool as is suggested by the absence of snails in the waters behind the spit on the south side of the lake. The trees and bushes bordering Crooked Lake in the region of the spits and bars, have no doubt greatly lessened the number of snails there. Few lakes offer more promising conditions, as far as protection from waves is concerned, but the deciduous leaves decaying in the quiet plant-grown waters of the bays will soon render snail life impossible.

The bar that is forming to connect the island with the land on the east side of Crooked Lake will form a new shore in whose shallow waters *Physa* may live. Presumably the island will be ultimately connected with the mainland on both east and west shores, thus dividing the present lake into two smaller lakes. The separation of the lakes will moderate the severity of waves and currents and this will in time alter present shore conditions. It is seen that *Physa* demands practically the same conditions for a habitat in a lake and pond as those in streams, although they may be formed in very different ways.

3. *Ponds and Swamps.* In this paper ponds are considered separately from lakes because although lakes tend eventually to become ponds, not all ponds were originally lakes. In the present study the largest ponds include bodies of water less than about 50 feet in diameter. This includes all the later stages of lake life and might include all small bodies of water cut off from the lake. The pond and swamp waters are, as in the river and lake, aerated by the overlying atmosphere. Whipple and Parker (1902) speak of the process by which water obtains air as breathing. According to the analysis given in their paper, and also those by Hoppe Seyler (1896) the upper layers of water are saturated with oxygen and contain but little carbonic acid, especially away from the cities. This is true for the shallow and for the upper layers of the deeper water. The oxygen decreases and the carbonic acid increases was the deeper layers of the water are reached. Birge (1908). Whipple and Parker also find that waters that are agitated take oxygen from the air and liberate much of their carbonic acid. The upper layers of some water, especially those that contain water plants, are found often to be super-saturated with oxygen. According to these results it appears that *Physa* as a rule lives in those parts of lakes and streams that are saturated with oxygen and contain but little carbonic acid.

There is another element, however, which, according to the authors above cited, tends to lower the oxygen content and increases the carbonic acid in many small bodies of water, namely, the presence of organic debris. In quiet waters, undisturbed by waves and currents, decaying vegetation occurs and takes up the oxygen from the water and liberates carbonic acid. In the small lagoons and behind bars and near the blind end of spits (as described for Crooked Lake) such conditions prevail and it is worthy of note few or no *Physa* occur there.

For the purpose of this paper, water plants must be considered not in their food relations alone, as they have been hitherto in the most favorable lake and river habitats, but also with reference to the amount of gas which they give to the water. In still waters, *Physa* has come to bear a double relationship to the plant, and depends upon it for food and perhaps somewhat for aerated water. This method of aerating water is one of the essential differences between stream and lake habitats on the one hand, and other small still water habitats on the other. Another difference has to do with the relative depth of the waters and the resulting difference in the length of their life histories.

Bodies of water, no matter what has been their previous history, when once they become small ponds, have much in common during their short life; they all tend to become dry land. The processes which cause these small bodies of water to become dry may work gradually, year by year filling may go on, or down-cutting of the outlet may take place, or the water level may become lower and lower during a year of unusual drought and the pond become dry. This may become of yearly occurrence for longer and longer periods of time until finally the pond becomes permanently dry.

a. *Relation of Pond Weeds to Physa.* Not only does the aeration of the pond water bring the snail into a new relationship with the water plant, but the drying up of the waters brings both plants and snail into a close relationship to each other. It may be remembered that in the study of lakes and streams, where quiet water prevailed, the pond weeds grew luxuriantly. The ponds with their quiet waters offer very favorable conditions for the growth of the water plants and it is only a matter of time until these plants entirely capture such an area. The question arises as to whether waters which have a very thrifty growth of water plants, offer conditions favorable to a good growth of snails, or in other words whether the optimum pond weed habitat coincides with the optimum snail habitat. This question can be answered only by a study of the conditions under which the different pond weeds grow most favorably and by observing the snail life under such circumstances.

In the examination of different bodies of water for *Physa* habitats a well marked correlation between the large pond weeds and the amount of motion in the waters was observed. The plants that were anchored to soil, such as *Chara* and *Elodea*, found their optimum in water where there was more or less motion at times, while the floating plants of the type of *Ceratophyllum*, *Spirogyra* and *Hypnum* were found to live in the very quiet water where there is more or less decaying debris. Two reasons may be given for floating plants inhabiting this sort of water, 1st, any motion of the water would cause an unanchored plant to drift, and 2nd, according to Pond (1905), the plant may absorb from the debris-laden waters the mineral matters which the anchored plant gets from the soil. The optimum habitat of some of the more common plants found in this study and their relation to *Physa* are as follows:

I. *Optimum Chara Habitat.* The most favorable *Chara* habitat was found in the pond of Kavanaugh swamp. This pond is filled with *Chara* almost to the very center and nearly to the exclusion of other plants. The shallow water near the shore is so filled that it comes above the surface on the south side, and great banks of it may be seen as the lake shelves off suddenly into deeper water. Kavanaugh Lake, lying north of these ponds a few rods, has no visible *Chara* on its wave-washed shores but the plant finds a foothold in its deeper, less active waters. It is in Crooked Lake, however, with its many shore modifications that one finds *Chara* showing a marked correlation to wave and current. Here, as in Kavanaugh Lake, the wind-swept shores have no visible sign of it; but if a small area of shore is slightly protected from the full sweep of the wind, little tufts of *Chara* not an inch in height and about two inches across may be seen growing here and there near the shore. All gradations in size and abundance of *Chara* are seen, depending apparently, upon the protection from waves and the amount of humus in the sand. *Chara* is found growing in a fairly rapid current in the ditch at Kavanaugh where the loose peaty substratum is held by it from being washed away. In shallow, quiet waters where *Chara* grows in abundance, no *Physa* are found, but in luxuriant growths of this plant, where the water courses gently over it, or where it grows in a minimum amount in quiet water, the snail thrives well.

II. *Ceratophyllum Habitat.* Very favorable habitats of *Ceratophyllum* are found in the sheltered quiet waters of Crooked

Lake behind bars and in small lagoons that are entirely cut off from the lake. The water that is cut off from the river, as the overflow at Geddes, Fig. 7, is more or less filled with debris. In the former practically no snails live, but in the latter there were many snails living upon the plants with several inches of clear water above them.

III. *Hypnum Habitat.* The best *Hypnum* habitats were found in swamps more or less shaded and having stagnant water. The old cedar swamps of Dayton, Tuscola County, Mich., furnish the optimum examined for this plant, although luxuriant beds of it were found in the ox-bow pond of Lima Center Creek and in small pools in Kavanaugh swamp. Where *Hypnum* grows in luxuriance, *Physa* is not found, but where there is a moderate amount of it, the snails are found in numbers.

IV. *Elodea Habitat.* There is an *Elodea* habitat in the little Railroad Creek where the stream is cutting a new channel in the bottom of its old one. Most of the water is flowing in the new bed but there is also a sufficient amount of water to cover the old bed to a depth of eight to ten inches. The deeper, swifter water has no plant life, but in the shallow quiet water of the old bed there is a great abundance of *Elodea.* So completely has it captured these quiet waters that no other plant is seen and it grows in such abundance that it is crowding above the water surface in places, as may be seen in the foreground of Fig. 5. No sign of *Physa* was found, either living or dead, in this habitat although it was present in habitats where *Elodea* was growing in less abundance a few yards farther up stream. An analysis of the optimum *Elodea* habitat and a comparison of it with the above described optimum creek bed habitat of *Physa* which lies but a few rods above it, serves to show the influence which water plants may play when they are present in great abundance. The *Elodea* habitat has the following conditions: Shallow water; full sunlight; quiet waters, perhaps more or less mingled with the flowing creek waters especially on the margin; very little decaying debris; no enemies observed; and an abundance of water plants. The only perceptible difference between the *Elodea* habitat and that of the creek-pool habitat is that there are more water plants and perhaps less currents flowing over them, yet this region was carefully searched without finding a single specimen of *Physa.* Other places in the creek in which *Elodea* grow in less abundance contained the snail, and the inference is suggested that the presence of this plant in abundance is not favorable in its food or oxygen relation to Physa.

Chara, *Ceratophyllum*, *Hypnum*, and *Elodea* are the more common pond weeds met in this study and it is a notable fact that they occupy the water of their optimum habitat almost to the exclusion of any other plants although many ponds of a few feet in area were found where they were all growing together.

The scarcity and often the entire absence of *Physa* is also noted where *Ceratophyllum*, *Chara* and *Hypnum* are growing in abundance. An abundance of these plants growing in a small aquarium will cause *Physa* to die within a week or two. Yet a moderate amount of these plants in an aquarium will support the snail in numbers. It therefore seems probable that it is the abundance of the plant and not the kind of plant that proves so disastrous to *Physa*. It also seems probable from the observations made in both field and laboratory, that relatively few plants in quiet water will serve both for food and aëration and that where the optimum pond weed habitat occurs *Physa* is near its minimum, and that the optimum of the snail is not the optimum of the water weeds. It may be remembered that the only places found where the plant optimum and the snail optimum closely approached each other were those in which water coursed gently over the weeds as in the brook ditch shown in Fig. 2, and those in which six to eight inches of water stood above the weeds, as at Geddes,—Fig. 7. In these cases, it would seem that whatever elements the plant growth added to or subtracted from the water was neutralized by the inflowing fresh water.

The following general conclusions seem probable from the above observations concerning the favorable conditions for plant growth, and their general relation to the snail habitat:

1. Where the pond weeds have captured quiet waters, there were found no snails living or dead.
2. Snails live in moderate numbers where there is a luxuriant growth of weeds if there be a considerable depth of water above the plants, or if water is gently flowing over them.
3. The snails occur in the greatest numbers where there is a moderate amount of water plants and organic debris.

These conclusions are based upon many observations made in widely different areas and they all point to the fact that an increase of plant life in quiet waters beyond a certain point, is very unfavorable to snail life.

This relation which the plant bears to *Physa* in point of numbers, brings us to an interesting phase in its local distribution. In newly isolated ponds *Physa* passes rapidly through its short lived optimum to its minimum as the pond weed captures the waters. It is clear that if *Physa* is to inhabit ponds in any numbers, that it can do so only when, by some means or other, the growth of the pond weed is checked or killed.

b. *Relation of Drought to the Pond Weeds and Physa.* In the present study of ponds two points arise for consideration: First *Physa* and its relation to the water plants, and second, the relation of the pond plants and *Physa* to drought. Since a definite relationship has been established for *Physa* and the water weeds, the next question to be considered is, What is the relation of the plant and snail to drought? The bearing that drought has upon the plant will be considered first, followed by a discussion of the desiccation of snails.

In the study of the river and lake systems the observation is made that wherever there is slack or sheltered waters there is generally a more or less abundance of pond weeds. These plants, however, are not found in all the ponds studied. Pond weeds are abundant in the ponds shortly after they are cut off from the parent body and continue to be so up to the time they are subject to drought. Many of the ponds contain the water plants *Chara*, *Ceratophyllum*, *Hypnum* and *Elodea*, and investigation shows further, that if these bodies of water have not as yet reached the stage where they dry up, they almost invariably contain at least one of these common plants. On the other hand, those ponds that are observed to dry up, or upon inquiry are reported to do so, contain none, except *Hypnum*, of the above cited weeds.

In the series of swamps studied below for snail desiccation, this plant seems to survive even though the swamps become perfectly dry year after year.

It is evident from these observations that drought is fatal to most of the pond weeds. These plants reach their maximum growth in the quiet water, and ultimately capture the water to the exclusion of other plants. At the first appearance of drought this luxuriant growth of pond weeds is killed and the pond henceforth takes on a new appearance. The perennial plants usually give place to annuals which are not so aggressive, since they take most of the summer to mature.

Since, in excess, the pond weed is very unfavorable to *Physa*, and since drought is so disastrous to the pond weed, it is necessary to ascertain the relation of drought to the snail.

A study of the most favorable pond habitat for *Physa* may throw some light upon the question and may show an equilibrium established between the plant and the snail in quiet waters so as to enable the latter to live there in large numbers. A small pond situated a few rods north of the University campus, Ann Arbor, is the remnant of a small, deep pond of glacial origin, which some twenty years ago had fully twenty feet of water in it, but which now does not exceed two feet in the deepest parts. Great numbers of *P. gyrina hildrethiana* are found on all sides of the pond reaching nearly to the center, instead of in a narrow belt of a few inches in width as is generally the case in such bodies of water. The conditions in this habitat are as follows: Shallow water throughout; full sunlight; no enemies observed; very little decaying debris; no pond weeds, but a very small amount of *Spirogyra*, and *Alisma plantago* L. in moderate numbers.

It was noticed that this habitat has none of the usual pond weeds, but a form of vegetation which is less aggressive. Upon a closer study of this pond a relationship was found between such pond weeds as *Chara*, *Ceratophyllum*, *Elodea* and *Physa*. As this pond dries up during seasons of drought and as these pond weeds have no means of withstanding such a period, and cannot as a consequence gain a permanent foothold in water of this nature, but must give way to plants less sensitive to drought; the following observations show that other means than drought retard the growth of pond weeds. This is the case at Dayton, Tuscola county, Mich., in a cedar swamp which has been nearly cleared, and in which water stands the year around. There were a moderate number of water weeds and a great many *Physa* were crawling about upon a soft clay substratum. This swamp is of long standing and the presence of a few water weeds together with a clean clay substratum is worthy of note; also the fact that the clay forming the substratum has been eroded from the surrounding hills and that it serves very effectually to keep the weeds in check so that *Physa* flourishes. This mode of checking or killing the water plants was also observed in the optimum habitat of Crooked Lake, where the soil has washed into the water from a neighboring field.

c. *Relation of Drought to Physa, or Snail Desiccation.* That some *Physa* can withstand a period of severe drought is well established, as in the case of the pond near the campus, but how often and under what conditions drought can be endured is the problem before us. To answer the question nearly a dozen swamps were examined in various degrees of extinction, from the last stages of standing water to dry land. These swamps are found in Dayton, Tuscola County, Mich., in a morainic region extending over an area of about two hundred acres. The swamps are isolated and have no natural outlet but lie side by side, surrounded by gently sloping hills of clay and sand. The two soils retain their own individuality, lying side by side in areas of an acre or so, and are not much intermingled. About fifteen years ago, white cedar is reported to have filled the swamps, and the surrounding region was covered with a dense growth of hemlock. Burning and clearing soon reduced the hemlock land to cultivated fields, while the cedar was cut and has given place to black ash. Most of the ash in turn has been succeeded by willow. Some of the swamps are completely cleared, thus giving the open water or pond condition.

These swamps were studied in detail for snail desiccation alone and in consequence will be classified according to the moisture conditions they showed during the middle of September of the unusually dry season of 1904. They may be divided into groups. The swamps of Group A contain more or less moisture throughout the year; Group B is subject to periodic drought, while Group C undergoes annual drought.

Group A—Swamp A ^{1}. This is surrounded by gently sloping, ploughed hills of clay and sand, with an open growth of young, soft maple and willows. Most of the swamp is dry and covered with a young growth of mesophytic annuals which have grown up since the disappearance of the water in early summer, but here and there in the lower depressions, are found pools of standing water in which grow a small amount of *Spirogyra*, but no other water plants are present. The substratum varies, some parts are of peat and sand, while others are clay. The sand and clay have been washed in from the hills, and in places completely hide the substratum of peat. The dry parts of the swamp were searched thoroughly for living water snails, both under debris and in the soil, and with the following results:

1. A few *Lymnaea palustris* and many *L. desidiosa* were found lying under the moist ground in the region of standing water.
2. In the drier parts, none of these snails were found living except in the bottom of cattle footprints which were deep enough to hold sufficient moisture. In one of these moist prints a cat-tail grew and three specimens of L. *desidiosa* were found sealed to its stem about three or four inches from the bottom of the depression.
3. Although the two species of *Lymnaea* were found scattered here and there over the swamp, there was no evidence of *Physa* living or dead, in the dry parts of the swamp, although in the pools of water it was found in abundance feeding upon algae, in company with a very few *Lymnaea*. Evidently for some reason, when the waters of the swamp began to recede, *Physa* followed them to their lowest depressions while the other snails did not.
4. No evidence of burrowing in the soil was seen among the mollusks of this swamp with the exception of some small bivalves *Sphaerium* which were found covered with soil to a depth of one to three inches.

Swamp A^2. This swamp differs from A^1, in the following respects: The swamp is skirted by clay hills covered with beech and maple; it has a sparse growth of black ash trees and a medium amount of *Hypnum;* there is no standing water except in one very small, shallow depression; the substratum is peat; no evidence of erosion except a very little clay washed from the hills at the very border of the swamp. A great variety of snail life was present, there being *Lymnaea desidiosa*, *L. palustris*, *Physa elliptica*, *P. gyrina hildrethiana*, and *Planorbis*—in addition to *Sphaerium.*

Many shells representing all the mollusca of the swamp, except *Sphaerium*, were strewn over the ground and moss, but only in the two following cases were there any living ones found outside the small pool of water. In one small area where the ground was damp, a number of *Physa elliptica* Lea and *Planorbis parvus* Say were found lying on the ground. It is a notable fact that when they had the aperture down they were living in more cases then when the aperture was turned up.

The border of the swamp was very dry. No snails were found living except three specimens of *Lymnaea palustris* which were found sticking, aperture down in the clay.

Swamp A ³. This swamp is cleared and is surrounded by open pasture lands. The swamp basin is shallow, very level and has no standing water, although the ground in many places is moist. It has no water weeds except *Alisma plantago*, also found in the pond near the campus.

Erosion on some of the hillsides had taken place quite rapidly; so that patches of clay and sand several feet square cover the peat on the border of the swamp. While there were many dead shells of *Lymnaea palustris* (the only mollusk in the swamp except *Sphaerium*, strewn over the surface), there were places moist enough, both on the sand and clay to support snail life. Many *Lymnaea* were found living on the clay washed from the hills, while few were found on the sand. A very remarkable instance of desiccation was found upon a large boulder which lay on one side of the swamp. About twenty snails were left upon the top of this stone when the water receded. One of them was found living, aperture up. Upon examination the snail was seen to have formed a complete mucous epiphragm over the aperture. This seemed remarkable as the snail lay fully exposed to the sun on the top of the stone which was fully a foot above the level of the bottom of the swamp.

Group B is very much the same as Group A, except that the ground is wholly dried up.

*Group B—Swamp B*¹. This swamp is surrounded by gently sloping hills covered with grass. All the trees have been felled and many of the logs are still lying where they have fallen. The ground contains moisture (although no standing water is seen) and is covered with an abundant growth of *Hypnum* six to eight inches in thickness, which, when the water was lowered, settled upon the logs and bed as a heavy blanket. Some of this moss was damp and one specimen of *Lymnaea palustris* was found alive upon it although hundreds of dead shells lay under the moss. Another specimen of *L. palustris* was found upon some dry *Hypnum* with its aperture up and a mucous epiphragm over it. No signs of an inwash from the surrounding clay and sand hills were seen and no evidence was seen of burrowing on the part of the snails.

Swamp B.[2] This swamp is a small, open area situated in a growth of poplar trees. Some willow trees skirt its borders and fill the substratum of peat with small rootlets. Rotting logs, brush and willow leaves are found on the swamp bed which has a growth of such mesophytic plants as the dandelion and thistle. No water plants were seen except some algae. A thorough search in this debris and peat for evidence of the habit of burrowing among snails revealed nothing but a number of living *Sphaerium* buried in places to the depth of three inches. Two specimens of *Lymnaea palustris* were found lying aperture down on the surface amid loose peat and dead shells. Several living *Physa elliptica* and *Lymnaea palustris* were found, aperture down, in a thin wash of clay on the border of the swamp. The ground around this swamp is grass-grown and the hills gently sloping; this perhaps accounts for the small amount of erosion found.

Swamp B.[3] This swamp is situated at the foot of low cultivated hills of clay and sand, some of which are in pasture, others in grain, and still others are freshly ploughed. The swamp is only partly denuded of its trees of white cedar and black ash, some of which are growing, while others have been felled and allowed to decay. A dense, thick border of willows skirts the swamp, causing it to be more shaded in these parts. The swamp has a dense growth of *Hypnum* which covers the logs and substratum.

In this swamp, of fully fifteen acres, there was found very little evidence of living molluscan life although there were many dead shells lying about upon the peat and moss. One or two living specimens of *Lymnaea palustris* were found on the border of the swamp in the damper places, and one or two were found sealed in the clay which had washed over the peat, but no other living mollusks were found except a few bivalves in the peat on the border of the swamp. Absolutely no signs of life were found in it, on or beneath the heavy blanket of *Hypnum.* Even the *Sphaerium* buried beneath the heavy growth of moss, were all dead and their shells crumbled when touched. This dearth of life is attributed to the great amount of vegetable mould collected upon and beneath the moss. The inwash from the ploughed fields covers the peat with a coating of heavy clay to a depth of six or eight inches leaving no surface trace of either plant or animal life.

Group C is the last of the series and represents the latest stages of swamp life.

Group C—Swamp C[1]. This little swamp or pond is surrounded by a hayfield and is wholly cleared, with no trees or bushes growing in or around it. The substratum is of stiff blue clay and it has no water plants except some traces of algae and a moderate growth of *Alisma plantago L.* The clay covers the whole swamp bed, no traces of peat are seen, which is due perhaps to the rapid deposition of clay, eroded from the surrounding clay hills.

The clay in the bed of the swamp is so dry that cracks from eight to eighteen inches in depth and from two to three and a half inches in width are found, caused by the long continued drought of the summer and early fall. Imbedded in this clay were hundreds of shells of *Lymnaea palustris* and two dead shells of *Physa gyrina hildrethiana.*

A portion of this clay with its imbedded shells, from one of the many tiny depressions of the saucer-like basin of the swamp is shown in Fig. 10. The shells are well scattered over the whole area, but more are in the center of these depressions, where, no doubt, the water lingered longer than in the somewhat higher portions. Nearly all of the more recent shells which had their apertures well sealed in the clay were alive and revive in a short time after being placed in water. All of these living shells that were sealed in the clay had a mucous epiphragm over the aperture. A careful study of the shells for the presence of a habit of burrowing into the soil, to insure the closure of the aperture in case of drought, revealed no indication whatever of such a habit. There were about as many shells with the aperture sealed in the clay as of those with the aperture exposed. All of the fresh shells that were sealed in the clay were alive, but there were also some old dead shells which were fairly well sealed; however, it was thought that perhaps the water of the previous season washed the clay around the aperture. It is therefore concluded that it is by chance if the snail is hermetically sealed and that this is due to the position the snail happened to be in when the clay grew so hard that movement was no longer possible.

The farmer who owned the land said that the swamp had been completely dry since early June. I have no reason to doubt this general statement as there were no signs whatever of young snails and probably the water dried up before they could develop. No other snails were found living. The specimens of *Physa gyrina hildrethiana* were not sealed; the bivalves could not bury themselves in such stiff clay and both species were dead.

Swamp C². Swamp C² is a few rods away from Swamp C¹, in the same hayfield and represents the next stage in drying up of Swamp C¹. It has the same clay basin but is shallower and has logs and sedges in it. Careful search revealed but a few fragments of decaying shells which serve to enable a prophecy to be made concerning the fate of snail life in Swamp C¹.

Swamp C³. This swamp is very much like Swamp B², in its physical makeup, but had no mollusca except *Sphaerium* which were buried in the peat. Fragments of shell were found but no whole ones. This indicates that none of the snails had succeeded in surviving some severe drought during the past few years. Another swamp was found that gave the next stage in their life history series, namely, one that had become too dry even for the bivalves whose decaying shells in the dry peat told the story of a long, severe drought.

Conclusion Concerning Desiccation. The following snails have only a slight burrowing reaction if any at all: *Physa gyrina hildrethiana*, *Physa elliptica*, *Planorbis parvus Say*, *Lymnaea palustris*, and *Lymnaea desidiosa*. Baker (1911) p. 39. *Sphaerium* burrows in the softer substratum but cannot in the stiff clay. The *Lymnaea* forms a heavy mucous epiphragm and in consequence has in any case a better chance of living through drought, which probably accounts for their presence in many waters to the exclusion of other snails. It was observed that all the above named snails lived for a time upon almost any kind of substratum providing it was moist. All may live for a few months when their apertures are turned down and buried in the clay, even though they do not form an epiphragm. Even in the clay, *Lymnaea* has the advantage over snails that do not form a mucous epiphragm. The sealing in clay is the result of chance; and depends upon the presence of clay and upon the snail assuming the proper position for sealing. In the presence of clay, *Lymnaea* will be one of the last gasteropods to inhabit a pond subject to severe drought, but if peat or sand is present *Sphaerium* stand a better chance because it burrows into the soil.

Much growing vegetation, as *Hypnum*, is very disastrous, both because it prevents the snail from reaching the substratum, and because it decays and thus kills even the buried bivalves. Moss and loose debris ordinarily furnish protection to *Sphaerium*. Too much erosion of clay is perhaps not conducive to the endurance of desiccation because it may bury the snails so deep they cannot get out. Perhaps much of the richness of molluscan life in many ponds that dry up is due to the advantages they offer through having a clay substratum and a moderate amount of vegetation. The majority of snails in the above studied swamp are *Lymnaea palustris* and *Sphaerium*. Comparatively few *Physa* were found. If a pond has no clay in its bed and is subject to drying, *Physa* is likely to die off with the pond weeds because it but rarely forms a mucous epiphragm. In general the survival of *Physa* in ponds that dry up is therefore dependent upon the presence of a certain amount of clay.

V. *General Discussion and Summary*. The physical conditions of the river system are very different from those of the lake and pond, yet the most favorable habitats for *Physa* have essentially the same factors. The following examples serve to illustrate how these conditions are brought about in stream and lake by widely different agencies. Snails are found protected from the current behind the stones in a stream bed and they also found shelter from the waves behind spits. The factors making up these habitats are essentially the same yet there are not many points of resemblance between a creek and lake or between the modifying agents, stones and spit which are effectual in producing like environments.

In general, the occurrence of the snail *Physa* in bodies of water about Ann Arbor, Mich., proved to be very general but very discontinuous. Streams do not offer conditions favorable for *Physa*. Springs and brooks, especially those not connected with streams, are practically barren, which is due perhaps to their isolation. The snail is quite generally dispersed in creeks but only an occasional favorable habitat is found, as behind stones and in quiet pools. Rivers contain but few snails, the most favorable places being in the slack water above dams, and in the quiet waters which have been cut off from the river such as, back-waters, flood-plains and deserted channels or ox-bows.

a. Physa Habitats in Still Water. The pond offers, on the average, relatively a much greater area of water that is sufficiently shallow for the snail, than do lakes and streams. The pond may not only offer a more continuous habitat around its margin but it may be shallow enough for the snail to live nearly throughout its whole bed. On the other hand, a pond may be of the sink-hole order with steep shores so that its waters, while relatively shallow as compared with a lake, may not be sufficiently shallow along its margin to enable the animal to live. The amount of decaying debris in a pond habitat is usually more than in rivers or lakes where currents and waves shift it about or carry it away. The amount of this debris varies with the growth of the vegetation which is necessarily less in ponds that are subject to periods of drought or where the inwash from the surrounding hills is sufficiently great in amount to bury the debris. In general, the snail occurs abundantly in lakes only in the littoral zone, as a rule the conditions are more favorable than those of the river. The shallow wind-swept shores of large lakes are barren and it is only in their beach pools that the snail is found. It finds protection from severe waves and currents behind spits and ice-ramparts that are formed in medium sized lakes and upon their sedge-grown shores. In the littoral zone of certain small lakes *Physa* is found even in unprotected places.

The very nature of the pond brings *Physa* into new environmental conditions of which nothing was known in larger bodies of water. The snail's relation to pond weeds and drought brings out possibilities of adaptation that would hardly have been suspected from a study of the snail in the waters of the river system and lake proper. The double relationship which exists between the snail and the water plant, namely, that of food and aeration of water, would naturally lead one to suppose that the optimum of the water plant would be consistent with that of the snail. This is, however, not true even in water that is in other respects essentially the same as that of the optimum habitat of *Physa*, as for example, the *Elodea* habitat. In the field *Physa* does not find an optimum among excessive plant growth. In the laboratory this same phenomenon holds true. Any one who has tried to keep snails in numbers in the laboratory has found that the water will soon develop a bad odor and become turbid if sufficient plants are not placed in it. While on the other hand, if the water is crowded with such plants are *Chara*, *Elodea*, *Ceratophyllum* and *Hypnum*, it remains clear, but the snail will die in a relatively short time. It is therefore seen that an excessive amount of plant life in the water is detrimental to snails.

It is interesting to note in this connection that Kofoid (1903) in his work upon plankton in the Illinois river observes that a luxuriant vegetation is unfavorable to an abundant production of plankton. He found wherever *Ceratophyllum* was growing in excess that the small microscopic plant and animal life was correspondingly scarce. I quote the following from his report, p. 392: " The dominance of the abundant vegetation is inimical to large plankton production. Other things being equal, plankton production is greater when the relative occupancy of the water by vegetation is decreased." Again on p. 484: "Other things being equal, bodies of fresh water free from vegetation (submerged macro-flora) produce more plankton than those rich in such vegetation." In a footnote upon this statement he says: " This relation of vegetation to the plankton may be formulated as follows: The amount of plankton produced by bodies of fresh water is, other things being equal, in some inverse ratio proportional to the amount of its gross aquatic vegetation of the submerged sort." Kofoid attributes the scarcity of plankton in the regions rich in vegetation to the fact that the plants use the dissolved nutrition in the water and the scarcity of plankton is due to lack of food.

Pond (1905) agrees with Kofoid's statement and interpretation of the scarcity of plankton only where there is an abundance of non-rooted vegetation. According to Pond the roots of anchored plants are true absorbing organs taking from the soil valuable mineral salts. I quote him (p. 522) in the following: " These rooted aquatics are important contributors to the plankton food supply, because when living they organize matter that may be used as food and in death they yield important salts and organic substances to the water."

However this may be for plankton, few or no snails are found where there is an abundance of both rooted and non-rooted gross vegetation. Nor can their scarcity in these localities be attributed to the lack of food since they eat the plants and probably do not take nourishment from solution in the surrounding medium. It is therefore evident that some reason other than the one given by Kofoid and Pond for plankton, must be sought to account for the inimical effect of excessive vegetation of the submerged sort on snails.

The effect of drought on the water plant is of great importance to the snail. To just what extent drought kills water weeds is an unsolved problem so far as is known to the writer. That drying kills the plant itself, there is no doubt, since it is easily demonstrated experimentally, but there is no experimental evidence known to me of the extent to which spores and seeds of these plants can resist drought. To be sure *Ceratophyllum* and *Elodea* produce seeds rarely and when they do so, it is in the middle or latter part of the summer. It is in this part of the season, however, that drought usually occurs in the ponds. Taking all together, the chances indicate that drought is fatal (at any rate in this region) to such pond weeds as *Elodea*, *Ceratophyllum* and *Chara*, since all the ponds known to dry up are devoid of these plants.

Means of withstanding drought are sooner or later of great importance to snails that inhabit ponds or swamps. It is seen that a pond or swamp may dry up, but as long as the ground remains damp, all the above mentioned snails may live. All species of mollusks studied, except the little *Sphaerium*, can live if there is a clay substratum for some weeks even in severe drought. The pond near the University campus is a good illustration of this.

Where the substratum of a pond or swamp is of loose texture and there is but a small amount of clay present, few snails are likely to survive and restock the pond because the sealing is a matter of chance. The formation of an epiphragm greatly enhances the chance of survival in time of drought irrespective of the substratum. A pond with a sandy substratum was examined and no snails but *Lymnaea* were found and no pond weeds were present. This pond was found to be subject to drought. Evidently *Lymnaea*, through its ability to form an epiphragm, survived while other species were not so favored.

The current belief is that snails can withstand drought by burrowing into the ground when a pond dries up. In many of the swamps that were dry when examined, most of the snails were dead, hundreds of dead snails lay upon the moss and ground. Neither dead nor living shells were found buried.

In ponds and swamps subject to severe drought, the formation of an epiphragm and the sealing in clay are the only effectual means of the continuance of snail life. Small bodies of water reach in time, the stage where severe droughts may occur yearly, and snails in order to live must be able to form an epiphragm or the substratum must contain more or less clay. *Physa*, therefore, has but little chance in a pond subject to drought unless there is more or less clay, but *Lymnaea* has a good chance whether peat, sand or clay prevails. *Physa* inhabiting swamp waters differ greatly in appearance from the same species found in the open pond. The difference is so great that Mr. Bryant Walker identified the specimens at once as swamp forms without a previous knowledge of the locality from which they were taken.

Lewis (1855, p. 120) remarks upon the variation of *Lymnaea*, due he thinks to such conditions as locality and temperature. "I have found that all these shells which abound equally in the Erie Canal and the Mohawk River at this place, have local peculiarities, by which I can determine at a glance, almost, which of the two localities a certain number of shells may have been taken from."

The most formidable condition for *Physa* in small bodies of water may be said to be too many pond weeds and too much decaying debris. While drought may be said to be disastrous to *Physa* in bodies of water that have a loose substratum, and dry up completely, yet it is essential for a pond optimum that it is sufficiently severe to kill the pond weeds but not the snail. These conditions which enable *Physa* to withstand drought are seen to furnish the basis for the popular opinion that it prefers ponds and ditches that dry up.

b. The General Relation of Physa to Its Environment. The conditions under which *Physa* lives in the different habitats apparently varies greatly and there is a corresponding variation in the number of snails found in different situations. However, an analysis of the five habitats having the largest number of snails shows a striking similarity in the conditions, as may be seen from the following table:

Creek-Bed Habitat	Beach Pool	Behind Ice-Rampart	Behind Spits and Bars	Pond near University Campus
Shallow water, from 1 inch to a foot.	Shallow water, from 5–8 inches deep.	Shallow water, from 2–10 inches deep.	Large area of shallow water from 1–6 inches deep.	Large zone of shallow water from 1–12 inches deep.
Running water	Water supplied from the lake without severe wave action.	Exchange of water from the lake.	Free exchange of water from the lake.	Still, shallow water.
Growth of *Cladophora* upon stones.	Small amount of Algae.	A medium number of plants.	Comparatively few plants.	Medium amount of *Spirogyra* and *Alisma plantago.*
Little or no debris.	No debris.	Little or no vegetable debris.	Very little debris.	Medium amount of debris.
Gravelly substratum.	Clean, sandy substratum.	Clear, gravelly substratum.	Clear loam substratum.	Clay substratum.
Full sunlight.	Full sunlight.	Little or no shade.	Practically no shade.	Shade from *Alisma plantago*, when mature.
No enemies observed.	No enemies observed.	No enemies observed.	No enemies observed.	No enemies observed.

In all the different habitats studied, *Physa gyrina* Say, *Physa gyrina hildrethiana* Lea, *Physa anatina* Lea, *Physa ancillaria* Say, *Physa heterostropha* Say and *Physa elliptica* Lea were found. *Physa gyrina* was the most common. Four of the above species, namely, *Physa gyrina*, *Physa ancillaria*, *Physa heterostropha* and *Physa hildrethiana* Lea have an optimum with the following conditions: Shallow water; minimum amount of shade; few or no enemies; minimum amount of debris; protection from waves and currents; moderate amount of water weeds; and well aerated water.

It is clearly not a question of food which causes these snails to collect in numbers in these habitats, as snails are well known to be almost omnivorous in their habits. Neither is it the kind of food since the same kinds that occur in the most favorable habitat, are found in greater abundance in neighboring places that have no snail life.

According to the work of Whipple and Parker (1902) and Hoppe Seyler (1896) the shallow water of these habitats with its water plants is often saturated and even supersaturated with oxygen. This is brought about by a diffusion from the overlying atmosphere and is known as a breathing process. Water plants are well known to add to the amount of oxygen of the water when they are subjected to direct sunlight. According to the above cited authorities water that is agitated takes oxygen from the air by mechanical processes and liberates its carbonic acid. The water that breaks over stones in the creek-bed habitat and the water that is lashed by the waves through a gap in an ice-rampart or into the open end of a spit-formed pool, is probably well aerated and contains little carbonic acid. Direct sunlight favors a moderate amount of decomposition which in turn directly affects the amount of oxygen and carbonic acid. It seems that *Physa* is living in parts of the water which have the highest percentage of oxygen and the lowest percentage of carbonic acid. Experimental evidence corroborating these observations will later be considered in detail.

Aside from the question of enemies, the conditions common to the optimum habitats resolve themselves into that of the gaseous content of the water, and indeed later experiments show that the snail reacts very positively to oxygen and is strongly repelled by carbonic acid.

II. MUCUS AND MUCOUS THREADS OF PHYSA.

I. Secretion of mucus; its properties.
II. Formation of an epiphragm.
III. Food and mucus correlated.
IV. Nature and process of spinning.
V. Conditions affecting spinning.
  1. Food.
  2. General activity or tonus affecting spinning.
  3. Habitats affect spinning.
VI. Some principles underlying spinning.
VII. Biological significance of spinning.
VIII. Brief discussion of the literature on spinning.

1. Secretion of mucus; its properties.

Mucus is secreted over all the exposed parts of the snail's body but does not flow perceptibly from the glands except upon the ventral side of the foot. The presence of slime on any exposed part of the animal's body may be easily demonstrated by touching the integument with a fine rod or bristle. The mucus may be felt sticking to the rod or, when the bristle is withdrawn, may be seen to be stretched out into a fine short thread. The experiment may be tried when the snail is crawling on the substratum either in or out of the water but the demonstration of slime on the integument is rendered much easier if snails are taken that have become accustomed to being handled, otherwise they may retreat into their shells at the slightest disturbance of the water. The slime, secreted by the snail's integument has presumably the same nature whether found on the ventral side of the foot or on the other exposed parts of the body. The description which follows is for the former alone.

The mucus or slime varies in physical properties according to the length of time since its secretion. Freshly secreted mucus is a clear, viscous, jelly-like substance, resembling in appearance the white of an egg. (When it is fresh and under water or in a thin layer on the substratum it is practically invisible and difficult to study.) Fresh mucus is at all times more or less stringy and may be pulled out into threads of greater or less length according to the physiological condition of the snail at the time. The ordinary thin trail of the mucus is not visible at any time under water unless the snail has crawled over a layer of sediment, in which case the incorporation of particles of sediment into the mucus at once renders it visible, as will be shown by later experiments. The invisible trails of the snail in the water may be detected by passing the hand across the substratum over which the animal has crawled.

Fresh mucus is not soluble in water. This is easily demonstrated by placing a mass of it in water and watching it from day to day until disintegration takes place. It does, however, undergo changes in the water. If fresh mucus be exposed to water for a few moments it gradually becomes visible, taking on an opalescent and later a blue-white hue. This occurs, however, when the mucus is in mass several mms. thick, and not when it is, as stated above, in a thin ribbon adhering to a solid. The mass of mucus soon shrinks and becomes less viscous, less elastic and somewhat brittle. As the mucus thus becomes more dense it loses part but not all of its elasticity as will be shown by a later experiment. Fresh mucus exposed to the air in sheets, dries, becomes brittle, and resembles in appearance a thin sheet of mica or of dried collodion.

Physa holds its head a millimeter or so from the substratum or the surface film and is thus able to move it freely in all directions. The mucus forming the ribbon apparently begins to flow on the broader anterior part of the foot and apparently moves backward in straight lines from the point from which it started. Perhaps this is the only part of the foot that does form the ribbon, since if mucous glands were situated over the middle and posterior part of the tapering foot, the ribbon would be uniformly thicker in the center. The apparent flow of the mucus backward, in straight lines may be easily verified by placing small objects on the fore part of the foot and watching them as the animal crawls on the surface film. As they pass backward they always remain in the same position relative to the plane of symmetry of the foot and also relative to the borders of the ribbon of mucus. Their apparent progress back over the foot in straight lines is due to the fact that the mucus as fast as it is secreted depends from the surface film and remains there without further movement, so that the snail crawls ahead under the mucous ribbon as it is laid down. Thus the ribbon has the appearance of moving back over the foot. Since the mucous ribbon is depending from the under side of the surface film it does not come into direct contact with the air. The phenomenon of the mucus flowing from the wider fore part of the foot results in a mucous ribbon being laid down the width of this part. Perhaps the relation of the snail to its mucous ribbon may be made clearer by the following illustration. A hollow triangular flatiron is made to move forward with its broad end in advance, thus crudely imitating the foot of *Physa*. This hollow flatiron is filled with tape the width of a slot which extends across the whole broad end of the iron. The tape passes out of the slot and extends under the iron and as fast as the iron is moved forward the tape from within is unwound. Now if we imagine the tape adhering to both the solid beneath and the iron above, while the iron is being pushed over the upper side of the ribbon by muscular force while the lower side of the ribbon is left adhering to the substratum, we have in a very crude way imitated the relation the snail bears to its ribbon of secreted mucus, except that in the snail the mucus does not flow from a slot or linear area as in the case of the illustration. The flow of the mucus attends the movement of the snail forward whether it be on solid, film or thread.

If the animal is moving forward there may be seen upon close examination small areas of muscular contraction over the whole sole of the foot, but more numerous and plainer on the border of the fore part of it. This is especially well shown on the foot of *Lymnaea stagnalis* while crawling on the surface film. These muscular contractions are not in regular waves as they so plainly are in *Helix*, but are small and irregular, and result in parts of the foot being momentarily slightly depressed here and there over the surface. These momentary slight depressions of the surface of the foot cause its mucus to reflect the light (as may any slight roughness of a bright surface), and they are thus made visible. This muscular activity always accompanies the flow of mucus as it always does locomotion. Whether it plays a part in locomotion or in the flow of mucus is not known. If a snail retracts its foot into the aperture of its shell this muscular activity is not seen, nor is mucus seen to flow (though the foot is still visible). In the experiment described later to show the mode of forming an epiphragm, the mucus was gently removed from the contracted foot which would otherwise have formed an epiphragm, and there was then in no case an epiphragm formed. The animal did not protect itself by secreting more mucus to form a second epiphragm, but retreated into its shell as drying occurred, and remained with the aperture of its shell fully exposed. Walter (1906, p. 7) makes the following remarks upon the relation of the flow of the mucus and locomotion: " When a snail has been allowed to leave the water and to crawl around upon an absorbent surface until its mucous supply is temporarily exhausted, it is unable to resume locomotion, on being returned to the water."

To get a reliable record of the flow of the mucus when the animal is moving and at rest, the following observations and experiments were made: Some neutral non-soluble powder such as chalk or talcum was thoroughly mixed with water and then allowed to settle on the bottom of a dish. Snails were allowed to crawl over this substratum. The powder incorporated with the mucus caused it to become instantly visible. Walter (1906, p. 7) used carmine particles for this purpose.

The edges of the ribbon are formed by the glands in the broad anterior part of the sole and are not at any time covered by the tapering posterior portion. Thus, if one is looking down upon the moving snail, this edge of the ribbon may be studied as fast as it leaves the glands of the foot. The mucus covers the path which the snail has plowed, through the powder, and when loosened from the substratum, looks like a white gauzy ribbon. The center of the ribbon may be much thicker than either of the two edges and vice versa. It may appear mottled, i. e., irregularly thick and thin, and there may be places in the snail's path where no mucus has been deposited at all.

When a snail stops on the substratum, even for some time, there is no accumulation of mucus formed where it rested on the powder. This would seem to be evidence that mucus stops flowing with the cessation of the movement of the foot. An interesting case of the secretion of mucus without the formation of a ribbon may be seen when a snail is quietly feeding on the surface film. This happens with *Physa* and other fresh-water pulmonates observed, but is especially well shown in *Lymnaea stagnalis*. The fore part of the foot stretches gently back and forth while the snail is feeding, but the foot as a whole does not move from its position on the surface film. The minute areas of muscular contraction may be seen in the fore part of the foot, but not at all on the posterior and middle portion, and it is worthy of note that the flow of mucus is seen only in the parts where these contractions occur. The consequence is that the mucus from the fore part of the foot does not leave it as a flat ribbon stuck to the surface film, but flows back to the somewhat hardened mass of mucus on the middle foot and is pushed up over it. Thus, when the animal remains feeding for some time in one place on the film, a mass of mucus becomes heaped up in the center of the foot.

II. Formation of an epiphragm.

The dried mucus may form an epiphragm over the aperture of the shell when the snail is exposed to drought. The epiphragm consists of a thin sheet of dried mucus stretched usually just within the aperture, so that it forms a thin partition between the retracted snail and the dry substratum of air. The epiphragm may be formed (1) when the animal is in the drying mud, (2) on a grass stalk or other perpendicular solid, or (3) when it is turned aperture up. In the early part of this research, a series of swamps was studied for the purpose of learning something of the effect of desiccation on snails. *Lymnaea palustris* was found to have formed an epiphragm in all three positions above mentioned. To determine the way in which this epiphragm was formed, a number of *Physa*, *Lymnaea palustris* and *Lymnaea stagnalis* were placed in a dry glass beaker and observations made upon them from time to time.

The snails crawled upon the dry substratum for an hour or more. At first they moved with apparent ease with the foot quite fully extended, but gradually the mucus on the foot began to get drier and drier until further movement was impossible and the snail finally remained quiet in its track. The foot gradually retracted into its shell as movement ceased and finally remained for some time just within its aperture. The foot was contracted into the center of the aperture surrounded by its retracted mantle, both together forming a smooth, plane surface. The mucus could be seen to become dry and glassy over the surface of both mantle and foot. Soon after this condition was reached, gentle muscular contractions of foot and mantle could be seen; and gradually they retreated farther into the shell leaving a hardened curtain of mucus stretched across the aperture.

It was observed that all species of snails did not form an epiphragm. Some had formed entire epiphragms, some nearly perfect ones, and others had mere pieces of the dried mucus sticking to the edge of the aperture. Most of the shells were sealed to the glass wherever any part of the shell about the aperture came in contact with it. *Physa* was rarely observed to form an entire epiphragm and it was equally rare to find *Lymnaea palustris* not doing so. Pilsbry (1896, p. 96).

Probably the physical properties of the mucus, which may vary with the individual and the species, together with the size and shape of the aperture of the shell, determines in a large degree whether or not an epiphragm is formed. It has already been pointed out that with the aid of its epiphragm a snail may withstand quite a severe drought, even when the aperture of its shell is not sealed in clay. Of course, an entire epiphragm is of great value, and there is no doubt that it was this that enabled the snail *Lymnaea palustris* mentioned in the description of Swamp A^3, (p. 34) to survive its nineteen dead mates, when they were left on the top of a large stone by the retreat of the water.

The ease with which some of the *Lymnaeidæ* form an epiphragm accounts for the occurrence of this species in some small ponds and ditches to the exclusion of other species. Yet in seasons of extreme drought few of these snails succeed in withstanding the severe conditions. Possibly the survivors are those whose epiphragms most securely sealed them in their shells. This presumably accounts for their scarcity in ponds in years following a severe drought. A snail whose aperture is not wholly sealed may withstand adverse conditions but only those hermetically sealed can withstand a more severe drought. This same economic use of mucus is cited by Poulton (vol. 34 of Nature, p. 617) for slugs. He placed a number of slugs in a box with some earth, forgot about them and left them in his study for several months in the hottest weather. He thought, of course, to find them dead and was surprised to find the majority living encysted in mucous capsules. Some had died immediately but the rest were curled up and living.

Presumably the formation of the capsule about these slugs took place in the same manner as that of the epiphragm of the above named snails. As soon as the earth began to dry so that the mucus about the slug began to harden, the animal retreated away from it and a capsule was the result. Those that died may have been the ones whose capsules had been ruptured while the snails were withdrawing from the mucus. Some of the land pulmonates, especially *Helix*, are known to form an epiphragm during long hibernation. Several layers of mucus are formed one within the other, with a greater or less space between them.

Dr. Binney (1878) after watching the process for some time, described the formation of the epiphragm of *Helix hortensis*. He says that the aperture of the shell was up and the collar of the animal was brought level with it and a quantity of gelatinous matter was thrown out. The pulmonary orifice was then opened, and a portion of the air within suddenly ejected with such force as to separate the viscid matter from the collar, and to project it like a bubble of air from the aperture. His description of the formation of the epiphragm of the land pulmonate, *Helix*, refers presumably to the epiphragm formed over the aperture of this snail during cold weather. In drought I have observed that these snails form an epiphragm which is very similar in appearance and is formed in the same way as that of the fresh water pulmonate *Lymnaea palustris*. In such a condition of drought the land pulmonate forms but a single epiphragm which is frail and by no means always entire and no mucus is shot out to project over the aperture like a bubble, but the epiphragm is formed from the mucus left on the foot when the animal ceases to crawl. Observations were made of the formation of the epiphragms which *Helix* produce during cold weather. They are found to be much thicker, have several layers, and look as if they contained a substance like lime. It is possible that this epiphragm may be formed by glands different from those on the foot from which the drought epiphragm is formed.

III. Food and mucus correlated.

There may be, as is suggested above, a constitutional difference in the viscosity of the mucus among the different genera of fresh water pulmonates, but it is certain that the viscosity of the mucus in any given snail varies from time to time according to the amount of food taken. The following experiment will serve to show the changes: Mucus was gathered from the foot of a poorly fed snail while it was crawling on the surface film. *Lymnaea stagnalis* furnishes a larger mass than a *Physa* and hence is better for the purpose of demonstration. The mucus was found to be jelly-like and, when attempts to stretch it were made, broke in thick chunks with but short connecting strings. If this same snail was well fed for 20 to 30 minutes and its mucus examined, it was found to be much thinner and stretched into longer strings without being lumpy. Indeed, this difference may be seen by trying to hold back a snail by its ribbon when it is crawling on the film, when the animal is well fed and again when it is hungry. The poorly fed snail may be drawn in any direction one pleases by pulling back on the ribbon of mucus, but this same snail well fed will not be much affected, because it is not adhering strongly to its less viscous ribbon and glides easily from under it. This difference in viscosity may also be plainly noted by causing poorly fed and well fed snails to move over the powdered substratum. If the thick mucus of the hungry snail is laid down in a homogenous trail, it shrinks away from its path on both sides while a like ribbon of thinner mucus remains intact.

This change in the viscosity of the mucus due to the physiological conditions of the snail has been described for *Limax arborum* by Harte (1862–3) and his observations agree with those for the fresh water snails. He says that it has been observed that when this species is gorged with food, its slime is thin and watery and unable to sustain its weight, but that, after the process of digestion has been performed, the mucus again becomes thick and tenacious.

When *Physa* is taken from food and placed in conditions where it must fast for some days, its mucus passes from a thin watery consistency to that of a thick jelly. As the flowing mucus becomes thicker it diminishes in volume and finally after four or five days there is no visible flow. On account of this condition of its mucus the animal in the fasting condition has some difficulty in remaining attached to the substratum when its lung is full of air.

IV. Nature and process of spinning.

The process of spinning as found among mollusks is not spinning at all, in the sense in which that term is used for spiders or silk worms. The snail leaves the substratum, floats upward through the water by reason of its buoyancy and leaves behind it a fine invisible mucous thread to which the posterior end of its foot is attached. The spinning consists in the formation of this mucus into a filament. There are no special glands or organs for the purpose and the mucus of the thread is nothing more than the mucus of the foot which ordinarily, when the snail is crawling, is left behind on the substratum in the form of a thin ribbon. The thread differs from the ribbon in that it is cylindrical and passes up through the water and is fastened at one or both ends. The snail always begins the spinning of a thread while it is on a solid.

Before entering into a somewhat detailed account of spinning some of the reactions of *Physa* to mechanical stimuli will aid in a better understanding of its behavior. The following observations were first made on the reactions of *Physa* to the stimuli received in its undisturbed environment, and they were subsequently repeated by the use of artificial stimuli applied with a slender glass rod. The reaction following a stimulus varied with the strength of the stimulus. In general, allowing for the difference in physiological state, a weak stimulus produced a positive reaction, while a strong stimulus produced a negative reaction.

A moderately strong stimulus upon the top of the head or tentacles such as a snail receives, when it strikes the sides of a containing vessel as it is moving along at a moderate pace of about forty seconds per inch, causes it to pause momentarily and raise the head. It then moves on. A like stimulus upon the side of the head and one tentacle causes the animal to turn toward the source of the stimulation. A strong stimulus on one tentacle or on the side of the head or on both at once when a snail is moving about one inch in twenty seconds, causes the animal to turn away from the source of stimulation. This may also be seen when the animal strikes these parts against the side of a dish or stone when it is traveling at a rapid rate. A very strong stimulus on the top of head such as a snail receives when struck by a rapidly moving animal causes it to retreat momentarily into its shell.

Any mechanical stimulus on the ventral side of the head and foot causes, at the point of contact, an indentation of the surface. If the animal is still, the muscles of the foot contract so as to form a cup-like depression about an object, but if the animal is moving, the depression becomes trough-like as the foot moves along under or over the object. The depth of the depression corresponds to the strength of the stimulus. If a pencil point is run along the foot of the snail with some firmness, a deep furrow is produced, but if the foot is more lightly touched, a corresponding shallow furrow is formed. This also is true of any object laid upon the ventral surface of the foot when the animal is crawling upon the film. If it is light and floats on the film, no perceptible indentation follows, as the foot moves along it; but if the object is heavier and depresses the surface film, a deeper indentation occurs. This is also true for the edges of the foot, and it would seem that the muscles in the snail's foot sense weight much as the human hand recognizes it.

The thread is invisible when freshly spun and can be seen only after it has remained in the water some time. Long before it becomes visible, however, the snail has left the thread and all opportunity for studying its behavior on it is lost. Warington (1853) gives the method of passing a rod under the creature. This shows the existence of the thread by swaying the animal to and fro. In the present study the following method was employed to study spinning: When the snail began to spin, carmine mixed in water was injected from a pipette into the region of the snail. Great care was taken not to disturb the snail when the carmine left the pipette. The particles of carmine settled down upon the freshly spun thread and enabled one to watch the process. If snails are used that are not accustomed to being handled, they react when spinning, much as they do upon the substratum. The slightest disturbance causes them to either stop or retract somewhat into the shell, and if there is no further disturbance they may then continue the spinning. The chances are that they will either turn about and descend the thread if thus brought to a standstill or expel the air from the lung and sink to the bottom. A slight raising of the anterior part of the snail's foot from the substratum is the first indication that the snail is about to spin a thread.

As the foot leaves the solid, it begins to curl along its margin into a more or less closed cylinder. The curling begins at the anterior end of the foot and runs backward as fast as the foot leaves the substratum, so that the foot curls in very much the way it does when one draws a pencil point along its axis as it is spread out on the film. The tip of the foot is last to leave the substratum and the thread is attached to it. As the snail's position changes from the horizontal to the vertical its attitude remains to all appearances unchanged except for the curling of the foot lengthwise. This composure is in marked contrast to the behavior of the snail when it is unexpectedly dislodged from the substratum, or when, as it sometimes happens, the flow of mucus which forms the thread is retarded and the snail is brought to a standstill in its upward journey. In the latter case the snail loses its composure and stretches its head upward and downward and twists its body from side to side as though trying to break itself loose. If it is successful, it regains its calm demeanor, but if it fails, it turns about and descends the thread to the substratum. The snail's position in ascending a thread varies; the longitudinal axis of its body may be perpendicular to the substratum and its tentacles straight out in front of the head, or the body may be more or less bent. The snail ascends through the water with a smooth, even glide and with no apparent movement of the body. Indeed, the snail's tranquillity while ascending a thread may make the impression that the mucus is being stretched from the substratum into a fine thread by the upward pull of its body. This, however, is far from the truth. The following observations show that the ascending snail is secreting mucus and leaving it in its track just as it does when on the substratum, except that the mucus is in the form of a thread suspended in the water. (1) One may easily be convinced that the mucus cannot be thus pulled into a thread of so great a length if an attempt is made to stretch a piece of the freshly secreted ribbon 40 or 50 times its original length. (2) If the snail comes up on a thread it stops almost instantly when its tentacles touch the film. The same upward pull is exerted on the thread when the snail is thus at rest as before. Yet the thread does not stretch so as to bring the animal perceptibly nearer the film. (3) If a carmine mixture is lodged on the thread as the animal is spinning, the particles retain the same position relative to one another throughout the process, thus showing that the thread is not being stretched during spinning. (4) It may also be noted that there is seen the same muscular activity of the fore part of the foot that accompanies the flow of mucus under other circumstances.

The mucus, which is constantly secreted, passes backward through the funnel formed by the curled foot and adds new length to the thread as the snail goes up, just as the mucous track lengthens as the snail crawls over the substratum. This process may be made clear, perhaps, by referring again to the illustration of the unrolling of the tape from the front end of the hollow flatiron. If the triangular face of the flatiron be curled into a tube, as the iron moves over the substratum, the tape instead of being formed into a ribbon is rolled into a thread. As a rule the flow of the mucus is so continuous that the snail glides gracefully through the water as though impelled by some invisible power. Tye (1878) describes the process of spinning in the following admirable way: "When a mollusk is forming a thread the lateral margins of the foot are brought together, forming a channel for the natural flow of mucus down the sides of the foot to the tail; thus adding to the thread, which is gradually extended."

When the animal has come up on its thread so that its tentacles touch the film, it usually stops, the shell is swung around at right angles to the foot and the siphon elongates and opens to take air on the film. Air being taken, the snail usually turns about and begins to crawl down the thread head first. In turning, the foot may or may not come in contact with the film. If it does so, the mucous thread adheres to the film and thus the thread becomes fastened at its upper end. The film is drawn down into a small concavity where the mucous thread touches it. This is due to the fact that the thread is stretched taut by the upward pull of the snail and presumably also by the shrinkage of the mucus through exposure to the water. Should the foot of the snail not touch the film as it turns to descend, the thread is fastened at the lower end only. The foot fails to touch the film oftener than it touches it, hence there are more threads attached at the lower ends only than there are attached at both ends. It may readily be seen that the chances of the snail's foot touching the film depend largely upon the distance the animal is from the film when it stops to get air. Approximation to the film, in turn, depends upon the length of the animal's tentacles and the quickness with which it stops when the film is perceived. This latter has to do largely with the rate of movement of the animal in its upward ascent on the thread. The turning of a snail to descend its thread is very characteristic and usually consists of a doubling over of the foot which brings together the extremities of its ventral surface. The snail descends its thread head first with its tentacles straight out as in the ascent. The foot is wrapped about the thread in the same relative position that it had when the animal ascended. When the animal crawls down the thread, it thus adds to it a coat of mucus that gives it almost double its former diameter. One may always tell whether a thread is attached at one or both ends by the position of the snail in descending the thread. If the thread is attached to both film and substratum, the long axis of the snail's body is nearly perpendicular to the two parallel surfaces to which the taut thread is fastened, since the foot is wrapped about the thread. If the thread is not fastened to the film the posterior part of the foot is bent over into the form of a hook. This phenomenon is brought about by the thread falling down as soon as the snail crawls over it and thus bending the posterior part of the foot. The snail upon nearing the bottom strikes its tentacles on the substratum and lifts its head and crawls off, leaving its thread where it has fallen on the substratum.

It has been shown that it is possible for a snail to spin a thread upward because the animal's specific gravity is less than water, so that it is buoyed upward as soon as its foot is free from the substratum. It is clearly impossible for a snail to spin a thread down through the water when its lung is full of air. It will be shown later that the snail, on the surface film, takes air frequently, consequently, it nearly always has a specific gravity less than the water. This means that the animal on the film with its lung full cannot descend beneath the water unless upon some solid or upon a previously spun thread. Its only other method of leaving the surface is to give up the air from its lung and sink.

That a downward thread may be spun by *Physa* is illustrated in the following experiment: A very thin sheet of collodion was placed on the water in a bacteria dish and a snail without air in its lung was made to crawl on the underside of this artificial film. Every time the snail approached the edge of the collodion and attempted to take air it was made to turn back by stimulating it on the head with a glass rod. After this had been repeated several times, the snail had increased its speed, through being thus disturbed, so that when it came to the edge of the collodion it was moving so rapidly that it crawled off the collodion film and went to the bottom, and as it descended it spun a thread the end of which was fastened to the edge of the collodion film. Another instance of a snail's spinning a thread downward, but not from the surface of the water, is seen when the animal crawls upon a straw, or filament of alga which extends but part way to the surface of the water. If the animal is coming up at a quite rapid rate the fore part of its foot may leave the end of the filament before the snail has slackened its speed. In case the animal's specific gravity is less than water, the snail continues upward on a thread, but if the snail's specific gravity is greater than water it sinks to the bottom suspended by a thread. Its descent differs from that observed when the animal gives up its air and drops to the bottom in that its foot is not contracted into its shell, and it goes down with an easy gliding motion. Ordinarily *Physa* does not crawl off the edge of a solid, as does the slug *Arion ater;* but it follows the different surfaces of the solid, keeping its head in close contact with them. It has been observed that threads are not spun downward frequently. It happens sometimes that the thread is not spun to the surface of the water, but that the snail's upward progress is hindered for a brief time or that it is obliged to turn around and go back to the sub-stratum, owing to the failure of the thread to increase in length. It also may happen that the thread breaks when the animal is part way up, thus throwing it to the surface with some violence. In the first case where the spinning ceases temporarily and the snail turns and goes down the unfinished thread, its behavior may possibly be made necessary by a failure of the mucus to flow.

The thread that is attached to the surface film is left standing when the animal descends and crawls away and may serve for other snails to crawl to the surface upon or to descend upon.

The thread, if used by the snails to any great extent, attains considerable size since every time a snail crawls up or down it leaves a coating of mucus. Observations show, however, that the threads are of very short duration since the mucus becomes brittle and easily broken and is eaten by the snail, especially if food particles settle upon it.

The following are variations from the process above described in spinning:

1. Instead of the snail taking air, when it reaches the film and then descending in the usual manner as above described, it may crawl with its body partly upon the film and then turn and descend upon the thread.

2. The snail may crawl off upon the film after it has ascended upon a thread and may or may not stop to take air.

3. Several snails may crawl upon an anchored thread at the same time, one crawling over the other if it chances to be moving faster or if one is going up and the other going down.

4. When the thread chances to be spun near the side of a dish or other surface, the snail in taking air may touch the head or tentacles against this solid and may crawl upon it instead of on the thread or surface film.

5. Snails may crawl up on a thread, take air and descend; when they get to the bottom, turn, ascend again, take air, and repeat the journey up and down the thread several times without stopping. They may crawl off finally on the film or on the substratum.

V. Conditions affecting spinning.

1. *Food.* Spinning may be largely controlled by the food supply. This may be proven experimentally at any time that the snails are in good condition, but are not spinning, by feeding them upon apple or raw meat. Repeated experiments show that snails brought from the field and placed in an aquarium with a good food supply, spin very actively while those in a control aquarium with little or no food do not spin, although they move about actively engaged in eating from the sides of the aquarium and are in general in good condition. Now if this experiment is reversed and the well fed snails are given no food and the control snails well fed, the spinning will gradually be reversed. It is rare to see a poorly fed snail spin a thread and equally rare to see a well fed snail refrain from

spinning for any length of time, other things being equal. Food and spinning are very closely correlated, and snails are nearly always seen spinning very actively either upon their food or in its immediate vicinity. A snail that had not been spinning was caused to spin by the following device: A tube, the ends of which were closed with fine wire netting, was placed in the aquarium with snails. The tube was filled with the pulp of apple, only the juice of which penetrated into the surrounding water. Some snails were soon attracted and presently began to spin before the wire netting. This experiment is significant in that the snails did not eat the food, but the flow of their mucus was affected in much the same way that our saliva is stimulated by the odors of attractive food.

It is not known why spinning in *Physa* accompanies feeding. The mucus as shown above is much thinner shortly after food is taken and this may have an important bearing on the initial act of spinning, namely, the detachment of the snail from the substratum. Hart's (1862–3) remarks on the effect of food upon the spinning of the land pulmonate *Limax arborum* are interesting in this connection. "It has also been observed that when this species is gorged with food, its slime is thin and watery and unable to sustain its weight, but after the process of digestion has been performed, the mucus again becomes thick and tenacious." From this it is seen that the mucus when spinning takes place is much more tenacious in *Helix arborum* than in *Physa*. The thread of the land pulmonate is spun down from the edge of a solid through the air, while the water snail spins its thread usually from the surface of a solid up through the water. The snail *Helix arborum* is much heavier than *Physa* and would of necessity require a stronger thread. It also has a reaction above mentioned that *Physa* has not, i. e., the crawling off from the edge of a solid instead of keeping its head in and following the surfaces. It is thus seen that the initial act of *Limax arborum* in spinning is to move straight off from a solid while the foot of *Physa* must be loosened first from the substratum and it is probable that the thinning of the mucus makes this possible.

2. *General activity affects spinning.* The general tonus modifies spinning in that it affects food taking and the general activity of the animal. Light may be shown to accelerate

activity and darkness to have a quieting effect. These facts may be shown by observations upon snails kept in the laboratory by comparing them in the day time and at night when they are placed in a well lighted position. It is noticed in the field that the snails do not become very active until late morning, reaching their maximum in the middle of the afternoon and then continuing active during the early part of the evening. Temperature and light both undoubtedly play an important part in this behavior. An increase in the temperature of the water always causes an increase in the activity of *Physa* even to the thermal death point.

Walter (1906) has shown by an experiment that *Physa's* movements are accelerated in higher temperatures, its rate of movement being as high as an inch in 18 seconds in bright sunlight and as low as an inch in 98 seconds in diffused light. This fact is also brought out on cold mornings and evenings, and during cold weather in spring and fall and in winter hibernation. Spinning is at its maximum in the warmer months. Even in the laboratory it does not go on at a uniform rate during the year. After the snail has been kept in an aquarium for several months, the general tonus of the animal is lowered and its spinning is greatly lessened.

3. *Habitats affect spinning.* It may be readily seen that the habitat in which the snail is living affects the amount of spinning. *Physa* living on stones in such swiftly flowing water as is found in the creek-bed habitat and those living on *Elodea* submerged under quite rapidly flowing water were never observed to spin threads. It is evident that if they did so it would not take long to deplete the habitats of their members, since they would be swept away by the currents as soon as they become loosened from the substratum. These snails, however, move about and eat as do those in still water habitats. If placed in still water they spin as readily as any of the snails of their species, yet in situations where great danger attends the process, no spinning occurs. It can be readily shown that the snail hugs the substratum more closely when the water is agitated than when it is not, i. e., the animal exerts muscular energy at times when needed to keep from being swept away. This may be demonstrated by throwing a stream of water upon a moving submerged snail; it stops and hugs the substratum and if the water

is continuously disturbed it moves about with its shell held closer to the glass. Just how long this muscular exertion can last is a question. Probably in a habitat such as that of the creek-bed above cited, the snail may relax behind a sheltering rock. There is no doubt in my mind that this same muscular energy is exerted to keep it from being floated to the surface when its specific gravity is less than water, and when at the same time mucus ceases to flow for brief periods of time. This is also true perhaps in cases where snails are fasting and but little slime is secreted. A habitat having debris of moderately coarse stems, straws, or grasses has been observed to be favorable to spinning. Snails may be seen spinning from the stems or fine leaves of the plants in such a habitat much oftener than in a habitat with a smooth substratum unobstructed by this coarse vegetation.

VI. Some principles underlying spinning.

Tye (1878) and Warington (1853) believe that all fresh water pulmonates possess this thread spinning power. Tye bases the ability of the snail to spin wholly upon the fact that it can rise to the surface of the water, when its lung is sufficiently full of air. He says (p. 402), in speaking of the method of respiration of the pulmonate snails: "It is on this simple fact hangs the capability of the mollusks to spin an upward and downward thread." While we must agree with Tye that the specific gravity of the snail is important, nevertheless the fact is that all pulmonates do not spin threads. I have kept *Planorbis trivolvis*, *Planorbis tricarnata*, *Lymnaea stagnalis*, *Lymnaea palustris* and *Lymnaea reflexa* under constant observation for two years and have never seen any of them spin a thread except in the case of a very few individuals of the last two named species. These snails have been placed in a variety of the most favorable conditions to produce spinning, but without avail.

On the other hand some individual mollusks of a well known spinning species never spin a thread. Some large *Physae gyrina* from one of the creeks of Kavanaugh swamp illustrate this type. There is but little doubt that the reverse may be true and that certain few of the snails of a species that do not spin threads may be found to spin. This gives rise to a diversity of opinion among different workers. All of these snails have a specific gravity less than water when their lungs are full of air, and all too, secrete a mucous ribbon; therefore it is obvious that reasons must be sought other than the one offered by Tye to account for the fact that some species of these genera spin and others do not. A characteristic difference in the shape of the foot between the spinning and non-spinning gastropod suggests an explanation. Without exception, the snails that spin have slender, tapered or pointed feet, while those that do not have bluntly pointed ones. The more slender and pointed the foot, the greater the ability of the snail to spin. Thus *Physa* stand as the type of spinning mollusk and *Planorbis trivolvis* as a type of the opposite extreme which cannot spin at all. Variation in the shape of the foot may account for the variation in spinning.

VII. Biological significance of spinning.

A snail cannot spin when its lung is not sufficiently full of air to buoy it to the surface. When it is submerged with an empty lung it is obliged to crawl upon some solid to the surface film. It cannot therefore be urged that the spinning is resorted to in time of greatest respiratory need. It is perhaps true that in any habitat where spinning may occur, the animal by spinning gets more oxygen than it otherwise would. It probably has also more frequent access to the food that may be on the surface film and hence there may result both respiratory and food advantages which the spinning snail has over the non-spinner. Spinning may also furnish a means, in some habitats, of reaching the surface film where no other means are available. The greatest advantage perhaps that spinning gives the snail, is that it may leave its submerged food upon a thread, get air, and usually return to the same spot and to its food supply since spinning usually takes place in a food environment. While a spinning snail may get more oxygen and more and perhaps a greater variety of food than one that does not have this habit; yet spinning cannot be thought to be of vital importance to the animal since it will be shown later that the animal breathes by means of both lung and integument and that food is abundant in most localities to so great an extent, in fact, that the animal is more in danger of too much than too little food, since abundance may lessen the oxygen content of the water.

VIII. Brief discussion of the literature on spinning.

The spinning of mollusks has been known since Montagu (1803) recorded the following observations: "*Physa fontinalis* spins a filament by which it lets itself down from the surface after floating." Warington (1852) gives an interesting account of the thread spinning of *Lymnaea glutinosa*, *L. stagnalis*, various species of *Planorbis* and *Physa fontinalis*. He ends by saying that, "All fresh-water snails are possessed of this power." Reeves (1863) does not believe that Montagu and Warington are right in their observations of the spinning mollusks. He gives the following account of his observations: "The *Physa* especially *P. hypnorum* are active in habit, whether swimming foot uppermost, on the surface of water, holding themselves stationary at different depths in the water, or gliding through it in sudden jerks by a hydraulic action of the foot. By bringing the lateral margins of this organ into contact the animal constructs a tube for inhaling and suddenly expelling the water either upward or downward. Montagu stated, and the statement has been repeated by Jeffrey, that the animal spins mucous thread for letting itself down in the water and rising again for respiration; but I have not succeeded in confirming and have great doubts of its accuracy." Tate (1866) in speaking of *Physa* says: "that it ascends at will to the surface in a direct line, or returns to the bottom, or holds itself suspended in the water with facility." "This little *Physa* can raise itself in the water or sink at pleasure, without having resource to plants to assist its progress; in descending through the water the movement is gradual and uninterrupted, and is affected by means of a thread affixed to the surface, a mode of progress analogous to that of some of the land slugs which I have referred to as spinning a line of gelatinous secretion from the skin." Tye (1878) did more and better work than any one else on the subject of thread spinning. He takes occasion to severely criticise Reeve for so coolly doubting Montagu and overlooking Warington and says that the mollusk is capable of "holding itself stationary at different depths in water" when attached to a thread and that no "hydraulic action" of the foot takes place.

I have already quoted Tye's view that spinning is wholly dependent upon the amount of air in the lung. He would therefore echo Warington's statement that all fresh water snails having lung respiration have spinning power. He says in speaking of the thread: "I have never seen a member of this order descend by a thread unless it had first ascended by one, in which case it might return upon the same thread. It would no doubt be possible for it to descend by a thread if its air chamber was sufficiently empty to allow of its sinking; but atmospheric air being essential to the creature's existence, it very rarely voluntarily descends without a supply, and never in such a case by a thread." "The method of anchoring these threads to the surface of the water is singular. A minute concavity at the upper end acts like a small boat, and thus sustains the thread. When one of these mollusks descends by the thread it spins in ascending, it generally carries back the thread with it, gathering it together by a muscular action of the foot; although these threads are sometimes fixed and made to last a considerable time. The longest threads I have seen are those of the *Physa* and I have had in a vessel containing 14 inches depth of water. a number of them fixed by *P. hypnorum*, up and down which they were creeping for eighteen or twenty days together. Permanent threads are kept in position and strong enough for use by the addition of a film of mucus each time a mollusk crawls over them; and I may here explain what I wish to convey by saying that the process of spinning is to a certain extent an involuntary act. When a snail crawls (either a terrestrial or an aquatic species) it leaves behind it a trail of mucus, which is discharged for the purpose of lubricating the foot in its passage over any surface, and if the continuity of this mucus be not ruptured, we have a thread in all respects analogous to those I am speaking of." Tye says that the use of these threads seems to be: (1) "They enable the mollusks to reach the surface of the water gently when no other means present themselves, and to return to its original station, which it often does, after having ascended to the surface of the water and opened its bronchial valve for the entrance of more atmospheric air. (2) It is a much easier method of locomotion. (3) It is a much quicker mode of traveling; for if the surface traversed be smooth, as the sides of a glass vessel, it will take the mollusk twice the time to creep as to float by a thread, while if the surface be uneven, as the sides of a pond, or the leaves of a plant, it would be longer still in creeping. (4) As a great part of the life of the *Lymnaeidae*, especially the *Physa*, is spent in floating upon the surface of the water, where they feed upon the particles of decaying vegetable matter, this property of thread spinning seems admirably suited to their requirements."

Tryon (1882) speaking of the spinning of *Physa* says: "They come to the surface to respire the free air and sometimes may be observed gliding shell downward, on the surface of the water, anchoring or letting themselves down occasionally by means of a glutinous thread." Adams (1896) speaking of *Physa fontinalis* says: "The habit may be watched in an aquarium, where the threads may be seen passing perpendicularly downward from the surface of the water and upward from the bottom."

Perhaps on account of the invisibility of the thread these observers except Tye, were led into the error of supposing the snail could spin a thread downward from the film. Tye went much farther. He clearly saw that an upward thread could not be spun unless the snail could be made lighter than water and that a downwardly directed thread was impossible unless the snails were heavier than water. He did not, however, go far enough, since he attributed the spinning wholly to this ability of the snail to change its specific gravity through pulmonary respiration. According to this, all fresh water pulmonates should have equal power to spin; yet he himself notes that they do not.

Tye seems to be confused upon the subject of threads. He first speaks of all threads being anchored to the film without telling us how, then he says that "where one of these mollusks descends by the thread it spins in ascending, it gathers it together by a muscular action of the foot, although these threads are sometimes fixed and made to last a considerable time." Tye speaks of several other things which would bear a word of discussion:

1. He says the great advantage of spinning is that it is a quicker mode of travel. While this is true it is difficult to see, however, where there is a great necessity for hurry when it has been demonstrated that the snail is in no pressing need of either air or food since it can spin only when fed and when its specific gravity is less than water.

2. He asserts that the greater part of the life of the *Lymnaeidae*, especially the *Physa*, is spent in floating upon the

surface of the water. My observations in field and laboratory failed to confirm this statement. In the field, one finds the snails most of their time on the bottom or among weeds, according to the kind of habitat. In the laboratory, they reach the surface of the water often but do not stay crawling on the surface of the water for long at a time. The reason is obvious if one watches a snail on the film, especially in a small aquarium. When the animal comes within a cm. or so of the side of the dish or other like solid, it seems, at least to the uninitiated, to hasten its speed and crawls under the water as though relieved to get upon a solid. In reality, however, the reason the snail's speed is thus increased when it comes within a certain distance of the glass sides of the aquarium is due to the approximation of two bodies that will not wet, the glass and the snail. The snail's head is brought up against the glass with some force which causes it to lift the head away from the film and to crawl at once down the side of the glass into the water. This is an almost invariable result if the snail is approaching the side of the dish head first. It often happens that the snail comes up to the side of the dish and eats with its foot partly on the glass and partly on the film. The action of the surface film causes the snail, however, to be brought back against the side of the dish, usually with force enough to cause it to crawl down in the water. It is thus seen that, while a snail comes up to the film quite frequently in a small aquarium, its stay there is limited. Tye speaks of some species of snails spinning when young but ceasing to do so when they grow to be adults. I have made no observations which substantiate this view. *Lymnaea stagnalis* has never been seen to spin although it has been reared from the egg in the laboratory.

Walter (1906) has the following to say upon spinning: "Occasionally a snail will be seen dangling in the middle of an aquarium without any visible means of support, but by passing a brush gently through the water a mucous thread will be discovered anchoring the snail, usually to some object at the bottom of the aquarium. A snail thus attached to the bottom by a mucous thread may be seen to gradually spin its way to the surface, the foot meanwhile being rolled into a tube instead of spread out flat. Again, a snail, made light by air bubbles, will sometimes climb down such an anchorage, in which case a stroke of the brush through the water will demonstrate that it has left no mucous trail behind. Possibly the explanation of this curious feat is that since there is nothing to which a new trail may be attached, none is spun out, and consequently nothing is left behind to catch the brush, while the old track becomes entangled in the foot, and is, in a sense, reeled up. Still again, a snail may be found dangling from a thread of mucus let down from some support at the surface. Obviously this is not possible except when the snail has altered its specific gravity by emptying its lung until it can sink in water. In all these various forms of dangling the snail was always seen to carry the foot well out of the shell and at the same time to expend considerable muscular effort in twisting about." From this it would seem that Walter is not aware that the snail can attach its thread to the surface film.

III. FOOD OF PHYSA.

I. Nature of food.
II. Mucus as a food and as a means of collecting food.
III. The effect of drought and temperature upon food taking.
IV. The sensitivity of *Physa* to food.
  a. Sensitive regions of the snail's body.
V. Positive and negative response tochemical stimuli.
VI. Relation of mechanical and chemical stimuli to food taking.
VII. The influence of physiological state upon food taking.
  a. Experiments on food reactions of well fed snails fresh from the field.
  b. Experiments on the food reactions on fasting snails.
  c. Experiments on the food reactions of very well fed snails.
VIII.—General summary.

I. Nature of its food.

Physa lives upon a variety of animal and vegetable food either fresh or partly decayed. Its vegetable food consists of green plants and decaying plant tissue, and it will also eat fruits and vegetables. The green plants that it eats are mainly algae, but it devours as well the tender green shoots of other water plants such as *Chara* and *Elodea*. Such leaves as grass, maple and elm are eaten very commonly when watersoaked and partly decayed but never when they are fresh and hard. Oak leaves are never touched unless the snail is very hungry, and then but little. Leaves are not wholly devoured; the pulp is taken from the vascular bundles on each side, thus leaving the skeleton. Even the smallest veins and veinlets are left intact so that an excellent method of obtaining skeletonized leaves is to place them in an aquarium with hungry *Physa*. *Lymnaea* eats not only the pulp but much of the fine vascular system of the leaf as well. This difference is due perhaps to a difference in the jaws in the two species: the jaw of *Physa* is simple while that of *Lymnaea* is composed of one upper and two lateral pieces. It is no uncommon sight to see a water soaked leaf floating near the surface of the water buoyed up by a number of *Physa* which are feeding upon its pulp. This leaf raft is unique in that the animal is supplied at once with air and food as it crawls about on the surface of the leaf. *Physa*, *Lymnaea stagnalis*, *L. palustris* and *L. reflexa* greedily eat both stale and fresh meat. *Planorbis trivolis* and *P. tricarnata* are vegetable feeders, at least they have never been induced to eat meat in the laboratory.

All of these flesh-eating snails have been seen eating dead houseflies, Mayflies, fish, beefsteak and snails. They will eat such meat fresh, although they seemingly prefer it stale. I have seen them eating dead snails, when the odor from the food could scarcely be endured in the laboratory. The *Lymnaea* cited above have cannibal traits, a character which is especially noticeable in *L. stagnalis*. I have seen this species devouring struggling flies, moths and young snails that have become entangled in its slime. It also attacks and eats its injured mates, leaving nothing but the shell. These observations upon the food habits of *Lymnaea* verify many similar observations of other writers. Semper (1874) observed *Lymnaea stagnalis* eating a live newt (*Triton taeniatus*) although vegetable food was easily accessible. Ullyett (1886) records its overpowering and devouring healthy specimens of the common stickleback in an aquarium. Baker (1902) found *Lymnaea palustris* feeding upon the carcasses of cats and dogs. Walter (1906) says: " The writer also observed that a dozen or more specimens of *Physa sp.* confined in a glass of water with a few amphipods (*Gammarus sp.*) in three days devoured the crustaceans, shell and all." In this case however, there is no evidence that the crustaceans were killed by the snails. I have never seen *Physa* eat anything living, although small snails and other animals have been caught in its slime. The struggle of the animal held in the slime serves to startle *Physa* and causes it to react by drawing violently away from the entangled animal. This allows the latter to escape. Indeed, *Physa* does not make an attack upon other snails even though it is in a starving condition. The ones that succumb to hunger first, however, are greedily devoured by the remaining snails.

The habitat in which the snail is living necessarily determines the kind of diet that it must feed upon. For example, aside from the microscopic animal and plant life, a snail living in running water such as is found in the creek-bed habitat must feed almost entirely upon *Cladophora*. On the other hand, in the pond habitats a mixed diet can readily be obtained, since all debris of dead animals and plants must needs be left to decay where it falls.

II. Mucus as a food and as a means of collecting food.

One cannot watch an active snail like *Physa* moving continuously about leaving a track of mucus behind it wherever it goes, without wondering at the secretion of such great quantities of mucus. In fact, it does not take an active snail long to secrete a mass of mucus the size of its own body. This mucus is insoluble in water and hence if a number of snails are kept in a small aquarium, we should expect to find a perfect interlacing net work of mucous threads such as Pearl (1903) found with his planarians. No such accumulation of mucous threads occur, however, since they are eaten by the snail.

It is a common thing to see *Lymnaea stagnalis* (and other fresh water pulmonates) turn about and eat from the foot the mass of somewhat hardened mucus together with what foreign bodies this has incorporated. Linden (1892) has observed the dexterity of *Lymnaea* in obtaining food from the foot, while the snail is moving upon the surface film. Brockmeier (1898) describes this process as "plankton fishing." The mucus serves not only as a food itself, but is a most efficient means of collecting food for the snail, both on solids and on the film. The trails of mucus left on solids remain sticky and serve as a trap to catch minute plants and animals and other foreign particles. The snails eat continually from the solids, devouring the mucus with all that is caught in it. It thus happens as Walter (1906) records for *Lymnaea*, that the snail may even "engulf and retain the fæces of other snails." This scouring habit of snails is well known and on account of it they are commonly put in aquaria with other animals. The use of the mucus in collecting food may be clearly shown if the animal is on the surface film by sprinkling some fine bread crumbs on the surface of the water. The crumbs collect in masses in the floating ribbons of mucus and soon the snail begins to eat crumbs and mucus together. Gradually the ribbon is pulled into the mouth and thus the snail is enabled to gather food from distant parts. The animal however, scrapes off a great many microscopic plant and animal forms from stones and plants in its habitat, independently of the mucus. The collecting power of the mucus may be satisfactorily demonstrated by examining it under the microscope. Quantities of small animal and plant forms are stuck to it and are thus devoured by snails. In the strict sense of the word, therefore, even *Planorbis trivolis* cannot be said to be a vegetarian. It may be seen also that a great deal of non-nutritious substance is taken into the body of the snail in this wholesale house-cleaning process. Indeed, it is difficult to find clean mucus even when the animal is kept for some time in clear water, as waste epithelial cells and other waste products of the body are thrown off with the mucus.

As has been shown above, the more hungry a snail becomes, the less slime it secretes. At first the slime becomes thick and, as the fasting proceeds, it ceases to flow freely. Consequently one cannot pick up a ribbon of mucus from the surface film behind a fasting snail. The lack of mucus may be also noticed when such a snail moves upon the substratum in that the snail sticks to the surface of the smooth aquarium with difficulty and thus is floated many times to the surface of the water. This would be an advantage to the snail in a region where food is scarce, in quiet water, in that it might feed more often from the surface film, and, in moving water it would be transported to another locality with perhaps a more abundant food supply.

Although *Physa* eats its own and other snail's slime, yet I have seen it while fasting leave its egg masses unharmed, sticking to the sides of the aquarium. Occasionally I have seen a snail while feeding from the sides of a vessel apparently try to ingest an egg mass that chanced to be in its path. Failure to do so was probably due to the tough, resistant capsule in which the eggs are incased.

III. The effects of drought and temperature upon food taking.

The snail takes no food for months during its winter sleep and during desiccation. In the laboratory, however, active snails may die of starvation in four or five days at room temperature, the time varying greatly with the individual snail. Some of these have been revived by feeding even after they had fallen on their sides through hunger.

The snail loses visibly in size from day to day during this period of fasting, the foot being most conspicuous in this shrinkage. In this condition the general activity of the animal is greatly lessened, the snail remaining quiet for long periods at a time even in bright sunlight. The temperature of the surrounding water seems to have a very marked effect upon the snail in its food relations. Eagerness for food is greatly lessened if the temperature of the water is lowered, and increased if it is raised. This is demonstrated by the following experiments: Snails that were kept at room temperature and accustomed to being fed cracker and apple would not respond in the morning to this food if the water in the aquarium had become about ten degrees cooler during the night. If, however, the temperature of the water was raised by the addition of warm water, they would respond to the food immediately and become much more active. Snails that have fasted for some time and have in consequence become very weak and inactive will also go about with greatly increased activity of movement, and the reflex action of the jaws will be greatly accelerated if the temperature of the water is raised.

IV. The sensitivity of *Physa* to food.

As *Physa* feeds, whether upon the surface film, bottom or sides of a pool or containing vessel, the oral surface of the head is alternately applied to the surface and withdrawn from it. As the head is brought in contact with its food, the radulæ close upon its surface and the head is then withdrawn about 1 mm. By this means small pieces of food are torn away so that they may be ingested. Thus the food reaction of the snail consists of a double set of activities; the alternate application and withdrawal of the head from the food accompanied by a rhythmical action of the radulæ. If a snail senses food it turns toward it and gives this food reaction. A piece of fresh meat was placed in the center of a bacteria dish and *Physa* were watched to see how far away they could detect its presence. Maps were made of the snail's paths as they wandered up and down, now on the film and now on the substratum. They would pass within a cm. or less of the meat and not detect its presence; and indeed, might even touch a tentacle against it while moving rapidly, and yet pay no more attention to it than if it were stone. Meat that was soaked in water for about twenty-four hours and then placed in fresh water was seemingly more readily detected than fresh meat used in a similar experiment. Possibly this is due to a difference in the rate of diffusion of the juices in the two pieces of meat. A tube filled with crushed apple, whose juices could be seen to radiate through the fine wire gauze fitted over each end was placed in the aquarium. The snails seemed to detect this for a greater distance than a piece of solid apple. This was due perhaps to a greater concentration of juice in a given area. They would start to cross the path of the radiating juice and then would pause and turn toward the end of the tube.

Different kinds of food were placed in the aquarium to find, if possible, which would be the more readily detected by the snail. Pieces of apple and pear were more easily found than meat, and when crushed more snails collected upon them in a shorter space of time. This was due no doubt, as Pearl (1903) found for planarians, to a greater diffusion of the juices of the food in the surrounding water. It was also found that a food that had an odor was more quickly detected than one that was odorless. Snails seemed to be able to find stale, ill-smelling meat more easily than fresh meat; this is probably the reason that more collect on it than on the fresh meat.

The distance at which the snail, moving at a slow rate, can detect a given food depends largely upon the odor of the food and the rate of diffusion of its juices. The distance is short at best, being on an average not much over 1cm. *Lymnaea stagnalis* as experiment showed, is much more sensitive and can detect food at a greater distance than *Physa;* responding to both strong and weak odors more keenly. Yet this large snail cannot be compared to the graceful *Physa* in general activity. It would seem that natural selection had operated to sharpen the senses in the slowly moving *L. stagnalis* and had left them less specialized in *Physa*, since it had selected in this little creature a sufficiently compensating motor activity.

a. *Sensitive regions of the body.* Experiments were made to locate the regions that were sensitive to chemical stimuli in the exposed parts of the snail's body. It was found necessary, for reasons which will appear later, to use snails fresh from the field, and to select for this experiment only those that were not giving the food reaction at the time. It was early learned that, if the snails were once stimulated with food, their jaws would begin to work and would continue to do so for perhaps an hour or more, even if the animal was placed in fresh clear water. The starting of the snail's jaws into activity and an accompanying lowering and raising of the head are the only means one has of knowing whether or not the food has been sensed by the snail. Thus after the food has stimulated the jaws into activity the same snail cannot be depended upon (at least for some time) to give reliable data as to the sensing of food by other parts of the body. In this experiment such foods as sugar, bread, pear, apple and meat were used at different times, with the same result in each case. The food substance was very lightly touched to the exposed parts of the snail's body, or held in close proximity to them. All parts of the head and the first few mms. of the ventral surface of the foot were found to be sensitive to food. A snail was found to give the food reaction when foods with strong odors such as apple or pear were gently waved several mms. above the snail's extended foot as it moved upon the surface film. The region of the foot that is sensitive to food thus held in the air is the same that is sensitive to food when applied or approximated under water. It could not be determined whether this whole area is sensitive to food stimuli or only some localized parts of it.

It would seem from the above experiments that *Physa* and *Lymnaea* have a sense similar at least, to the olfactory sense, in some of the land snails. The organ of smell in *Physa*, according to Lacaze-Duthiers (1872), is a large ganglion, the osphradium, situated in intimate connection with the lung cavity. So far as can be ascertained this region of the lung is not sensitive to chemical stimuli. The snail does not give the food reaction when food is gently touched to this region or held above it. It would seem probable that this ganglion is more intimately connected with the process of respiration than with food taking.

V. Positive and negative responses to chemical stimuli.

Physa does not respond to all chemical substances alike. This may be conveniently demonstrated by applying chemicals with a glass rod to the region about the mouth when the animal is crawling upon the surface film. *Physa*, *Lymnaea palustris* and *L. stagnalis* respond to chemical stimuli in the same way; but this reaction may be more clearly demonstrated in *L. stagnalis* on account of its size and, perhaps, because this snail is more sensitive. Snails should be used that are accustomed to being handled and ordinarily well fed. By this is meant that the snail should have access to such food as water-soaked grass, or maple leaves and algae, that it would get in the field. If small pieces of bread, meat, apple, or sugar are gently applied to the mouth region, the snail shortly gives the food response, its head often reaching up out of the water. If the side of the head is touched gently, the animal will turn toward the source of the stimulation and give the food reaction. Food with a strong odor such as pear and apple, causes these positive responses when gently waved in the air a mm. or so above these parts.

If a glass rod is dipped in five hundredths per cent. hydrochloric acid and gently touched to the mouth region, the snail momentarily withdraws its head from the film and does not give the food reaction. If it is applied to the side of the head, the snail turns away and does not give the food reaction. Diluted onion juice, pieplant and the juice of a walnut husk also cause a negative response.

The snail responds to a neutral substance, such as chalk, when it comes in contact with the head region, as it does to any mechanical stimulus. The reaction of *Physa* to a food substance may be observed if dry cracker crumbs are scattered near the animal as it is moving slowly on the surface film. When the crumbs are within a mm. or so of the snail's body they are pulled with some force toward the animal. This pull is the result of a surface tension which exists between two substances that form like surface curves, such as two pieces of dry cracker, or a piece of dry cracker and a snail's integument, which are not wet with water. As soon as the cracker crumb becomes wet it is not pulled toward the snail. A cracker crumb that comes thus in contact with the snail's head gives a sufficiently strong stimulus to cause it to withdraw its head momentarily. The crumb remains usually in contact with the head and causes the animal to give the food reaction, i.e., the movement of the jaws and the depressing and raising of the head. The distance to which the snail lowers its head below the film is in direct proportion to the depth at which the crumb rides in the water. The deeper the crumb floats the further the snail depresses its head. After repeated trials the crumb will, perhaps, be brought over the mouth and ingested. If however, the particle passes back over the mouth, the head of the snail rises up out of the water and bends toward the food, the jaws moving the while. An indentation is formed on the surface of the head around the food so that it is held in a cup-like depression. If the crumb is of considerable size, the foot bends toward the head and its edges curl in so that the whole snail is wrapped about the food. This phenomenon is well shown if a piece of meat is given to *Lymnaea stagnalis* when it is on the film. The snail has been seen to hold its food thus wrapped in its foot for hours together while it feeds. If the food once passes from the sensitive region, i.e., the head and the first mm. or so of the foot, the chances are that it is lost, at least, for the time being. It may however, be regained if it chances to be caught in the slime that has hardened on the foot of the snail in the way previously described. The snail bearing a heap of hardened mucus on its foot, turns toward the mass of mucus almost immediately after it has ingested or lost its food, still giving the food reaction. This turning is due, possibly, to the fact that when the animal starts to move forward a pull is felt on the foot from the hardened mucus. In this way it may recover the lost food almost immediately.

VI. The relation of mechanical and chemical stimuli to food taking.

The food of *Physa* is solid, and contact with it necessitates the snails receiving a chemical and mechanical stimulus together. In order, therefore, to interpret the snail's behavior towards food the observer must bear in mind that different food substances, as meat and onion, evoke different responses, some positive and some negative and that the quickness with which the food is perceived depends upon the diffusion of its juices. The snail usually turns away or gives a negative response to a mechanical stimulus of medium strength, and turns toward or responds positively to a gentler mechanical stimulus. The strength of the mechanical stimulus received by the snail in its undisturbed habitat depends upon the momentum with which it is moving when it comes in contact with a solid. A snail moving slowly (about an inch in ninety seconds) strikes a solid and receives a gentle mechanical stimulus which causes it to respond positively; while the same snail moving with greater rapidity (about an inch in twenty seconds) strikes the same solid and receives a stronger stimulus with the result that a negative response is evoked.

In one case a *Physa* was moving slowly toward a piece of meat which had been placed but recently in its path. The meat was fresh and its juices were diffusing very slowly and in consequence the snail actually touched it with its tentacles before it turned toward the food. In this case it is impossible to say which stimulus, chemical or mechanical, produced the reaction, as both would produce the same result.

A *Physa* was observed as it moved slowly toward a piece of onion which had been freshly cut and washed to prevent too rapid diffusion of its juices. The snail touched the onion with its tentacles before it reacted to its presence. It first turned toward the onion, paused, and then turned away. It would seem that in this case the snail responded positively to the gentle mechanical stimulus and then negatively to the chemical stimulus of the onion. The two responses are in different directions, with the result that the snail first approaches and then retreats from the source of stimulation.

If *Physa* was moving at a moderately rapid rate when it came in contact with the meat, it received a sufficiently strong stimulus to cause it to turn away, to pause and then turn back. It would seem that the mechanical stimulus was not only sensed first but obeyed, and then the chemical stimulus was in turn sensed and obeyed. If the onion was used in place of the meat in this experiment, the snail turned away, paused and then continued to move away. The reaction to the two kinds of stimuli were both in one direction;

the mechanical stimulus was obeyed first, then came a pause, and the chemical stimulus was sensed and the resulting reaction was in the same direction as that to the mechanical alone. The experiment was again tried when the snails were moving very actively. In this case they turned sharply away from both meat and onion, and made no pause whatever. The mechanical stimulus alone was obeyed and it is a question whether the chemical stimulus was even sensed.

It would seem from the above experiments that *Physa* senses and responds to a mechanical stimulus quicker than to a chemical stimulus. These are the usual reactions to chemical and to the mechanical stimuli of the ventral surface of the foot and head of the snail. It is necessary to employ the word usual since there is some variation of reaction depending on different "physiological states" as set forth by Jennings (1904) and Pearl (1903). In interpreting the results of the stimuli given in the experiments or received by the snail from its environment, one must gauge the momentum of the moving snail. If this is not considered it may lead to an exaggerated notion of the amount of variation that occurs in responses to stimuli from time to time in a given animal observed. I have found it very difficult to gauge the strength of a stimulus when the animal is moving. Indeed, I find it almost impossible to give a gentle touch enough to cause the snail to turn toward the source of stimulation when it is moving at a lively rate. This difference in the strength of the stimuli depending upon the rate at which the animal is moving, is well illustrated in the snail's relation to the surface film. When the snail is moving up through the water, it strikes the film with a blow that varies with its velocity. In the great majority of cases the animal receives a stimulus of sufficient strength to cause it to throw the head back, thus touching the new surface, the under-side of the film, upon which it then moves away. Sometimes a snail moves very slowly up through the water, in which case the film is so gently touched that it goes on through the film and up into the air. This same phenomenon may be seen in the snail's relation to the mud on the bottom of its habitat. Ordinarily the animal crawls down into the water at a rate fast enough to get a considerable stimulus upon reaching the substratum; unless the mud is exceedingly soft, and even in this case it turns presently and crawls over it. But where the snail moves very slowly downward, it enters the mud for some distance before it gets a strong enough stimulus to cause it to turn around. These examples are sufficient to show that the rate of movement of the animal so affects the usual stimuli received that the resulting behavior brings the animal into a new relationship with its environment, which may even prove dangerous to it. This may be true when the snail is crawling out of the water in the way described above. The chances are that it may slide back into the water, but it has been seen at times to remain stuck fast by its mucus to the dry surface and so to perish. See Walter (1906 p. 29).

The nature of the substance giving the stimulus must also be considered in accounting for the reaction. The stimulus received from a soft substance is weaker than that received from a hard one, if the rate of motion be the same. This may be seen when a snail touches with its tentacles the side of a glass dish as it moves along. The stimulus is sufficient to cause it to turn away sharply. If it strikes the soft parts of a fellow snail or other like substance, however, when moving at the same rate, it reacts positively because it receives a more gentle stimulus.

The experiments on reactions to chemical stimuli were made upon snails from the field. It is clear, that generally speaking, a chemical causing positive reaction may be compared to the gentle mechanical stimulus, and one which causes the negative reaction may be compared to a strong mechanical stimulus.

VII. Influence of physiological state on food taking.

All experiments upon food reactions thus far described, were performed upon snails fresh from the field. The snails used in the foregoing experiments are believed to have been in like physiological conditions, since they were taken from the same environment and used at once. Early in the work it was discovered that reactions of snails obtained from different sources gave very conflicting results, and that no conclusions could be drawn unless the physiological condition of the snail at the time of the experiment was known.

In the following experiments the snails are divided into three groups according to the relative amount of food they had taken. (1) The first group includes *Physa* taken from the field where food was present. These have not been fasting, nor are they satisfied as they always show a readiness to eat. I term their condition well fed. (2) The second group includes those that had had no food near them for several days. They may be spoken of as in a fasting condition. (3) The third group consists of those that have been very well fed in the laboratory.

In performing the following experiments, each snail was placed alone in a clean bacteria dish filled with filtered tap water. The experiments were performed upon the animal while it was crawling upon the surface film. It was found that this position of the snail was by far the most satisfactory one for the operator, since the action of the mouth could be watched conveniently while the chemical was being applied. When two chemicals were given to the snail, one after the other, the animal was washed off after the first application and removed to fresh water, to insure against any trace of the first chemicals remaining before the application of the second. A solution of .05% of hydrochloric acid was found to call forth a negative response if used in small quantities. The chemical was applied by dipping a glass probe into it and touching the snail with it in the immediate region of the mouth. Granulated sugar was found to give a positive reaction and was applied by placing a granule near the mouth. When onion and apple were used, they were crushed and small pieces laid upon the ventral part of the head, or a probe was first dipped into the juice and then in turn touched to the animal's mouth.

a. Experiments on the food reactions of well fed snails fresh from the field.

(1) Mechanical stimuli applied to the mouth or head of a well fed snail, if its jaws were not moving, did not induce the reflex action of the jaws seen in feeding. A stimulus of this nature was given with a glass rod or a piece of chalk applied to the head and on the mouth.

(2) If the snail chanced to be moving its jaws before the experiment then it would continue to do so, and would not close its mouth when touched or when the chalk was brought in contact with the head. Indeed, it would take particles of chalk that were floating on the film into its mouth and continue to do so for half an hour or more at a time. Thus it is seen that the chalk particles did not start the food reaction, but when the reaction was once started, the chalk was ingested. This

experiment was also tried upon mosquito larvae (*Culex* and *Anophles*) with the result that they would fill themselves with powdered carmine or ground red pepper.

(3) If the jaws were not in motion when the animal was brought upon the film, a grain of sugar laid upon the mouth would cause an almost instantaneous response, the jaws beginning to move. This action was not necessarily long continued unless more sugar was applied.

(4) If the action of the jaws was started before the experiment began, one or two touches on the mouth with the acid would serve to cause the mouth to close. In the above experiments a fresh snail kept under the same conditions was used each time.

(5) If acid was applied to the mouth of a fresh snail, the mouth closed or remained so, regardless of whether or not the reflex action of its mouth had been previously started. It then required a steady application of sugar for some time to cause the snail to give a positive response. In one case a snail was lightly touched with the acid on the mouth three times in two minutes, and it took twenty-seven minutes of steady application of sugar to get a brief response of the jaws. After this the periods of response grew gradually more and more frequent. A fresh snail responds to an application of sugar almost instantaneously.

(6) If a fresh snail was given the sugar first and then followed by acid, the animal would respond for some minutes to the acid as if it were sugar; then with the repeated application of acid, the periods of reflex activity of the mouth caused by it grew less and less.

b. Experiments on the food reactions of fasting snails.

The following experiment was tried to see whether reflex action of the mouth could be started by mechanical stimuli alone. Snails fresh from the field were washed thoroughly, their shells being cleaned with absorbent cotton in filtered water. After they had been rinsed thoroughly, they were severally placed in bacteria dishes which had been thoroughly cleaned and filled with distilled water. This precaution was taken so that they could not eat from their own and other's shells, and thus start the reflex by chemical stimulus or odor. At first the snails went about giving the reflex action of the jaws, but as time went on, they became more quiet and few were seen scraping the sides of the dish. This quiet period did not last over an hour or so, the time varying with the individual snail, then they were seen to again give the food reflex. It was found that any mechanical stimulus, such as a glass rod touched to the head or mouth, or bits of chalk would start the action of the jaws. At the end of four or five days of fasting, the snails could not be turned around on the film or disturbed without causing the jaws to open and close and to continue to do so for long periods of time. If the temperature of the water was raised a few degrees, it seemed to make the snails much more ravenous so that they moved about with increased activity and opened their mouths wider, showing a greatly increased food reaction.

1. When the snail was brought to the film for study it was usually giving the food reflex. If now a grain of sugar was placed upon its mouth, the snail responded by an increased opening of the mouth and a raising of the head.

2. If upon the mouth of another snail acid instead of sugar was placed, the animal at once responded by increased action of the jaw and a raising of the head. The animal behaved for the first three or four minutes in just the same way that it did toward the sugar. Absolutely no difference could be seen between its behavior and that of the sugar fed snail unless a large drop of acid was given, in which case the snail drew its head back into its shell, but came up to the film directly and took in the acid as before. After the first three or four minutes the snail closed the mouth for longer and longer periods of time, if the acid was applied every time the reflex started.

3. Now, if the acid was given a hungry snail for five minutes and then sugar given, the snail did not respond immediately as when given sugar at first. If another snail was fed acid fifteen minutes, i. e., whenever the reflex started, it took longer for it to respond to the sugar than it did when the acid was fed but five minutes. This period of indifference to the sugar increased as the time of feeding acid was increased. In one case acid was touched to the mouth of the snail for an hour every time the animal began the food reflex; it then took over four hours for the animal to open its mouth to sugar although its mouth was continually bathed in it during this time.

4. If sugar was given first, then acid applied, the snail ate

acid for nine or ten minutes before it could be made to close its mouth for an instant, and much longer periods elapsed before the snail closed its mouth for any length of time. It might be thought that the constant application of a chemical such as an acid would render the snail insensitive to it; but this does not seem to be the case in these experiments; in fact, the longer the acid is applied the more sensitive the snail seems to be to it and the less number of applications of the acid it takes to cause the mouth to close.

c. Experiments on the food reactions of very well fed snails.

1. A very well fed snail differs from a well fed one in that its chemical sense seems to be blunted. At any rate crushed apple waved over the head of a snail in this condition will not cause the food reflex. It may, however, respond to the apple, if touched to its mouth even though the odor of it failed to call forth a response.

2. Apple may be eaten while cracker crumbs placed around the snail's head elicit no more response than pieces of chalk do.

It is a notable fact that the above results with acid and sugar on the snail in its different physiological states can be obtained by onion and apple or cracker, or even by their odor alone. The following results may be obtained with the onion, cracker or apple.

a. If onion is brought near a well fed snail which is not at the time giving the food reflex, it does not open its mouth but turns away or curls its head into the shell, according to the strength of the stimulus. If it is giving the food reflex, however, it stops and soon refuses to open its mouth again for some time after the removal of the stimulus. If cracker or apple is given first, the food reflex is started and if onion is then given, the well fed snail will eat it for about two minutes as readily as it did cracker or apple. If, however, onion is offered first, the snail does not respond to either apple or cracker for some time thereafter. A hungry snail responds equally well to cracker, apple or onion for the first three or four minutes and then there is less and less response to the onion.

The effect of quinine upon *Physa* is worthy of note. The hungry animal took the quinine powder into its mouth as it did cracker or sugar for the usual length of time and then followed short periods of inaction, but upon further application of the chemical, the jaw action became increased and continued for the two hours it was under observation. The snail threw its head back into its shell and upon the application of the powder it acted disturbed, but it took it into the mouth repeatedly. The foot and head after a time seemed to shrink and the mouth was sunken in somewhat. The snail was alive several days afterward. The quinine seemed to act as a strong stimulant poison, causing increased activity for some time. and then, although the animal became quiet the jaw action continued. In this case the food reflex seemed to have passed entirely beyond the control of the animal after the first few minutes, much as an engine might with the governor thrown out of gear.

VIII. General summary.

Physa is almost omnivorous in its food habits, feeding upon a variety of plant and animal forms, fresh or in various stages of decay. *Lymnaea stagnalis*, *L. palustris* and *L. reflexa* have carnivorous and cannibalistic traits while the genus *Physa* is not known to take living prey; *Planorbis trivolvis* and *P. tricarnata* on the other hand have a vegetable diet only. The conditions of the habitats determine largely the food eaten by the snail, the greater variety being found in still water.

Physa as a scavenger is highly desirable in water.

The mucus secreted by the snail's foot aids it in adhering to a surface and serves as a lubricant, as a food, and as a means of collecting food, since by remaining adhesive in water it entraps all kinds of microscopic plants and animals. Experiments show that *Physa* even if in a starving condition does not eat its egg masses. The physiological state of the snail due to the amount of food taken affects the amount and viscosity of the mucous flow of the foot. A fasting snail secretes but little mucus and it is thick and impedes its progress, while the mucus from the foot of a recently fed snail is rendered thinner and permits greater activity.

Drought and temperature affect food taking. The snail may live for months without food during hibernation and desiccation. Nevertheless, *Physa* will starve in a week or two if kept at room temperature without food. Lowering the temperature decreases the activity and desire for food and vice versa.

Physa can sense its food only at a comparatively short range. The distance depends in part at least upon the rate of diffusion and odor of the food. In spite of the fact that *Physa* cannot sense its food keenly, the snail probably is rarely without food, since the great variety and abundance of food in most habitats together with the animal's constant activity cause it to meet with nourishment continually.

The eyes of *Physa* are rudimentary and probably play no part in the collection of its food. Experiments show that the head and first few mm. of the ventral foot of the snail are sensitive to a food stimulus. If food is touched or brought into proximity to these parts, the animal gives the food reaction. This reaction consists of a lowering and raising of the head, accompanied by a rhythmical movement of the jaws. Experiment also shows that the parts sensitive to contact with food are also sensitive to some foods, if they are waved gently above the surface of the water as the snail crawls upon its film. *Physa* is positive in its reactions to some chemicals and negative to others. The snail turns toward a chemical which induces a positive response and gives the food reaction. In a marked positive response the snail, if it is upon the surface of the water, may raise its head above the film. Other chemicals cause the snail to turn away and fail to give the food reaction and, in marked cases, even to curl its head back into its shell.

Physa alternately approaches and withdraws its head from a food particle that it has sensed until the particle is brought over its moving jaws and ingested. If the food passes backward beyond the region that is sensitive to chemical stimuli the chances are that it is lost to the snail. The ventral part of the head and foot often form a cup-like depression about the food, serving to hold it while the snail feeds.

Table II sums up briefly the behavior of a fresh, well fed snail under a mechanical and chemical stimulus simultaneously received. It is a notable fact that the mechanical stimulus seems to be sensed and obeyed first, followed after an interval of time by the chemical. If the mechanical stimulus is very strong, the snail seems to fail altogether to recognize the chemical stimulus. The physiological state of the snail, due to the amount of food taken, affects its reaction to food. Conflicting results follow a study of the reactions of the snail to food if its physiological state is not previously known.

TABLE II

REACTIONS OF WELL-FED *Physa* TO A MECHANICAL AND A CHEMICAL STIMULUS SIMULTANEOUSLY RECEIVED.

Rate of Motion.	Kind of Solid Food.	Mechanical.	Chemical.	Resulting Reactions of Simultaneous Mechanical and Chemical Stimuli.
Slowly moving.	Meat.	Positive reaction.	Positive reaction.	Turned toward the meat. Positive reaction.
Moderately fast rate.	Meat.	Negative reaction.	Positive reaction.	Turned away, paused and then turned toward the meat. Negative and then positive reaction.
Fast rate.	Meat.	Negative reaction.	Positive reaction.	Turned sharply away from meat and did not pause. Negative reaction.
Slowly moving.	Onion or fresh walnut husk.	Positive reaction.	Negative reaction.	Turned toward the onion or husk, paused and then turned away. Positive, paused, and then negative reaction.
Moderate rate.	Onion or fresh walnut husk.	Negative reaction.	Negative reaction.	Turned away and moved on away from onion or husk. Negative reaction.
Fast rate.	Onion or fresh walnut husk.	Negative reaction.	Negative reaction.	Turned sharply away from onion or husk and did not pause. Negative reaction.

Table III briefly sums up the difference in behavior of the well fed, the fasting and the very well fed snails. A mechanical stimulus does not call forth a food reaction in a well fed snail but if the reaction is first started with food the snail will ingest large quantities of such neutral substance as chalk. A mechanical stimulus not only calls forth the food reaction in a fasting snail but the snail fails for several minutes to sense any difference between the chemical that ordinarily causes a positive response and the one that causes a negative response. The very well fed snail on the other hand, does not respond to foods by their odor and gives no indication that it senses some of its former food. Indeed, the power of *Physa* to discriminate its food substances increases with the amount and, perhaps, variety of food taken.

TABLE III

THE INFLUENCE OF THE PHYSIOLOGICAL STATE OF PHYSA UPON ITS FOOD REACTIONS

Physiological Condition.	Action at time of Experiment.	Application of Stimuli.	Resulting Reaction.	Application of 2nd Stimulus	Resulting Behavior.
Well fed *Physa*.	No food reaction.	Mechanical (Glass rod.)	No food reaction.		
Well fed *Physa*.	Food reaction.	Mechanical (Glass rod.)	Unchanged food reaction.		
Well fed *Physa*.	No food reaction.	Chemical (Sugar).	Immediate food response.	Application of Acid.	Positive response for some time, then gradual negative response.
Well fed *Physa*.	a. No reaction. b. Food reaction.	Chemical (Acid).	a. No reaction. b. One or two applications of acid. No reaction.	Application of Sugar.	Negative response for some time, then gradual positive response.
Fasting *Physa*.	No food reaction.	Mechanical.	Food reaction.		
Fasting *Physa*.	Food reaction.	Chemical (Sugar).	Increased food reaction.	Application of Acid.	Positive response for longer time than in well fed snail.
Fasting *Physa*.	Food reaction.	Chemical (Acid).	First 3 or 4 minutes as though sugar; gradual negative response.	Application of Sugar.	Will not respond to sugar for much longer period than in well-fed snail.
Very well fed *Physa*.	No food reaction.	Mechanical.	No response.		
Very well fed *Physa*.	No food reaction.	Acid.	No response.		
Very well fed *Physa*.	No food reaction.	Cracker or Sugar.	Probably no response.		
Very well fed *Physa*.	No food reaction.	Apple.	No response from odor, but may respond if applied to mouth.		

IV. RESPIRATION OF PHYSA.

- I. Pulmonary respiration.
  - 1. Lung.
  - 2. Process of respiration.
  - 3. Parts of the snail sensitive to air.
  - 4. Physiological state of the snail affects respiration.
  - 5. Relation between respiration and reaction to gravity.
  - 6. Relative buoyancy of *Physa*.
- II. Integumental or cutaneous respiration.
  - 1. *Physa* may live without atmospheric air.
  - 2. *Physa* affected by gases in the water.
  - 3. *Physa* reacts positively to oxygen and negatively to carbonic acid.
  - 4. *Physa's* reaction to shallow waters may be due to greater oxygen content.
  - 5. *Physa's* reaction away from an optimum pond-weed habitat may be due to a diminution of oxygen and an accumulation of carbonic acid.
  - 6. Pulmonary respiration in the young snail.
- III. Summary and discussion.

I. Pulmonary respiration.

1. *Lung.* The lung of *Physa* is a mere infolding of the mantle with numerous blood vessels, but without internal folds. It is situated on the left side of the aperture of the shell near its caudal end and close to the edge of the mantle. A portion of the pulmonary wall may be seen from the outside by looking at the ventral side of the snail while it is crawling on the surface film. This exposed portion of the lung is dome-shaped and shows the aperture, if closed, as a crescent-shaped line whose convex border lies close to the edge of the mantle. The region of the lung about the aperture is capable of elongating into a slender, tentacle-like tube, the siphon, the aperture of which is circular when opened upon the film.

2. *Process of respiration.* In the laboratory respiration takes place at intervals varying from a few minutes to an hour or more; in the field in such waters as the optimum Crooked Lake and creek-bed habitats, *Physa* was not seen to come to the surface for air. *Physa* may be observed to take air into the lung upon reaching the surface film. The snail, upon nearing the film from beneath stops, swings the left side of the shell about through an arc of about ninety degrees until its axis is parallel to the surface of the water. The foot, however, remains in the position which it had been when the snail came to rest The siphon is immediately protruded to meet the air; if the

snail has stopped close to the film, the siphon is extended but little and opens wide upon the film; but if the snail is not so close to the film, the siphon is elongated into a slender tube which opens with a small aperture. If, when the snail stops, it is too far away from the film for the siphon to reach it, it crawls up a short distance further without changing the relative position of the shell to the surface. If *Physa* takes air while crawling upon the film, the siphon is protruded only slightly but opens with a wide aperture; and the shell is raised slightly, but is not swung about as is the case when the snail comes up through the water to take air. The siphon opens upon the film with a sound like the sudden parting of moistened lips. The time during which it remains open varies from a few seconds to a minute or more, depending, presumably, upon the amount of air in the lung at the beginning and upon the size of the aperture. When the lung is first opened, the air is seen to be gently forced out in a bubble which breaks upon the surface film; presumably, the lung then expands so as to form a partial vacuum which becomes filled with atmospheric air. The snail may expel the air from its lung whether upon film or solid, bubble by bubble or in a stream of bubbles. The readiness with which *Physa* gives up the air from its lung when stimulated depends largely upon the strength of the stimulus and whether or not the animal is accustomed to being handled. A snail in this condition may be spoken of as "tamed." *Physa* tamed in this sense expels the air from its lung with reluctance a few bubbles at a time. unless subjected to a severe mechanical stimulus. An untamed snail, on the other hand, empties its lung in a stream of bubbles if the unexpected happens. *Physa* may start to expel a bubble of air and, when it is projected from the siphon, may slowly take it back, thus showing ability of the lung both to expand and to contract.

3. *Parts of the snail sensitive to air.* The tentacles of *Physa* are sensitive to the film or to the stimulus of oxygen. As the snail crawls up through the water, its tentacles touch the film when its body is still some distance away. No sooner do they come in contact with the film, than the siphon begins to protrude; the snail stops and swings its shell about in the characteristic manner above described. The time that it takes a snail to stop after it has received the film stimulus depends

upon its velocity. If it is moving slowly it stops before its head touches the film; if in rapid motion, its head may come against the film before it can stop itself to take air. The tentacles were removed but the snail, upon reaching the surface of the water, took air as before, the only apparent difference being that the snail's head came in contact with the film before the siphon began to protrude, or the shell to turn.

The snail's body was tested for its sensitiveness to oxygen in the following way: The animal was placed in a bacteria dish filled with water and a glass cover placed over it so that there were no visible air bubbles. When a snail was crawling upon the glass cover, a bubble of air was allowed to enter and was then moved so as to touch the different parts of the animal. If the bubble came in contact with the head region, the snail turned its shell at just the angle necessary for the siphon to open into the bubble and took it into its lung. Very small bubbles of air in the water do not produce this reaction; but if the snail's lung is empty, bubbles about two mm. in diameter are sufficient to cause the siphon to open. If the air bubble is brought in contact with the region of the lung, the siphon immediately opens and takes in the air; if it is touched to other parts of surface of the animal there is no response.

The fact that the siphon can sense oxygen independently of the head is demonstrated by holding the snail with its head under water and its lung region exposed to the air. The moist siphon opens almost immediately when it is left exposed to the air; if the snail is accustomed to being handled; but if not, the process may be delayed. The siphon opens and closes at more or less regular intervals much as does the lung of the land snails *Limax* or *Polygyra*. The lung continues to open and close until drying occurs; the snail then withdraws into its shell and all visible respiration ceases.

It is therefore seen that the snail can pick up air bubbles which are under the water, if either the head or the siphon chances to touch them. There is a biological advantage in the fact that the head and siphon region can separately sense air. The continuous exposure of the foot to the air while the animal is on the film precludes its functioning to release the pulmonary reflex. The head and siphon which are submerged seem to release this reflex whenever they come in contact with the film. The snail thus receives a greater number of stimuli to take air while it is under water or while crawling, shell downward, on the surface film. In the latter position, the head and siphon region are both beneath the film; these regions are, however, quite frequently exposed to the film when the animal reaches up for food which has passed back upon its foot; and also if it twists its shell from side to side. This twisting or rocking of the shell is occasioned by a hindrance to the snail's progress. In ordinary locomotion, the shell drags and the snail brings it forward with a jerking motion. This occurs whenever the snail moves, whether upon film or solid, but it is accentuated and modified by anything which still further impedes its movements. The ribbon of slime often becomes thick and filled with foreign debris, and the extra weight causes the snail occasionally to rock its shell from side to side. Thus the siphon is exposed to the film. This behavior may be brought about whenever the slime is sufficiently thick, by putting small shavings of parafin in the mucous ribbon or by attaching a piece of the parafin to the shell with collodion.

The condition of the habitat and the general activity of the snail greatly affect the number of times it is stimulated by oxygen and, consequently, the amount of gaseous exchange taking place in its lung. The solids upon which the snail may crawl to the film, the mucous threads spun, and the amount of food upon the film, are some of the factors which tend to keep the small snail near the surface of the water so that it will more frequently be stimulated by oxygen and consequently will receive more air into its lung.

4. *Physiological state of the snail affects respiration.* The siphon acts reflexly to the stimulus from the surface film but the head and tentacles do not respond as unerringly. There are times when both head and tentacles touch the film, and the snail responds to it without respiration following as though it were a solid. This occasional indifference to the stimulus from the film on the head and tentacles is due to the presence of air in the lung. A snail that has for some time been crawling on or about the film and has taken the air into its lung several times at short intervals, is for a time indifferent to it, much as it shows indifference to food after it has eaten until it is satisfied. In the majority of cases, however, when the head region

of the snail comes in contact with the film, respiration follows; if the lung is empty or partially so, the response is then as invariable as is that of the siphon itself. With this ready response to the film it might be expected that the lung would occasionally become greatly distended with air, so as to make descent into the water difficult. The following may be an instance. A snail started to go down the side of an aquarium, after it had been near the air for some time and, without being disturbed in the least, let a bubble of air escape from the lung. The snail had never before been seen to give up air except when disturbed by an unusual occurrence; it is probable that its lung was so distended with air that it found it difficult to crawl down and maintain its hold. This phenomenon has since been observed several times, but only when the snail has taken air frequently at short intervals of time.

5. *Relation between respiration and reaction to gravity.* If several *Physa* are made to give up the air from their lungs and sink to the bottom of the aquarium in which they are accustomed to live, they begin to crawl about until they reach the perpendicular sides, and then unerringly ascend to the surface film. All efforts to cause them to turn about and go down by giving mechanical stimuli of the usual strength are in vain. Upon the application of unusually strong mechanical stimuli they turn about, but the majority turn immediately back again and ascend to the film. They seem to be insensible to all stimuli but the one that impels them to go upward. Three bottles were stocked with *Physa* and left with the corks removed so that they could have free access to the air for several hours and thus become accustomed to the new habitat. The snails moved in all directions over the sides and bottoms of the bottles and were not seen to collect in any one region. The snails in the first two bottles were then made to give up the air from their lungs and sink to the bottom. The bottles were then filled with water and corked so that there were no visible air bubbles. The snails immediately crawled to the top in both bottles and remained clustered about the cork. The first bottle was then inverted and the snails began almost immediately to turn about and go up toward the bottom, where they remained clustered. The third bottle was filled and corked, as were the others, but the snails were not compelled to give up

the air from their lungs. All three bottles were then inverted. The snails in the first two bottles immediately began to crawl upward away from the earth, while those in the third bottle seemed indifferent to the change in position. They crawled about as before and did not cluster at the upper end of the bottle, as did the others. The snails in the first two bottles had empty lungs. They were so sensitive that upon tilting the bottle even to the least observable angle, they would immediately turn and go to the highest point. The response to the stimulus of gravity was very quick and unhesitating when the animal was in need of air, and it varied with the amount of air in the lung. The snails seemed indifferent to the stimulus when the lung was full.

From the above experiments the conclusion was drawn that snails are negatively geotactic when their lungs are empty, but when they have sufficient air they become indifferent to gravity and crawl in all directions. It can readily be seen that the relation that the snail bears to gravity is of great biological advantage to the animal. If the snail were at all times indifferent to gravity, it might at times lack air if its contact with the surface film were left to mere chance. On the other hand, if the snail were always negatively geotactic it would seek its food at as high a level as its habitat would allow. This would cut off the food supply greatly and indeed would cause many places that otherwise furnish optimum conditions to the snail, to be abandoned.

Physa is seen to be less sensitive to gravity after it has been deprived of air for some time, since it then moves about in the bottle, but is much less active. This behavior is adaptive in that it would be disastrous to the species if the animals remained at the highest points in their habitats when their lungs were empty, in as much as lung respiration is often interfered with by currents or waves and even prevented altogether. The habitat in which the snail lives has a great controlling influence upon the amount of air to which the animal has access. If it is living in swiftly flowing water it has little or no opportunity of reaching the air and even if it could do so it would find great difficulty in opening its siphon for air upon such a disturbed surface. In the creek-bed habitat, for instance, the snail could not reach the air unless it crawled to the side and up the bank; this would be even more impossible in the *Elodea* habitat since the water was deeper , swifter, and the banks were further apart. No snails were observed crawling up the bank; and it would be difficult to see how they would know where the banks were, unless they reached them by mere chance. The same difficulty attends lung respiration in water too deep for thread spinning in which there are no plants or debris upon which the animal may crawl to the film. In most of the habitats where *Physa* are found living, however, the snails have abundant opportunity to reach the air, although they do not always do so.

Relative buoyancy of Physa. Lung respiration causes the specific gravity of a pulmonate snail to fluctuate from time to time. If the snail is dislodged it falls to the bottom, if its lung is relatively empty; if the lung is full of air the snail is buoyed to the surface of the water. The buoyancy of a snail appears when watching a water-soaked leaf on the bottom of the aquarium upon which the snails are feeding. The leaf does not move if few *Physa* crawl upon it and begin to feed; but if eight or ten snails are upon it, the leaf rises to the top and remains there as long as the snails continue to feed. As one after another of the snails crawl away the leaf gradually sinks to the bottom. These changes in specific gravity are evident to a casual observer, but the question arises whether the animal changes its specific gravity by compressing the air in the lung sac. The following observations and experiments bear upon this point: Several *Physa*, while crawling on the film, were gently turned about by means of their mucous ribbons whenever they approached the side of the dish to crawl down into the water. After they had crawled about actively for an hour or more, they apparently grew exhausted but seemed unable to rest with their feet spread out on the film and their shells suspended beneath the water. They either clung together in masses on the film, an unusual thing for *Physa* to do, or slowly expelled the air from the lungs and sank to the bottom. They were accustomed to being handled and were unmolested at the time they expelled the air from their lungs. In no case were the snails able to leave the film and go down into the water, but by expelling some of the air from their lungs. *Planorbis trivolvis* sometimes expels air from its lung so gradually that it requires the closest observation to determine how it descends through the water.

The experiment was tried of keeping *Physa* on the bottom to see whether they could ascend through the water without a thread by means of the expansion of the air in their lungs. No snails were observed to have any such power.

Lymnaea stagnalis is frequently seen to be just heavy enough to barely touch the bottom with its spire. It may then sway around and round as on a pivot. Sometimes it is able to reach the bottom with its head, but it often is obliged to let air out of its lung in order to do this. A slight difference in buoyancy is apparent when its foot and head are extended as compared with times they are retracted. A snail may come up the side of an aquarium and crawl upon the film when its specific gravity is somewhat greater than the water. *Physa* has been seen to be so nicely balanced that, when the ribbon of mucus was gently lifted, the snail slowly sank without giving up any air. The condition of the snail's lung may be tested by gently turning over the snails that are crawling on the film. If they are lighter than water they float shell upward; if heavier, they sink. The snail does not crawl long, however, upon the film with its lung partly empty, since the chances are that either the lung region or the head will shortly receive the respiratory stimulus from the film. I have never observed that *Physa* employs any other means of altering its specific gravity than by changing the amount of air in the lung. This means is in principle what is now commonly held to be employed by Teleost fishes.

II. Integumental, or cutaneous respiration.

1. *Physa may live without atmospheric air.* *Physa* living upon the bottom of streams have little or no opportunity of reaching the surface film if the current is swift. Under these conditions repeated observations lasting over periods of half a day show that they do not take atmospheric air. This together with the fact that the snails avoid the waters which have the most carbonic acid and seek those that are the best aerated, leads to the view that integumental respiration is a continuous process.

Physa that had expelled the air from their lungs were placed in an aquarium with a few water-soaked leaves for food. A wire netting was stretched tightly across the aquarium about half way up, so that the snails could not reach the air. The water above the netting was aerated by passing bubbles of air through it. None of the bubbles were allowed to pass beneath the netting, but the movement carried sufficient circulation to keep the water around the snails more or less well aerated. The power of *Physa* to live without lung respiration was demonstrated by the fact that most of the snails were alive after sixty-two days. The snails that were breathing entirely through their integument were inactive; compared with a control series, they moved but little and kept near the upper or better aerated water. Shortly after the screen was removed the snails came to the surface, took air as before, and soon became more active. In the field, in habitats having well aerated waters, such as the optimum creek-bed and the optimum Crooked Lake habitats, the snails do not come to the surface and the oxygen which they use is supplied, perhaps, wholly by integumental respiration.

Physa has been taken by a number of observers from water so deep that there was no possible means of getting air. Forel (1869) who took some of the *Lymnaeidae* from a depth of over 250 m. in Lake Geneva, Switzerland, says that in every case the lungs of the snails taken from this great depth were filled with water, when brought into shallow water they began immediately to crawl up to the surface and to inspire air just as if they had never experienced abyssal life. It is impossible to speculate as to the length of time these snails had led a deep water life. They may have been bred there and their ancestors for years before them may have lived in this deep water environment. On the other hand, they may have been very recently swept from shallow water. Whether it was years or months that these snails and their ancestors had obtained their air supply from water, the fact remains that they had not ceased to be negatively geotactic when the lung was empty in shallow water, nor did they fail to respond to the stimulus of the surface film immediately, whenever circumstances permitted. It would be of interest to know how long it would take to modify or extinguish such reflexes or instincts if totally unused.

It is a question as to how the snail's lung became full of water in each case where found living as abyssal fauna, since the pulmonate snail never opens its lung under water unless to take air. They might have been swept into deep water by a strong current or wave while crawling along the bottom; if the snail's lung was full it either gave up its air through the force of the water striking it, or else it was dislodged and came to the top of the water. In the latter case, there would be absolutely no chance for the animal to go under water, unless it did so by expelling the air and falling to the bottom as did the snails which were kept from crawling down the sides of the aquarium. If the lung was comparatively empty it would be but a question of depth of water. The pressure of the water on the outside of the lung would be greater at a certain depth than that of the air within, and the latter would in consequence be displaced by the former. This reasoning is based upon the results of observations made in the field which show that *Physa* does not crawl into deeper and deeper water. Hence it would not in this way gradually reach say a depth of one hundred and thirty fathoms in which Forel found it. *Physa* reacts so delicately to depth that an increase of a few inches often serves as a barrier. Experimental evidence showing the part that depth of water plays in the local distribution of *Physa* is found in the history of the Cemetery Pool, Ann Arbor, Mich. Formerly, the snail lived only on the side of the pool where an inwash made the waters shallow. The bank was artificially filled and so graded that it was gently sloping on all sides. The limited and discontinuous distribution of *Physa* was thereby changed to a continuous one and the animal was found inhabiting the shallow marginal waters.

2. *Physa affected by gases in water.* If *Physa* are kept in a deep bottle for some days they gradually collect about the mouth, and they will remain close to the surface film if the water becomes foul. If snails are placed when their lungs are comparatively empty in water well saturated with carbonic acid, they will die in a short time; but if less of the gas is dissolved in the water, the snails crawl to the surface and rest against the film, or crawl half way into the air. If *Physa* are kept in boiled water, they crawl to the surface and rest just under the film. If, however, they are put in a bottle of boiled water which is so closed as to shut them off from the air, they become much less active and die several days sooner than snails kept in tap water under similar circumstances. If a *Physa* whose

lung is relatively empty is put into chemically pure distilled water which has not taken up air from the room during the process of condensation, it dies before it can reach the surface of the water. If, however, it is allowed to take up more or less air, or is shaken, the snail lives for some time but remains near the surface film. If the water is aerated by passing atmospheric air through it, the snail lives as in tap water. It is thus seen that *Physa* dies if air is lacking or carbonic acid is in excess in the water and that it collects near the surface film if the water is foul, if it contains little air, or has carbonic acid to a certain amount.

3. *Physa reacts positively to oxygen and negatively to carbonic acid.* An inverted bottle was partly filled with oxygen and a number of *Physa* were placed in the neck and allowed to crawl up to the oxygen above. Each snail ascended until its tentacles touched the surface film, when it opened its siphon and filled its lung with oxygen. The reaction was most positive, the snail even resting its head and foot against the film and crawled upon its under surface. They were allowed to breathe the oxygen for twenty-four hours, and the only difference noticed between them and the control snails breathing air, was that the former were more lively and seemed to be very hungry. This same experiment was tried with carbonic acid instead of oxygen. The reaction of the snails differed according to the velocity with which they came up the side of the bottle to the surface film. If the snail chanced to be moving very slowly, it would upon touching the film stop, withdraw its tentacles, then slowly protrude them again and touch the film again, withdraw the tentacles, turn and go down into the water for about an inch and then turn back to repeat the former procedure. The snail that chanced to be moving upward at a lively rate when it touched the film with its tentacles immediately swung the shell about and touched the film with the siphon. The moment the siphon touched the film, however, it was withdrawn and the snail turned immediately and went down. One snail moving more rapidly than the others reacted toward the carbonic acid as though it was air; opened its siphon and took in some of the gas before the negative reaction occurred. The snails that touched their siphons to the film, and especially the one that took in carbonic acid into the lung, subsequently

descended further into the water than did those that touched only their tentacles, i. e., the reaction seemed to be more intense. The lungs of the snails were partly empty and they were therefore negatively geotactic; nevertheless they reacted negatively to the film on account of the presence of the carbonic acid gas. The snails were left in the bottle for about twelve hours. At the end of this time most of them were to all appearances dead, while those that were still able to crawl were found down in the neck of the bottle as far away from the film as they could crowd. All of the snails revived after they had been kept in well aërated water for some time. *Physa* reacted very strongly away from the carbonic acid. Indeed, the snail's behavior to the gas was such that an observer might be inclined to say that it was very much surprised at finding something so disagreeable in the place of air and that it was loath to believe the impressions of its tentacles and siphon and went back to touch the film many times before it could be convinced that so unexpected a change had occurred. The snail that was crawling up to the film slowly, touched it, stopped, sensed the carbonic acid, and reacted negatively. The one, however, that was moving at a rapid rate reacted to the carbonic acid film as though it were an air film, before either the tentacles or siphon discriminated between them. The snail's reactions to carbonic acid gas and oxygen were modified by its momentum much as was its reaction to food and we may note that the effect of the mechanical again precedes that of the chemical stimulus.

The following experiments give an idea of the delicacy of the reaction of *Physa* to oxygen. A large number of *Physa* were placed in a galvanized iron tank six by four feet and containing water about five inches in depth. Water was allowed to fall into the tank drop by drop, from about one inch above the surface, and caused a slight foam to gather at the point where it struck. The *Physa* collected in great numbers about the foam in a circle about a foot in diameter. The greatest number of snails was found near the place where the water dropped into the tank and the number grew less as the distance from this point increased. Snails were not found to collect on the bottom of the tank in this region nor about the outlet pipe. The cause of this distribution admits of several possible factors being considered: (1) Light, (2) temperature, (3) mechanical disturbance of the water, (4) a greater oxygen content of the indropping water. These various possibilities were tested as follows: The water was allowed to drop into different parts of the tank by changing the hose from place to place. In every case in the course of a few hours the snails would collect as before; the time required depending upon the general activity of the snail. Light as a possible factor was thus eliminated. No difference in temperature could be detected in different parts of the tank. The fact that the water dripped into the tank slowly from small pipes exposed to room temperature, accounts for the uniformity of the temperature. There are two possible factors which may account for the gathering of the snails, disturbance of the water and the relative amount of oxygen.

After the water in the tank had become again equally aërated throughout, air was forced through it in different parts of the tank in succession, so as to produce areas of greater oxygen content. After a time the snails collected in the better aërated waters. There were about two hundred and fifty snails in the tank and at one time there were fifty gathered on the pipe where the water, agitated by bubbling air would break over them. Other like tubes dipping into the water but having no air or water leaving them had few or no snails upon them. About one hundred and fifty snails were found in the fourth of the tank in which the air was bubbling, but not in the most disturbed waters. The thermometer again showed no difference in temperature. The following experiments were performed to see whether the snails were attracted merely by the mechanical disturbance of the water rather than by aëration. A very thin rubber bag was placed over the end of the tube through which the air was passing in such a way as to transmit the motion of the air to the surrounding water but without aërating it; i. e., the air was allowed to escape through the mouth of the bag without touching the water outside. The snails did not collect in the region or on the bag. A stirrer, such as chemists use, was propelled by a water motor and made to stir the water in the tank. The paddle of the stirrer revolved in a horizontal plane at the bottom of the tank, so that the surface of the water was not disturbed and in consequence was not mixed with air.

The snails did not collect but, if anything, seemed to avoid the disturbed water. It seems, therefore, that *Physa* do not react positively to motion of this sort in the water, and that it is the aëration of the water that causes them to collect.

It is probable from the above observations and experiments in the laboratory that *Physa* in the field collect in certain habitats because they react positively to oxygen, and always go into waters which contain the highest percentage of oxygen (whenever suitable protection offers) and away from water which contains carbonic acid gas.

4. *The reaction of Physa to shallow waters may be due to greater oxygen content.* The extreme sensitivity of *Physa* to oxygen suggested a possible explanation of the fact that the snail is always found in very shallow waters in the field. The waters in *Physa's* most favorable habitats always have two and often three means of aëration.

1. According to Whipple and Parker, shallow water takes up air until it is saturated.

2. Submerged water plants are well known to add oxygen to the water.

3. According to water analyses quoted by the above authors, water may be saturated before, and supersaturated after being mixed with air in its passage over a fall. Water may also become supersaturated in lakes and rivers by wave action. In the optimum habitat of Crooked Lake all three of these means of aëration are present. The snails, however, were not found in abundance in water over fourteen to eighteen inches in depth, although other conditions remained the same. It was not because the water at this depth did not contain sufficient oxygen, but because the thinner sheet of water nearer the shore had probably a greater oxygen content and the snails collected there, responding as delicately to oxygen in the field as they did in the laboratory. The greater the distance from the surface of the water the greater the percentage of carbonic acid gas found in it and *Physa* reacts as negatively to this gas as it does positively to oxygen. Thus it is seen that *Physa's* negative response to carbonic acid and its positive response to oxygen may explain its gathering in the shallow marginal waters.

5. *The reaction of Physa away from an optimum pond weed habitat may be due to diminution of oxygen and an accumulation*

of carbonic acid. A preliminary examination of the water from an optimum *Hypnum* habitat and from an aquarium having an excess growth of *Ceratophyllum* showed that the amount of oxygen and carbonic acid varied with the day and time of day. Water from an optimum *Hypnum* habitat had less oxygen than tap water, and water from the weedy aquarium had less oxygen and more carbonic acid on the average during the day than did that from a less weedy one, which had the same conditions with relation to light. Unfortunately the work was cut short before precise and full data could be obtained and these incomplete results would not be mentioned did they not suggest an explanation of why *Physa* avoids an optimum pond weed habitat. Birge and Juday (1911, p. 115).

Water plants give off oxygen and consume carbon dioxide during the process of photosynthesis, which takes place in sunlight. In a crowded condition much of the plant is shaded; hence the process of photosynthesis is greatly lessened. In consequence a less amount of oxygen is liberated and less carbonic acid gas is consumed. Respiration, however, is in all probability normal during this time; hence oxygen is being consumed and carbon dioxide liberated during the full twenty-four hours. This may account for the lack of oxygen and the excess of carbonic acid gas in an optimum water weed habitat and for the small number of snails in such a habitat.

6. *Pulmonary respiration in the young snail.* In order to study the respiration of the young snail, a number of egg-masses of *Physa* were allowed to hatch in the laboratory. When they first came from the egg mass, the snails were found to be heavier than water; they could, however, crawl on the surface film. The young snail's lung was either full of water or had not been as yet inflated. If placed in the center of the bottom of the aquarium they reach the side and crawl up to the surface film with the directness of older snails whose lungs are empty. The newly hatched snail is not long near the surface film before it opens its siphon to the air. The lung can be seen to inflate as the air enters and its outline can be plainly traced through the transparent shell. The young snail may be said, therefore, to react to the film in respiration as does the adult. It is not as sensitive to air when it is first hatched as the adult, inasmuch as it does not open the siphon immediately to the film when

it touches it, but remains for some time in contact before taking air into the lung.

III. Summary and discussion.

1. *Physa* may fill its lung with atmospheric air while it is upon a vertical or horizontal surface. The extent to which the siphon is protruded and the size of the aperture depend upon the distance of the snail from the surface film.

2. The lung has power of contraction and expansion and is presumably filled by the formation of a partial vacuum. The shell is swung about through an arc of ninety degrees if the snail takes air while upon a perpendicular surface; if upon the film the body is merely raised slightly on the left side.

3. The head (except the ventral side) and the region of the siphon are sensitive to an oxygen stimulus. The snail can sense and pick up air bubbles under water. If the head touches the bubble the shell is swung about at just the right angle for the siphon to open into it. Pauly (1877) observed the *Lymnaeidae* picking up bubbles of air under the water; he thought that the snails he had observed which did not come to the surface for air received their oxygen supply in this way.

4. The siphon acts reflexly to a stimulus from oxygen. If exposed continually to the air, the lung opens at more or less regular intervals and resembles the pulmonary reflexes in the higher animals. The head does not respond to the oxygen stimulus as unerringly as the siphon does. If air has been taken into the lungs repeatedly at short intervals, the head and the tentacles may respond with indifference to the stimulus of the film, much as the snail failed to respond to a food stimulus after it is very well fed.

5. The amount of air taken into the lung at any given time depends upon the amount of air already in the lung, the frequency of oxygen stimuli received, the size of the aperture and the length of time the lung remains open. Pauly (1877) believes that the intervals between breathing depend upon the distance over which the snail has traveled to reach the film. Walter (1906) thinks that the amount of atmospheric air which is taken by any individual during the twenty-four hours depends not so much upon the number of times it opens its respiratory tube at the surface, as upon the length of time the tube remains open for inhalation. He noted that some snails kept the siphon

open a fraction of a second; others kept it open ninety-six seconds. Walter apparently does not take the size of the aperture of the siphon into consideration, and this would doubtless modify the length of time taken to fill the lung. He also cites the case of a snail that "took breath" several times in quick succession and "sets it down as an expression of individuality on the part of this individual snail, due to some internal cause." I have observed this behavior quite frequently in *Physa* and believe that it may be seen at any time in any snail that receives oxygen stimuli at short intervals.

6. Davenport and Perkins (1897) found that slugs were geotactic. Walter (1906) finds that pond snails "are negatively geotactic in direct proportion to their lack of oxygen" and "are positively geotactic when supplied with sufficient oxygen." He says, "When several snails (*Lymnaca elodes*) were put in a square bottle, stoppered under water to exclude bubbles of free air and then placed on one of its sides, they soon congregated on the upper surface and remained there. In this case negative geotaxis was stronger than any other stimulus which could cause them to travel back down in the way they normally would if they had received a fresh supply of oxygen." Again he says: "Upon placing the flask in an inverted position they crawled up to the highest point, but, receiving no air, they seemed to experience great difficulty in passing beyond the 'pole' and down the other side, although the substratum was continuous, presenting no barriers. After reaching the highest point in the flask and finding themselves unable to renew their air supply, their ordinary behavior, to which there were some exceptions, was to let go and drop like dead weights." *Physa* is negatively geotactic if its lung is empty but manifests indifference to gravity if its lung is full. It crawls upon or under the film, up or down the sides of the aquarium, upon a thread and upon the bottom. If *Physa* is placed in a bottle in which the air supply is cut off, it will if in need of air, come to the highest point. If the habitat is strange and the snails are not allowed to take air before the bottle is corked they do not collect at the highest point; if accustomed to living in the bottle before it was corked, they will gather about the highest point and the time they remain will depend upon the degree of familiarity with their habitat. *Physa*, after they have been denied atmos-

pheric air for some time manifest indifference to the influence of gravity, and scatter over the sides and bottom of the bottle. They have never been observed to "let go and drop like dead weights" upon being denied atmospheric air.

7. *Physa* has no power to change its specific gravity by expanding or contracting the air in its lung; a change in buoyancy is brought about only by taking air into the lung or expelling it. The snail may crawl upon the surface film even though its specific gravity is greater than water, since the foot and the slime ribbon offer an expanded surface.

8. *Physa* lived in the laboratory in aërated water for sixty-two days when denied atmospheric air. They were much more inactive than the snails in the control experiment which had access to atmospheric air.

9. *Physa* is affected by the gaseous content of the water. If water lacks air or contains much carbonic acid the snails will come to rest near the surface film. They die sooner in boiled water than in water that has not been boiled.

10. *Physa* reacts positively to oxygen and negatively to carbonic acid. Experiments in the laboratory show that the snail reacts very delicately to oxygen, gathering in those parts of the water that have the highest oxygen content. They thus corroborate the observations in the field.

11. In very well aërated waters such as the creek-bed and the optimum Crooked Lake habitats, *Physa* obtains almost its entire oxygen supply through its integument, as it rarely, if ever, comes to the surface for air. Moquin-Tandon (p. 81) kept *Lymnaea glabra*, *Planorbis rotunda* and *Physa sp.* without atmospheric air for four days. Saint Simon (1853) kept *Physa sp.* and *Planorbis contortus* four and twelve days and Pauly (1877) kept two specimens of *Lymnaea stagnalis* ninety-one and twenty-two days without air. Walter (1906) says that, "When *Lymnaea elodes* is prevented from coming to the surface for atmospheric air it dies." Walter's results are not conclusive as there is some reason to believe that his snails died from lack of oxygen rather than from the absence of atmospheric air. v. Siebold (1858) noted that *Lymnaea auricularia*, *L. mucronata*, *Planorbis carinatus*, *P. laevus* and *L. stagnalis* were not seen to visit the surface to take atmospheric air in shallow or running water. Pauly (1877) confirms the

statements of v. Siebold in observations made upon *L. auricularia*. The pulmonate snails taken from abyssal depths by v. Siebold (1858), Forel (1869 and 1874), Pauly (1877), Forbes (1888), Walker (1900), and Andre (1901), undoubtedly abstracted their oxygen supply from the water through the walls of their lungs, which were filled with water, and through their integument. Tryon (1882) observes, "The air-breathers that inhabit water are obliged to visit the surface frequently; and stale water is so inimical to the water-breathers that they soon attempt to escape from the confinement of a glass or basin unless the water is frequently renewed." Willem (1896) shows that, if water is aërated, *Lymnaea* and *Planorbis* can live without atmospheric air. He regards the cutaneous respiration as much more essential than pulmonary. Walter (1906) observed that *Limnaea elodes* came to the surface to take air twenty times in an hour if kept in spring water and forty-four times in boiled water; while he admits that pulmonate snails absorb a certain amount of air from the water, yet he thinks they cannot take the required amount in this way. He speaks of breathing without coming to the surface as abnormal and says "in certain rather rare instances, snails may be made to survive for certain periods when forcibly kept under water. Death ensues prematurely in such cases and the inability of the snail to adapt itself suddenly to extracting its air supply from water alone is clearly demonstrated." He evidently regards the absorption of oxygen through the snail's integument as a new adaptation and not as a process that is taking place continually, whether the animal is using atmospheric air or not. He regards the pulmonates that are living in deep water as those, "modified to such a degree that they extract all their necessary oxygen from air contained in water."

12. The reaction of *Physa* away from the deep water and toward the shallow is probably due to the greater amount of oxygen in the shallow water. Tryon (1882) has made the following observations: "The depth at which shell fish live is probably influenced by the quantity of oxygen which they require; the most active and energetic races live only in shallow water, or near the surface; those found in very deep water are the lowest in their instincts and are especially organized for the situation."

13. A preliminary examination of the water of an optimum pond weed habitat for its gaseous content, showed an abnormal amount of carbonic acid and a small amount of oxygen. If the observation is confirmed this condition of the water explains the reaction of *Physa* away from such habitats. The amount of oxygen and carbonic acid may be explained in the following way: Plants, crowded together are shaded so that photosynthesis is interfered with and, in consequence little carbonic acid is consumed and but little oxygen liberated. Respiration is normal and a large amount of oxygen is consumed and carbonic acid liberated from the large mass of water plants. Birge (1908, pp. 1286-7).

14. The lung of the newly hatched *Physa* is either filled with water or has not as yet been inflated. The young show, if their lungs are empty or filled with water, the same geotactic response as do the older snails. When but a few hours old they go to the film and fill their lungs with atmospheric air. Baker (1902) says regarding *Lymnaeidae*, "It is interesting to note that the young animals breathe through the water for a long time, but finally acquire the normal characteristic of the family, which is breathing the air directly."

V. SOME PSYCHIC PHENOMENA OF PHYSA.

I. Sensitivity of *Physa*.
II. *Physa* varies in its reactions, due to differences in experience.
III. Reaction of *Physa* to a new experience.
IV. Adjustment of *Physa* to a new experience.
V. *Physa* forms associated memories of its habitat.
VI. A young *Physa* differs from the adult in the character of its responses.
VII. Differences in the reactions of *Physa*, young and adult.
VIII. Summary and discussion.

I. Sensitivity of Physa.[1]

The response of *Physa* to oxygen and to gravity is rivaled in delicacy by its reaction to a disturbance of the general environment. The snail "hugs" the substratum if the aquarium in which it is living is slightly jarred. *Physa gyrina* living in water two inches deep, has been seen to react thus, while upon the bottom, to the slightest disturbance of the surface film such as is made by the breath.

Physa also reacts delicately to a localized mechanical stimulus. It is a common sight to see it whirl its shell quickly about, often

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[1] In this work, the writer has made no attempt to measure, in mathematical terms, the delicacy of the reactions of *Physa* to stimuli.

through an arc of one hundred and eighty degrees if another snail comes in contact with it. This reaction to a contact stimulus is not common in other mollusks and is perhaps due to the mantle of *Physa* being reflected over its shell. On account of this reaction, *Physa* are not usually found in contact with one another even though thousands are living in an optimum habitat. Occasionally, if the water lacks oxygen, they may be seen in masses about the surface film, or in the angles formed by the sides of a rectangular box or bottle. This latter reaction is marked in *Physa* and is similar to that which Pearl (1903) found in planarians and called goniotaxis.

II. Variations in the reactions of *Physa* due largely to differences in experience.

No exact statement can be made as to the delicacy with which *Physa* reacts to a general disturbance of its environment or to a localized mechanical stimulus, since there is a wide difference in response among members of the same species and in the same individual from time to time. Changes in the physiological state may be causes of the differences in the snail's behavior, but the cause underlying the diversity in the physiological state must be sought and in a measure controlled before the behavior of the snail can be analyzed with any degree of accuracy.

There is sometimes a considerable difference in the reactions among the *Physa* of the different aquaria. A snail in one aquarium may be so sensitive that it reacts to the breath upon the film while another snail in a different aquarium may be touched with a pencil before it gives a like response. Here the difference in responsiveness is due to the amount of handling to which the snail or the containing aquarium has been subjected, since all environmental conditions were essentially identical. The snail that reacted so delicately to a disturbance of the film had been kept alone and undisturbed for weeks, while the one that failed to respond so delicately had been handled and had been accustomed to the experience for some time. The experiment was reversed. The tamed snail was kept by itself, wholly undisturbed for weeks, and the sensitive snail was handled, with complete exchange of their physiological states as a result. This phenomenon was observed early in the work. In subsequent experiments on their reactions to various agents the snails were reduced to a like physiological state (i.e., they were accustomed to being handled) before the experiments were begun. Similar phenomena were observed in land pulmonates. The snails that were kept in an unfrequented room, would retreat into their shells if approached, while those that were kept in the busy laboratory where they were handled more or less, could be picked up without retreating into their shells. Indeed, they often became so accustomed to being handled that they would withdraw into their shells only after very rough treatment.

It was observed that, even in an environment (field or laboratory) free from human disturbance, great diversity in the character of the response to the same stimulus was manifest. This difference was due, at least in part, to a difference in the amount and kind of stimuli received by the snails in the different habitats. That the environment of these snails was not uniform may be seen by referring to Table IV, which gives the chief sources of mechanical stimuli in some of the most favorable habitats. Some of the reactions uniformly shown by *Physa* in its undisturbed habitats are as follows:

TABLE IV.

SOURCES OF STIMULI RECEIVED BY *Physa* IN FIELD HABITATS.

Optimum Crooked Lake Habitat.	Optimum Creek-bed Habitat.	Optimum Creek-ditch Habitat	Swamp Pool Habitat.	Pond North of the Campus.
Soft, clean substratum.	Stone and gravel substratum, mostly covered with soft Cladophora.	Many water-weeds used as a substratum.	Soft substratum, moderate amount of soft algae.	Clay substratum obstructed with rubbish.
Quiet surface film.	Disturbed surface film.	Moderately disturbed surface film.	Unbroken film.	Unbroken film.
Quiet water or nearly so.	Running water.	Gently flowing water.	Quiet water.	Quiet water.
A few weeds in some parts.		Weeds, brush and the like.	Substratum covered with waving Tubifex.	Many water plants but no macro-flora.
Many *Physa*.	Many *Physa*.	Many *Physa*.	Many *Physa*.	Many *Physa*.
No other animals large enough, at least, to give a stimulus.	No other animals of sufficient size to give a stimulus.	Some beetles and insect larvae.		A number of frogs, many tadpoles, beetles, etc.

It reacts alike to all stationary objects. The reaction resulting from contact with such an object depends, as has been previously stated, upon the momentum of the snail and the character of the substance, whether hard or yielding. *Physa* reacts to motion in the habitat in the following ways:—Gently flowing water does not visibly affect the snail, while rapidly flowing water causes it to contract and hug the substratum. Snails which meet, respond positively or negatively according to their momentum. The motion of the water caused by the swimming of tadpoles, frogs and insect larvae does not call forth visible reactions unless the moving object comes very close. If these animals touch the snails, the latter react momentarily. Tadpoles were introduced into a habitat in which the snails were, at least for some time, totally unused to the presence of such animals. The sudden onslaught of a tadpole caused the snail to contract violently, expel the air from the lung and drop to the bottom.

This reaction suggests, perhaps, the *Anlage* of fear in the higher animals. After the tadpoles had been in the aquarium for some time, the snails react when suddenly struck; but they do not expel the air from their lungs, and seem to receive less of a shock, perhaps the *Anlage* of a startled reaction in the higher animals. The snails in the aquarium have undergone a change in their physiological state and now react to the blow from a tadpole like the snails that are accustomed to these animals in the field.

From the lists of the environmental factors (see Table IV) that are capable of giving stimuli in the different habitats, it is seen that some snails are receiving many different kinds of stimuli per hour over and above the number received by others. Throughout the work with *Physa* it has been noted that snails from some habitats become accustomed much more quickly than others to being handled; in other words, they are more adaptive. Those that are accustomed to living alone in an undisturbed environment take longer to become accustomed to being handled than those living in a habitat in which a variety of animals are actively moving about. A snail may be approached without frightening or startling it, if some motion to which it is accustomed is imitated, while it is difficult to approach a snail that lives alone in a still-water habitat without startling it. It appears from the above, that under the same conditions, snails in like habitats are in a similar physiological state and react alike to objects of a similar character, stationary or moving, and that the more varied the experience a snail has, the more readily it adjusts itself to new experiences.

III. Reaction of *Physa* to a new experience.

A snail that was accustomed to being handled was taken from its aquarium and, after being compelled to empty its lung, by pressing upon its foot with a pencil, was dropped back into the same aquarium. It lay upon the bottom for a moment and then began to crawl about until it reached the sides of the aquarium. No sooner had its head and tentacles touched the sides of the vessel than it began to crawl up to the surface of the water with as much apparent purpose and directness as though it were traveling a familiar path. Repetition of this experiment always brought about like results, unless repeated until the snail was exhausted. *Physa* from the pond north of the campus were lifted from the water and placed directly in a glass jar, previously filled with water from the pond to the depth in which the snails were living up to the time of the experiment. They were handled as little and gently as possible; nevertheless they quickly expelled the air from their lungs and retreated into their shells,—the usual reaction of *Physa* resulting from an experience to which they are unaccustomed. In a short time they crawled about on or near the bottom of the jar for a relatively long time. Some of the snails ascended the sides in an aimless way and were liable to turn and go back even though they were within a few mm. of the film. They reacted like the higher animals that are lost or suddenly deprived of their sense of sight, and appeared from their aimless wanderings to be no longer sensitive to gravity. They reached the film finally, apparently by chance and required from five minutes to an hour or more. This was in sharp contrast to the apparently direct, purposeful reaction of the tame snail. After the snails had once found the film, they seemed to recover their sensitiveness to gravity and seemed to experience no further difficulty in orienting themselves in their new habitat if left undisturbed.

IV. Adjustment of *Physa* to a new experience.

During the time that the snails were wandering about in the jar in the aimless fashion just described, they were seen to project their siphons into long tentacle-like feelers and to tap with them upon the bottom and sides much as a blind man taps with his cane. This use of the siphon was not seen unless the snail was in a disturbed condition as will be again shown in later experiments. This tapping ceased as the snails reached the film and was not resumed unless they were again disturbed.

If the snails, after they had once filled their lungs at the surface, were again picked out of the water and dropped back as before, the process of reaching the film and the amount of tapping with the siphons was much as it was in the first instance with, perhaps, an appreciable diminution of time and in the amount of tapping. This procedure was repeated eight or ten times within an hour and a half, i. e., the snails, shortly after they had taken air, were picked up and dropped back into the water. Each time they came up to the surface, there was less aimless wandering and siphon-tapping until, at the end of this time, they came up to the film without hesitation and without groping about with the siphon. The snails appeared to have " learned " the way, and behaved in all respects as did the tame snails that were dropped back into a familiar habitat. The shock that attended the experience the first time gradually disappeared as it was repeated, and the snails adjusted themselves to their new environment. These experiments were repeated many times with snails fresh from the pond and always with the same result. It is also worthy of note that the length of time that the snails were held in the fingers and the roughness with which they were lifted from their habitat increased the time that they wandered aimlessly about tapping with their siphons. For example, *Physa* that chanced to be upon stems of water plants could occasionally be placed in a jar without taking them in the hand by trailing the stem through the water so as to imitate wave motion. These snails, while they usually expelled the air from their lungs, got less of a shock than those that were handled, and came to the surface much more directly and in much less time. *Physa* that were living in a pond with shallow, sloping shores were picked up and dropped back into the water again. They wandered about in any direction for some time, but they invariably at last turned toward the shore into the shallower water. Like the snails from the pond that were placed in the jar, they appeared to lose their sensitiveness to gravity and to reach the shore by chance, trial and error, or later by the return of the sense of gravity which would cause them to crawl to the highest point of the sloping shore.

The time which it takes *Physa* to adjust itself to a new experience depends, within certain limits, upon the frequency with which the experiment is repeated. Snails that had expelled the air from their lungs when lifted gently from the pond were placed in a beaker. They were left undisturbed for six hours, with only an occasional moving of the dish. The first time that the beaker was gently touched, the snails expelled the air from their lungs and fell to the bottom. As time went on, they grew less sensitive and would crawl upon the film without expelling their air while the beaker was moved about. This experiment was repeated with other snails from the pond. The beaker was carried about continually with but short intervals of quiet. The snails adjusted themselves to the new experience in less than half the time required for the first lot.

V. *Physa* forms memories of its habitat.

A number of tamed *Physa*, after being compelled to expel the air from their lungs, were dropped back into the aquarium in which they had been living for some weeks, and the aquarium was then filled and covered so as to exclude all atmospheric air. The snails came to the top almost immediately and most of them crawled upon the glass cover. Some, however, that were moving at a faster rate than others, swung the shell about and elevated the siphon as though to take air but, upon touching the glass, withdrew the siphon and crawled upon the glass cover. The head did not receive even a semblance of a film stimulus, yet the shell was swung about and the siphon projected as though it did. It would seem that the snail was acting from force of habit and that this was likewise the explanation of its behavior to the film formed by the carbonic acid and water in a previous experiment (p. 98). The snails were not upon the cover long, before they projected their siphons and began to tap here and there on the glass. They lingered upon the cover sometimes for hours, but most of the tapping was done in the early part of their stay. This experiment was repeated, and the snails, after they had lingered tapping with their siphons about the cover for a while, were placed upon the bottom and the air excluded as before. They came up to the top, but they tapped less upon the cover. After this experiment was performed six or eight times they ceased to tap and they did not linger so long upon the cover.

The above experiment was repeated with snails fresh from their natural habitat. They acted as in a previous experiment, lingering for a longer or shorter time upon the bottom, tapping and wandering aimlessly about until they finally reached the cover. Most of them upon reaching the top tapped no more, or differently, than they did upon the bottom or sides; a few opened the siphon against the cover. After they had crawled upon the cover, they scattered about the aquarium, tapping with the siphon occasionally. The snails were again placed upon the bottom of the vessel and the cover was replaced so as to exclude all atmospheric air. They remained much longer at the bottom than before and tapped but little anywhere, neither did they gather in any part of the vessel. This experiment was repeated four or five times. The snails became very inactive and ceased to tap or crawl and behaved as if in a stupor. After they had reached this state, the cover was removed and they were allowed to fill their lungs at the surface. Soon after filling their lungs, they moved about almost as actively as they did at the beginning of the experiment. They were again touched and again they expelled the air from their lungs and dropped to the bottom. All atmospheric air was excluded and the snails' behavior observed. As in the first trial, they lingered and tapped near the bottom and sides and upon reaching the top they lingered and tapped for some moments. This experiment of causing the snails to expel the air and then cutting off all atmospheric air until they had remained tapping upon the cover for a time, was repeated until they had taken air at the film a number of times. They ceased to wander about aimlessly, tapping upon bottom and sides, but upon reaching the top they remained upon the cover for some time. From these experiments it would seem that *Physa* remembers the location of the surface film.

Tamed *Physa* were transferred from a large rectangular aquarium to a cylindrical one having the same depth and temperature of water. The snails came up without hesitation but they tapped with their siphons now and again as they went up. After they had been dropped back into the new aquarium three or four times, they ceased to tap as they came to the surface.

Physa accustomed to living in a cylindrical vessel, were transferred to a globe aquarium having water of the same depth and temperature. They immediately came up the side but soon after crawling on the curved surface, began to tap with their siphons. After they had been dropped back and made to crawl up to the surface five or six times, they ceased to tap with the siphon and gave no further indication that they sensed a change in the sides of their aquarium.

Physa that were accustomed to live in a beaker were transferred to a bottle of the same size, with the same temperature and depth of water. The bottle, near the top, had shoulders which curved toward the neck. The snails came up the sides without tapping until they reached the rounded surface and then they felt about with their siphons. After they had been dropped back into the bottle five or six times they ceased to tap as they crawled over the shoulder of the bottle.

Tamed snails that had been living for weeks in water an inch deep in a cylindrical aquarium dish were made to expel the air from their lungs and were dropped back into the dish after it had been filled with water of the same temperature. They came up the sides of the dish without tapping until they had passed by about one-half inch the level at which they were accustomed to get air; then they began to tap with the siphons. They repeated this behavior if dropped back three or four times, but after that they came up to the surface without tapping at all. Since the snail can not see objects and the surface of the vessel was smooth, the snail could neither see nor feel "land marks," but must have formed an associated memory of the space over which it had passed from the time it left the bottom to the time it reached the film. Hence, we may conclude that the tapping in this case was due to association with the level at which the snail was accustomed to get air.

Physa that were tamed and had been kept in a bacteria dish for some time were removed to another bacteria dish whose sides were coated with vaseline and the water in which was of the same depth and temperature. The snails began immediately to crawl up the sides of the dish but upon encountering the vaseline, they projected their siphons and felt about and even opened them against it as though trying to get air. After several repetitions of the experiment they passed over the vaselined surface without tapping, but it took longer for them to become accustomed to this than to any other change in their environment that had been tested. It is possible that vaseline in contact with water retains a coating of air, and this, together with the yielding of the vaseline, may have served to cause a stimulus similar to that of the film.

VI. Young *Physa* differs from the adult in the character of its responses.

Young *Physa* are much less sensitive to general disturbances of their environment and localized mechanical stimuli than are the adults. Large snails readily expel the air from their lungs and quickly fall to the bottom of the pond, while the little ones may be held between the thumb and finger without doing so. This difference in sensitivity is also illustrated by the following. A large number of *Physa* were collected with a dip-net, brought to the laboratory and placed in a pail of water. Many seeds of *Alisma plantago* were collected with them and were floating together with a large number of *Physa* upon the surface. The water in the pail was stirred briskly so that the snails would fall to the bottom; but upon removing the seeds from the surface the young snails were found among them. The young snails had thus not reacted by falling as had the adults.

In the experiment in which *Physa* was seen to adjust itself to a new experience, the adult snail wandered about aimlessly for a longer time before it reached the film than the younger one did. Perhaps owing to its greater sensitiveness, it received a greater shock from the unaccustomed experience and in consequence was longer in recovering from it than the younger one. Repeated observation and experiment show that an increased sensitiveness to general disturbances of the environment and localized mechanical stimuli does not seem to come on gradually as the snail grows, but there seems to be an abrupt change when it is about five mm. in length.

VII. Differences in reactions of *Physa* young and adult.

Young *Physa* of various sizes were taken from the pond and made to expel the air from their lungs. They were then placed in a beaker of water of the same depth and temperature as the water from which they were taken. As the snails crawled up and about the beaker they did not tap with their siphons as much as the older ones. The younger snails, observed through a lens, were not seen to tap with a siphon at all. Snails of about five mm. diameter and larger tap occasionally but not as often as snails several times this size. There is a noteworthy difference in the manner of tapping with the siphon in the young and in the adult *Physa*. The adult snail when it taps with its siphon does so by projecting it between the shell and the foot, touching the glass at one or several points without noticeably swinging the shell or stopping. When it takes air at the film while upon a vertical surface, it swings its shell about horizontally; when it takes air upon the film, the siphon side of the body is slightly elevated; but the shell is not swung about in the least. The little snail, on the other hand, stops in its upward progress, swings its shell about in a horizontal position and projects its siphon upward in exactly the same manner that the adult snail does when it takes air while on a vertical surface. It is very amusing to see the little snail stop every now and then on its way to the film, swing its shell about, and elevate its siphon as far as it can reach. If the beaker is full of water and all atmospheric air excluded, the young snail swings its shell about upon the glass cover in the same way that it does upon the side of the dish. All gradations of swinging the shell about and reaching up with the siphon are seen in snails of different ages. The younger ones swing their shells about horizontally but with increasing age there is less and less movement of the shell, until in the adult it disappears altogether. When the young snail first begins to tap, it projects its siphon straight up in one direction, while in older snails there is more and more of a tendency to feel about.

VIII. Summary and discussion.

Physa is sensitive to contact stimuli and its response to a general disturbance of the environment is so delicate at times that it rivals that observed in the leech by Whitman (1898) and the planarian by Pearl (1903).

The character of the response of *Physa* to both localized mechanical stimuli and to general disturbances of the environment so varies in members of the species and in the same individual from time to time that no general statement can be made unless the physiological state is known.

The physiological state of *Physa* varies with its experience; and its experience varies with the environment. The greater variety of experience to which it is accustomed, the more readily it may be approached without producing the physical reactions which are a correlate to the physical state of fear in the higher animals, and the more readily it is tamed. A physiological state in *Physa* can be transposed by transposing the conditions which produce it. A new experience produces a shock to *Physa* which seems to deprive it temporarily of its sense of gravity. The snail becomes accustomed to the experience, if it is repeated eight or ten times within an hour and a half; so that it reacts to it as do other snails to which the experience is familiar.

By the use of the siphon, *Physa* shows that it distinguishes changes in its environment. By a process of association it "remembers" the location of the film, the character of the sides of the aquarium and even the relative depth of the water. It also shows the development of neural habit.

The young are much less sensitive to stimuli of their environment. Very young snails show none of the reactions which are the correlate to the physical state of fear in the higher animals, but these quite suddenly disappear when the animal is about five mm. in diameter. The sudden appearance of these reactions is due, perhaps, to a rapid development of the nervous system (Donaldson, 1898), rather than to a sudden appearance of a delayed instinct, as Herrick (1901) believes to be true for birds; since there appear at the same time associations of the habitat.

The tapping reaction of the young is the same as that of the older snails, when it takes air at the film. This reaction changes as the snail grows, and is modified into the better adapted one of the adult.

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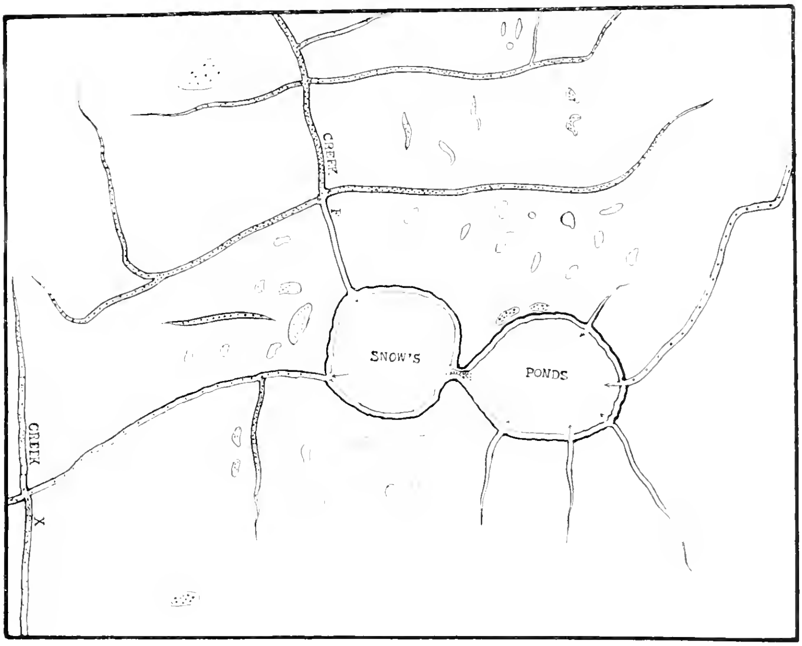

FIGURE 1—Diagram of the swamp at Kavanaugh Lake, Washtenaw Co., Michigan. The presence of *Physa* in the water is indicated by fine dots.

FIGURE 2—Brook-ditch, showing a *Physa* habitat, near Kavanaugh Lake.

FIGURE 3—Railroad Creek, showing *Physa's* optimum habitat behind stones in the channel, Ann Arbor, Michigan.

FIGURE 4—Railroad Creek, showing conditions very similar to those in Fig. 3, but lacking *Physa*. (Perhaps due to a deposit of silt.)

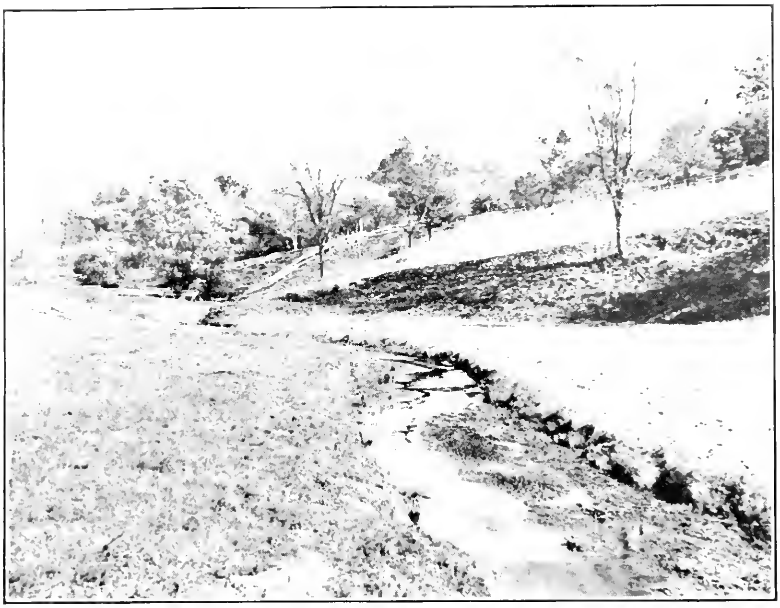

FIGURE 5—Railroad Creek, showing optimum *Elodea* habitat, where *Physa* was lacking.

FIGURE 6—Ox-bow pool, showing a favorable *Physa* habitat. Large amount of water weeds in the foreground with few *Physa*. Lima Center, Michigan.

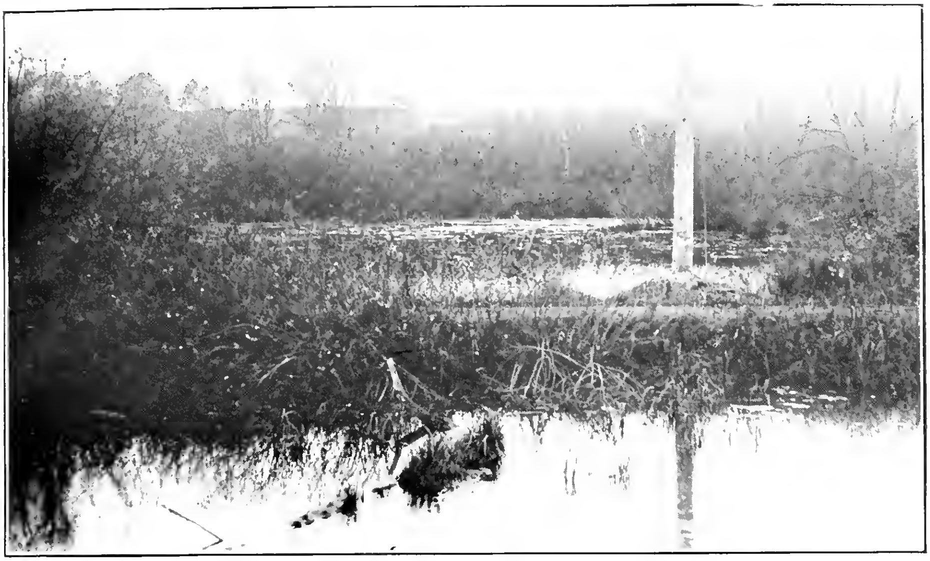

Figure 7—Overflow on Huron River at Geddes, Michigan, showing a favorable habitat.

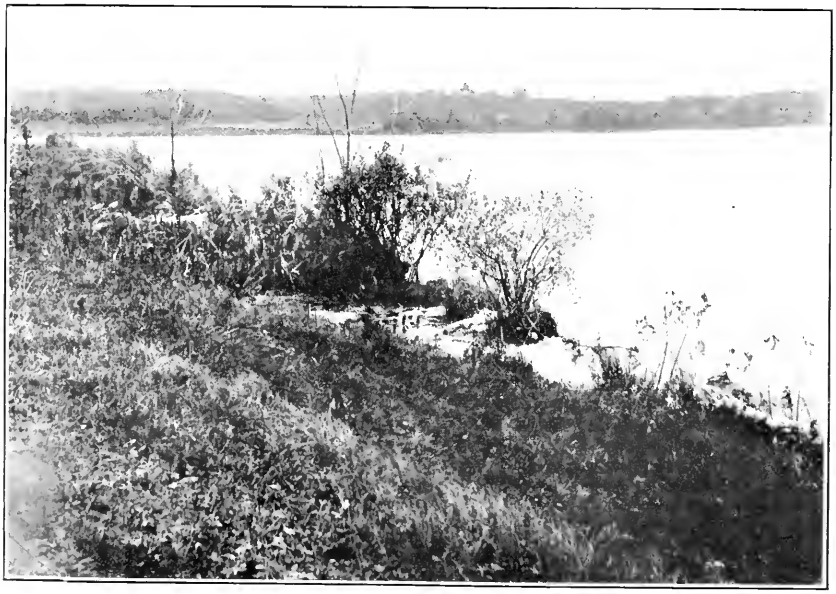

Figure 8—Ice-rampart pools at Kavanaugh Lake.

FIGURE 9—*Physa* habitat at Crooked Lake formed behind spit. Optimum near the center of the picture.

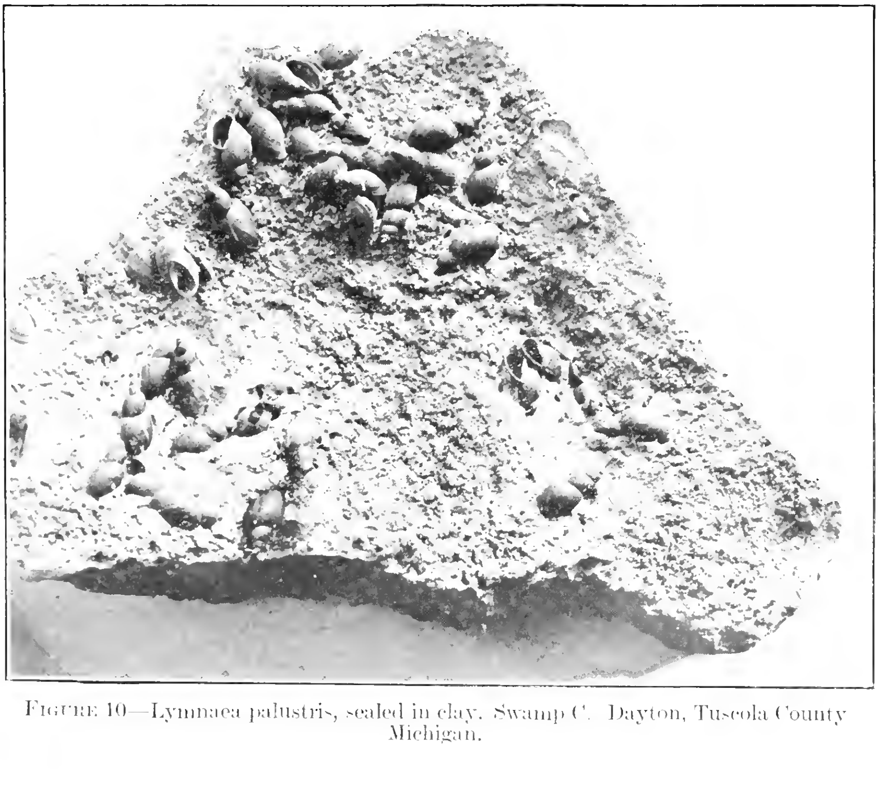

FIGURE 10—Lymnaea palustris, sealed in clay. Swamp C. Dayton, Tuscola County Michigan.

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Edited by JOHN B. WATSON
The Johns Hopkins University

The Function of the Vibrissae in the Behavior of the White Rat.

STELLA BURNHAM VINCENT

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at Cambridge, Boston, Mass.
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NINETEEN FIGURES

Contributions from the Psychological Laboratory of the University of Chicago

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PART I. LABYRINTH EXPERIMENTS

A. Introduction

The immediate incentive to this study was a desire to supplement an histological investigation of the tactile hair of the white rat with some functional data which should serve to explain its structure. The complexity of the organ and its marvelous innervation forced the conclusion that its real nature and use were of greater significance than had as yet been shown although it had been the object of much study.

The follicle of the tactile hair of the white rat, like those of the usual body hairs, consists of invaginated skin layers which form an outer and an inner root sheath. Besides these it has a dermal sheath which encloses within its layers large blood sinuses. Of these sinuses the inferior one is filled with erectile tissue and is separated from the superior ring sinus by an outgrowth of the root sheath, composed of loops of capillaries and connective tissue called the ringwulst.

The sensory supply to the follicle is from the trigeminus. A large nerve, consisting often of 150 fibres, enters from below and spreads out over it in a thick plexus the main fibers of which lie almost parallel to the long axis of the follicle. These fibers finally terminate in a mantle of touch cells in the outer root sheath. In addition to this there is a second innervation. Branches run down from the dermal plexus of the skin and form a nerve ring about the neck of the follicle.

So large and so complicated a nerve supply would indicate a high degree of sensitivity which would be still further enhanced by the nature of the tissue in which it lies, the vibratory character of the stimulus and lever-like application of the hair itself. The details of this innervation and discussion of the structure are given in another paper.*

B. Historical

Hair is a peculiar characteristic of mammals and is found on every mammalian species so far as known; even the whale has some about the mouth. If only a few hairs are found on the

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*To appear in vol. 24, Jour. of Comp. Neurology.

animal, Wiedersheim says, they are usually confined to the lips, eyes and cheeks, in other words to the tactile hairs. "Die Tast-oder Spürhaare sitzen zumeist in der Lippen-, Augen-, und Wangen-gegend, d.h. andern Stellen des Körpers, wo am frühsten die Behaarung auftritt und von wo sie wahrscheinlich die verbreitung über den ganzen Körper genommen hat."[1]

Anatomists and physiologists have studied both the structure and function of the tactile hairs for many years. Zoologists have frequently removed them from different species but have apparently been content to note merely the immediate effects of the removal and so far as I know no more extended observations have been undertaken. We are accustomed to think that experimentation with animals is confined to recent times and in view of this belief the following incident which Lyddeker gives is interesting:—

"In their active life, bats being mostly crepuscular or nocturnal while their eyes are relatively small, it is obvious that they must be provided with some special means of avoiding contact with objects during flight. This appears to be effected by the extreme development of a sense more or less akin to our sense of touch, by which the neighborhood of objects is perceived without actual contact; and it was demonstrated as long ago as 1793, by the cruel experiment of depriving bats of sight and then allowing them to fly in a room across which silken threads were stretched in such a manner as to leave just sufficient space for them to pass with outstretched wings. The unfortunate bats not only succeeded in passing between these threads without contact, and likewise avoided the walls and ceiling of the room, but when the threads were placed still nearer together, they contracted their wings in order to be able to pass without contact.—In the great majority of bats it appears that this sense of touch is situated in the wing membranes and in the delicate and frequently enormously elongated ears which are often provided with a kind of secondary inner ear known as the tragus. There are, moreover certain bats provided with an additional organ of perception, which takes the form of expansions of skin from the nose and adjacent parts of the face, forming what is generally known as 'nose leaf.'—The various membranes forming these nose leaves are always fringed with long fine hairs,

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[1] Wiedersheim, R.: Vergleichende Anatomie der Wirbelthiere. 1902, S 27.

which evidently correspond to the whiskers of the cat; and we may accordingly regard these nose leaves merely as an excessive development of the cat's whiskers accompanied by leaflike growths from the skin of the nose."[2]

The labyrinth method, which has been so much used in the study of animal behaviour recently, also is not new. Broughton, in 1823, gave a brief description of the nerve of the tactile hair of the cat and then says:—

"So large and particular distribution of an exquisitely sensible nerve, it is reasonable to suppose, must be for the purpose of some sensible function. To ascertain this, I put it to the test of experiment in the following manner:—

I placed walls of books upon the floor, so as to resemble the streets of a town opening into each other; and, having closed the eyes of a kitten completely, I set it down to find its way through the lanes of books. It continued to move on wherever a free communication presented itself, holding its head cautiously down close to the floor, and very adroitly avoiding contact with the sides of the walls, the corners of which it also turned without approaching closer than just sufficient to touch the tips of the whiskers slightly, when it always drew back instantaneously. At length it found its way out freely; and I then cut off the whole of the whiskers close to the face, and again set it down to observe whether this would produce any alteration in its manner. The kitten now showed evident signs of having lost the only remaining means of guiding itself. It struck its head repeatedly against the sides of the walls, ran against all the corners, and tumbled over steps placed in its way, instead of avoiding all these as before the removal of the whiskers.—From these facts I imagine that certain animals are supplied with whiskers for the purpose of enabling them to steer clear of opposing bodies in the dark. The mammalia having lips and considerable facial development are probably furnished with these bristles, or fine tubes of a compact substance, which, whilst they readily yield to pressure, convey the impression or excite the simple sensation of contact; just as the antennae of the sepia, the lobster, the snail, insects, etc., are to all appearances constructed for the sense of touch.

Animals which seize their prey by night, and such as explore

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[2] Lyddeker, F.: Natural History, vol. 1, p. 249.

dark passages, are furnished with whiskers. The bat is supposed to avoid walls and houses by the exquisite sensibility of its wings: it seems, however, probable that it is indebted for its safety in this respect to its whiskers, or feelers as they may be termed."[3]

The anatomists have, as a rule, been more interested in these organs than the physiologists or psychologists and they usually have something to say as to function.

Odenius, who studied these hairs in 1866, thought that their great innervation had to do with nocturnal habits, their superior nerve supply making them peculiarly sensitive and useful in determining the nearness of objects or the size of openings.[4]

Bonnet, in 1878, made a most exhaustive study of the innervation of the follicle of the tactile hair and says in conclusion:—" For the present one may only assume with certainty a quantitative difference in the power of touch based upon the greater or less degree of innervation," and that " Only experiments with living animals can give more certain results." He also calls attention to the fact that the term touch, as ordinarily used, includes the perception of two points, temperature, hardness, etc., and proposes to abandon this name for the hair, which probably serves none of these, and regard it simply as a feeling hair which gives spatial relations in the near as vision gives the far.[5]

One might cite other authors and other experiments but they all follow the same general lines and we will pass at once to some more recent work, and on the experimental side more carefully controlled.

Small studied the development of the young white rat and some of his notes are as follows:—

First day: " Gave little response to light pressure as with a hair except upon the nose which seems to be very sensitive."

Seventh day: " Dermal sensibility becomes more acute, though susceptibility to pressure is still greater on the nose than anywhere else on the body. Especially greater when tickling is involved. A bristle drawn across the body elicits scarcely any

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[3] Broughton, S. D.: On the Use of Whiskers in Feline and Other Animals. *London Medical and Physical Jour.* 1823, vol. 49.

[4] Odenius, M. V.: Beitrag zur Kenntniss des Anat. Baues der Tasthaare, Deutsch. *Archiv f. mikro. Anat.* 11, S. 436.

[5] Bonnet, R.: Studien über der Innervation der Haarebalge der Hausthiere. *Morph. Jahrb.* 1878 Bd. 4, S 361.

response; but applied with the same pressure to the nose, evokes squeaking and vigorous head shaking.[6]

Dr. Watson made some careful tests to determine the function of the vibrissae in the formation of the labyrinth habit. He first used a group containing two blind rats, two anosmic, and two normal rats that had previously learned the maze. These two were tested to make sure that the coordination was perfect and then their vibrissae were cut close and they were given two trials afterward. He found that there was marked disturbance at first which lessened during the succeeding trials and which had entirely disappeared twenty-four hours later.

He then tested four other rats, cut their vibrissae, but did not put them in the maze until forty-eight hours had elapsed, and found but slight disturbance. His conclusions so far as the labyrinth habit goes are as follows:—

"First, under normal conditions the rat probably uses his vibrissae to assist him in making proximate orientation in the maze; second, in all probability the rat does not discriminate his turns by means of any data contributed by the vibrissae; third, the immediate effect of the loss of the vibrissae upon the 'steadiness' of the rats reactions in the maze is only transitory—the steadiness of the reaction being not at all affected if the rat is allowed to habituate himself to the environment of his living cage after the removal of the vibrissae."

This is qualified by the following note in regard to the possible use of the vibrissae under normal conditions: "Be it understood however, that we have no crucial positive evidence in support of this assumption. The evidence as it stands here proves unquestionably that the animal is not disturbed by the removal of the vibrissae if time is given him to wear off the unaccustomed 'feel of their absence'—but it does not give unequivocal positive evidence that they are even normally used by the rat in sensing openings, walls, etc."[7]

Miss Richardson in some experimentation with problem boxes requiring the opening of a door in various ways concludes: "The impulses furnished by the sense of touch seem to play an important part in the adaptations of the animal to these several

---

[6] Small, W. S.: Development of the Young White Rat, *Am. Jour. Psychol.* 1899, vol. 11, p. 82.

[7] Watson, J. B.: Kinaesthetic and Organic Sensations, *Psychol. Rev. Mon. Sup.* 1907, vol. 8, no. 2, p. 75.

experimental situations. A very great difficulty arises when an attempt is made to separate the function of the tactual from that of the kinaesthetic or organic. The tactual impulses alone, or in the complex, are the stimuli to the digging movements in Problem I, and in part to the movements of pressing down the plane in Problem II. In the Problem III, certain familiar tactual impressions are evidently the stimuli to the discovery of the latch after the rat has arrived at the locality of the door. Contact *seems* to be the cue to movements which result in the raising of the latch, during both the learning process and the period in which the movements are habitual."[8]

She also experimented with the rats in some jumping tests and from her notes these extracts are taken:—" Up to a certain distance the rat was able to step across with little difficulty, and the contact of the snout or vibrissae with Platform II seemed to be the essential stimulus in the majority of cases."[9]

" This (blind) rat would not allow his fore feet to leave the platform unless his vibrissae reported contact with some object. When the platform was beyond the reach of his vibrissae the experimenter touched their tips with a pencil, whereupon he put out his fore feet to step over."[10]

" She used her vibrissae to locate the platform."[11] (Another blind rat.)

Her conclusions are given on page 99. " Touch as a partially controlling factor does, however, enter into the early adjustments of the blind animals, since they will more readily form the habit of jumping if the snout or vibrissae are stimulated by the platform to which the animal has to jump. This latter statement applies in some degree at least even to animals possessing vision. Once the habit is formed, however the initial tactual impulses can be dispensed with."

" In regard to the function of the kinaesthetic impulses in the case of the blind animals it seems safe to affirm that they soon come to usurp whatever functions tactual impulses from the snout and vibrissae exert in the learning process." (Jumping.)[12]

We will postpone a discussion of these conclusions until it

---

[8] Richardson, Florence: A Study of Sensory Control in the Rat. *Psychol. Rev. Mon. Sup.* 1910, vol. 12, p. 68.

[9] Ibid p. 73.

[10] Ibid p. 80.

[11] Ibid p. 81.

[12] Ibid p. 99.

can be made in the light of some experimentation now to be described.

C. General Description of Problem

All learning, human as well as animal no doubt, consists in the attainment of new or more perfect sense discriminations or in new or more perfect motor adjustments and all advance is made either by the formation of new sense impressions to relieve the demand of a motor situation or of a new coördination to relieve the stress of a sensuous stimulation; but both these factors are inseparable and both are concerned in every advance.

Nevertheless we may arrange experimentation so as to throw one or the other into prominence, to see how the habitual act is broken up or disturbed by the addition or subtraction of sensory stimulation, and what sense factors are requisite for a given coördination.

The following experimentation concerns itself with the acquirement of a labyrinth habit and the discrimination of surfaces.

It was believed that Dr. Watson was quite right in asserting that his animals learned their maze by the use of kinaesthetic sensations alone and that they learned it as perfectly and accurately without vision, olfaction, etc., as before; but the maze which he used was essentially a non-sensory maze for these animals. It was made of wood, unpainted, therefore practically uniform in color and brightness so that the keen sight of man would scarcely have been any help in such a situation far less the notoriously poor sight of the rat. The odor was fairly evenly distributed except in the immediate vicinity of the food box where there was always halting and hesitating in the early trials of an animal and the tactual and auditory conditions were, so far as could be seen, not more marked in one part of the maze than in another.

But one cannot reason from this maze to all mazes, nor from conduct in such a situation to conduct where sensory factors are more strong and more varied as they are in conditions of nature where animals run in the open either for food, from danger, or to their holes.

It cannot be argued that because animals can learn an intricate coördination without vision, hearing, etc., that if strong visual elements were present they might not help or hinder, as the case might be, the formation of the coördination.

Dr. Watson's results are largely given in terms of time. Now kinaesthetic control may perhaps quite fairly be thus measured since these motor attitudes are so closely linked with the physiological mechanism of the body as to be almost machine-like.[13] Hence control involving such sensations may be more nearly expressed in terms of time than any other sensory control. But when the action depends for the greater part on other sensory cues, especially those of the distance senses, then certainly the process cannot be fairly measured in terms of time and must take more account of the number and kind of errors.

This is in no sense intended as a criticism of Dr. Watson's conclusions but only to show how his work might be supplemented. The particular part of this investigation bearing on the maze was begun under him and he has seen the other experimentation in its later stages.

D. Apparatus

It was determined to build a maze which it was hoped would throw the cutaneous, tactual situation into relief and especially give some light upon the use of vibrissae in the acquirement of a labyrinth coördination where the loss of these members might be felt. Evidently the walls of the labyrinth were the source of most of the contact experiences of the vibrissae and the walls were the thing to take away.

A maze was made with elevated runways, unconfined by walls but separated by spaces wide enough to preclude jumping. From previous experiences, both of our own and others, with the animals, it was believed that they could not learn the problem by sight because vision was so poor: at least conditions which permitted the use of vision would not lessen the difficulties greatly. It was also thought best to make the problem a fairly simple one.

The maze as constructed is shown in Fig. 14, Plate I. It was made 54″ x 54″, with runways 4″ in width separated by 6″ spaces. It was made of ½″ stuff and the runways were elevated by strips which ran lengthwise and vertical to them beneath. These strips were stayed below by a few cross pieces and the whole mounted on a frame on castors which raised it about

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[13] Washburn, M. F.: The Physiological Basis of Relational Processes, *Psychol. Bull.* 1909, vol. 6, p. 369.

two feet from the floor. The walls which should have enclosed the runways were hinged to the sides so that they dropped below the floor but they could be raised and hooked together if one wished to enclose the paths. The food box was surrounded where it faced the maze by sides 4″ high.

Upon this maze were used rats with and without vibrissae; rats with the vibrissae cut on the right side, on the left side, and from birth; anosmic rats with and without vibrissae; rats with the fifth nerve cut, and blind rats with and without vibrissae. All of these rats were two months old or as near that age as possible when the experiment began.

E. Mode of Experimentation

The mode of experimentation was similar to that previously described by others who have used the maze in this laboratory. The animals were thoroughly tame, were kept in the room where they were used, and were fed in the maze three days before the experiment began. The maze was kept clean and was washed at the close of each day's work with a weak solution of carbolic acid. The animals ran under a slight stimulus of hunger, three times a day except at the very first when the time taken for one run prevented more. For our purpose the coördination was considered learned when the animal made eight out of ten perfect runs and this record extended over a period of three days. They were then usually taken from the problem and this necessitates a word at this point as to the way in which the graphs which show the learning process have been made.

F. The Learning Curve

Mr. Thorndike was the first to apply the graphic method to the results of comparative psychology.[14] His curves are time curves in the learning processes of single animals. It has been objected by others that the time curve is not truly a learning curve but there are reasons for believing that this curve may represent the labyrinth type of coördination better than any other because this type invoves the use of the oldest and most mechanized reflex and instinctive motor systems. These single animal curves all showed a sudden fall at the beginning followed

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[14] Thorndike, E. L.: Animal Intelligence, *Psychol. Rev. Mon. Sup.* 1898, vol. 2, no. 4.

by a more gradual decline the significance of which has been fully discussed by others. Aside from these two main features, the great variability of the curves prevented any generalization from them save the mere fact of variability. The graphic method as used in other sciences has usually been applied to masses of statistics of which the curve was the general concrete exponent and later investigators seizing upon Thorndike's method have grouped their results and shown them in general curves plotted from many animals.

To my mind it is manifestly unfair to call this curve a learning curve, What the curve really shows is physiological and environmental conditions which affect the whole group from day to day. But often the curve is plotted from data obtained from groups of animals which have been used at widely separated intervals so that it does not have even this daily significance.

A problem is said to be learned when it can be performed relatively free from error. A coördination never becomes entirely free from error and the degree of excellence must be based upon a standard artificially set, dependent upon the conditions and the complexity of the problem. Because of their great variability one animal may learn a problem in ten trials which may take another forty. Suppose these animals are given fifty trials and the numerical results either of time or errors are plotted in a curve. Something is obtained then which is very unlike either of the original records. The automatisms of the one come in to modify the errors of the other, the errors of the one to disturb the automatisms of the other. Taken individually up to the place where the problem is learned the curves if plotted separately for each animal are much alike except that the irregularities in the one due to the process of learning are distributed over a greater length of time. A curve has been plotted here which seems to be a truer representation of the learning process. It does not exhibit daily conditions as does the other nor does it show the actual length of time taken which may easily be shown in other ways, but it is believed it does demonstrate that under similar experimental conditions practically the same course is taken by animals in learning a problem whether it takes them ten or fifty trials to accomplish the task.

In this experimental work an animal's trials were discontinued when the problem was learned or one period past such time.[15] The numerical results of time and error for each animal were then divided into an equal number of serial groups, say ten, regardless of whether in the learning he had taken twenty or forty trials. In the one case there would be two numbers in each group and in the other four. The averages were then taken by groups and thus there was obtained for each animal a series of ten numbers. If there was an excess it was always distributed among the beginning groups. Suppose instead of twenty there had been twenty-two, and instead of forty, forty-five trials in the illustration used and it was still desired to make ten groups. Then the first two divisions of the first animal's records and the first five of the second animal's records would contain an additional member. The quantities for all the animals were then averaged in serial order and there was obtained in this way numerical data for plotting a curve in which the beginnings of the learning process corresponded as did also the second, third and end stages. In the old curve as usually plotted only the beginning stage was fairly representative of all.

A curve made in this way should represent the learning process in its successive stages with the individual variations eliminated in proportion to the number of animals used. It admits of better comparison between different lines of experimentation and with different species of animals. Direct comparison of these curves will be made in connection with the discussion of the results of the experimentation.

G. Experimentation

Experiment I. *Normal rats on the maze with sides up.* For the purpose of comparison we used a set of five males on the maze with the sides to the runways up. This first experiment was made to give us data to compare with that obtained from succeeding groups where the walls to the runways were down. The vibrissae brushed the sides as the animals ran but, if they were of service, the exact way in which they were functioning was hidden by the apparatus. The conduct of this group will not be described since it differed in no way from that which has been described for so many similar mazes before. The general

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[15] NOTE:—Except in some cases where the experiment was continued for the sake of comparison with the published results of others.

results of the experimentation are shown in the summary and graph which follows. (See fig. 1.)

Summary of the results of Experiment I.

Average number of errors in the first twenty-five trials.	41.
Average number of errors in the first trial	18.
Average number of trials in learning	16.5
Average time of the last ten trials in learning	11 sec.
Average time of the last of these ten trials	8.5 "
Slips and falls	none

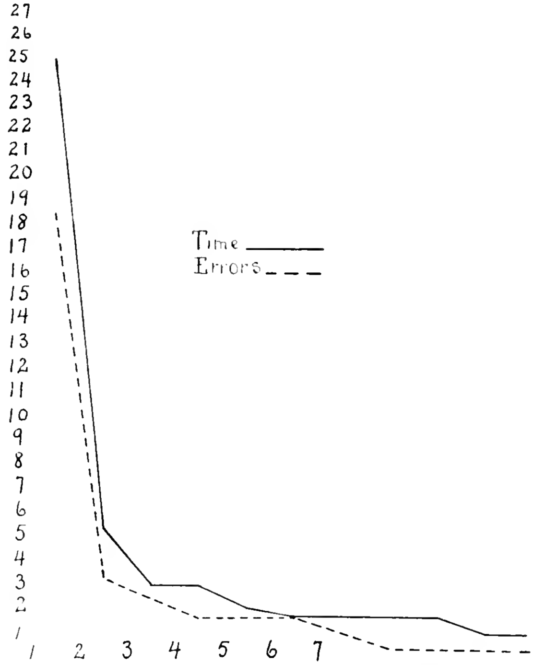

Fig. 1—Learning curves, time and error, of normal rats—maze with sides up.

Experiment II. Rats with vibrissae; maze without sides. Two sets of rats were used upon the maze with sides down, four females in June and five males in September 1911. The two groups gave very similar results although the males were a little quicker in learning. In computing the errors an entrance into a *cul de sac* is counted as one, a return, no matter how far, as one, but a return with an entrance into a cul de sac, as two.

General description of conduct in Experiment II:—The rats were very slow in venturing from A* where they were put upon the maze. Their heads were often over the sides and they tried to get off on the frame below, in which endeavor they occasionally succeeded. They often tried to jump from " K " to the food box and frequently attempted to get from "A" to " S." This latter attempt became more pronounced toward the end of the experiment. In moving off after they were put on the maze, they went, at first, along the very edge of the platform, with their vibrissae dragging and their heads over the edge as if to see the floor. They often raised themselves on their hind legs as if looking but of course both this act and the one mentioned before may have been for olfactory purposes. They curled their toes over the edge of the platform as if loath to let go. This was so marked that as the animals increased in speed they sometimes showed a gaït like that of a pacing horse. The noses were for the most part held close against the floor, often drawn along the edges and much used in corners. The first trials were cautious and there was only an occasional fall but as the newness wore off there was more recklessness in movement and more falls. These happened chiefly at the ends of the paths or at turns but frequently also from the sides midway.

If an animal lost its way all these peculiarities became more noticeable the nosing at edges and corners, the dragging of vibrissae, the rising on hind feet, the curling of toes over edges, the following of edges, etc., as if every available sense quality were being exploited. But as time wore on, the errors dropped out, falls became less frequent, the rats ran more confidently, and finally most of them stepped out daintily with heads up and ran the whole distance in six or seven seconds. (Fig. 15, Plate II.)

The general behavior thus differed much from that observed in the ordinary maze. The use of nose, vibrissae, feet and apparently eyes was most marked. In other mazes one only notices this incidentally. The less confident running was also evident. That this cannot be due entirely to the raised platform and to the dangers from falls later work shows.

One advantage of this maze is that every move and turn of the animals can be seen as they cannot in a maze enclosed by sides. Besides differences in behavior there are also to be

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* See fig. 6.

observed differences in the general numerical results of time and errors, as shown in the summary. (See fig. 2.)

Summary of the results of Experiment II.

Average number of errors in the first twenty-five trials	35.
Average number of errors in the first trial	9.5
Average number of trials in learning	16.5
Average time of the last ten trials in learning	11.8 sec.
Average time of the last trial	8.8 "
Average slips and falls in the first twenty-five trials	2.5

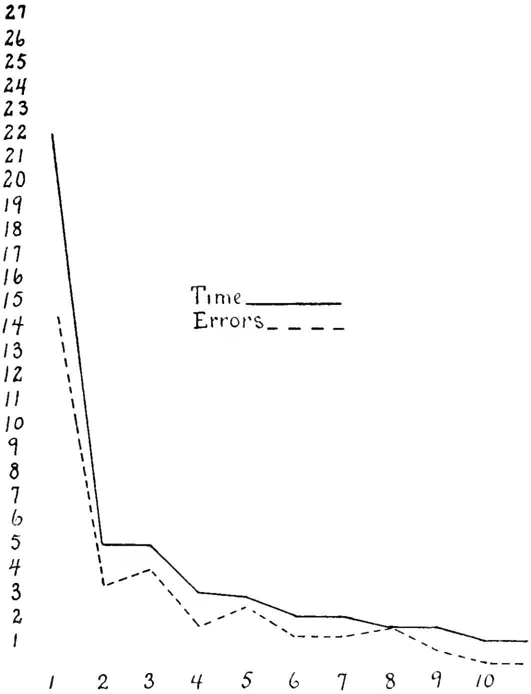

Fig. 2—Learning curves, time and error, of normal rats on maze without sides.

If the figures for this experiment are compared with those for Ex. I, it will be seen that the average number of errors for the first twenty-five trials is somewhat greater in the maze with sides than in the maze without, and markedly greater in the first trial. In spite of this fact the time of learning is the same and the average speed is practically the same. That something is influencing the different distribution of errors in this maze is evident but unless it should prove to be connected with the vibrissae it will not be discussed in this place.[16]

In order that there could be no charge of temporary disturbance the group of rats without vibrissae which followed these had their vibrissae cut from birth.

Experiment III. Rats with vibrissae removed from birth. The rats used in this experiment were born in the laboratory the first week in October. They were always kept in the room where they were used and always fed by me. They were three months old when they were first put upon the maze and in perfect condition, three males and three females. Their vibrissae which grew very rapidly were cut twice a week from birth.

Behavior:—This was very similar to that of the set preceding except that there was not the same timidity in venturing out upon the maze, nor the same slowness in traversing it. The animals flattened their bodies close against the maze and crawled. At first they kept to the middle of the path a characteristic feature in the work of this group, but later they went from side to side of the pathway always nosing for edges and as time wore on walked the edges. They hung over the sides as if looking below but went steadily to work and learned the maze in almost as good time as those of group two. As a whole they kept far more to the middle of the path than those of the other groups. They always preserved somewhat of the flattened crawling gait and never while they were being used lifted themselves high and ran confidently and with heads up.

Summary of the results of Experiment III.

Average errors in the first twenty-five trials	44.
Average errors in the first trial	8.
Average time of learning	(trial) 22.
Average time of the last ten trials in learning	18.5 sec.
Average time of the last of these trials	7.5 "
Slips and falls 72, average	12.

As will be seen the average time of the last ten trials is longer

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[16] Note:—In basing my conclusions upon these figures I have not neglected the mean variation. It has not only been carefully computed but in many cases has been carefully plotted for individuals and for groups. As between groups, however, the variability is not altogether a matter of chance and since the question which arises is one which does not concern this problem the figures are not given here. In another paper reporting a long series of experiments already finished the whole problem will be treated.

than that found in experiment two, but the last of the ten reaches a low point. The time of learning is slightly longer than those of group two and the errors are considerably increased. The noticeable thing however is the great number of slips and falls—five times as many as found in group two.

Compare the learning curve in fig. 3 with that in fig. 2 and remember that these rats were absolutely tame and that no emotional factors were observed which would account for the high time curve or for the irregular error curve.

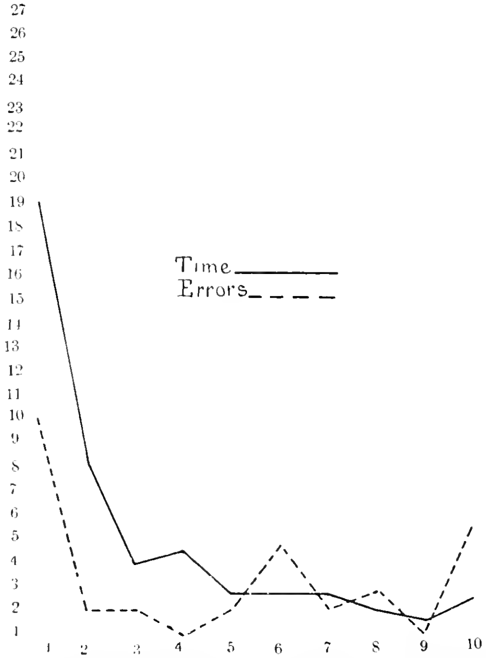

Fig. 3—Learning curves, time and error, of rats without vibrissae on maze without sides.

How shall we explain the difference? Although the other animals were perfectly gentle, these were handled every day from birth and had never been out of the room where they were used. No doubt some of the emotional conditions were lacking in their reactions which were present in the others. This may account for the few errors in the beginning. There is however, a distinct type of behavior as described above, the slips and falls are excessive, the rate of running is one-third that of the Hampton Court maze, and although this is a more simple maze, the errors approximate those made in the other. The irregularity of the error curve must also be explained.

We are not quite ready to say that these differences were due to the lack of vibrissae yet this was the only difference known between these two groups save that perhaps this group was tamer.

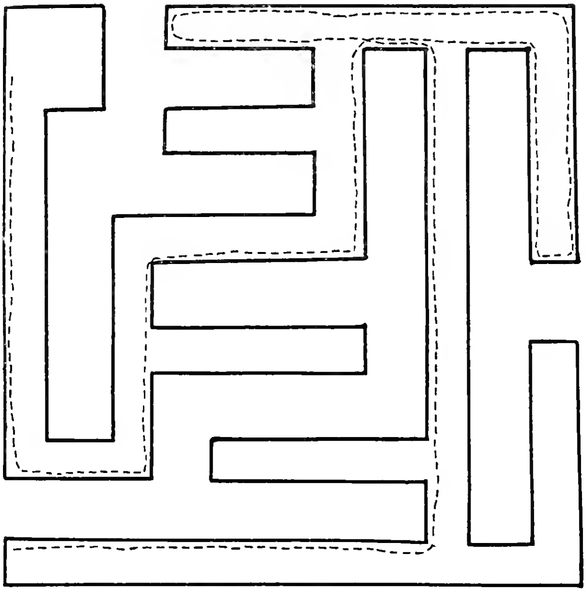

Fig. 4—Fourth trial of " Baby "—vibrissae cut on the right side.

We next used two sets of rats with the vibrissae cut upon one side only to see if possibly differences in behavior might not be revealed in this way.

Experiments IV. and V. Rats with vibrissae cut upon one side only. These experiments were tried with two sets of rats at two different times but the behavior will be discussed as a whole. In the first set the vibrissae were cut upon the right side as it was believed that more errors were made upon that side and therefore the loss on that side would be more severely felt. The results were strangely at variance with what we had expected but were confirmed by cutting the vibrissae on the left side of four rats.

These animals were all males with the exception of 1 and 2. Seven of them about two months old were sent out by a dealer in the city. They were as unpromising material as one often sees, dirty, with sore ears, bitten and bloody where they had fought in the box, wild and savage. Later three other animals were bought and added to this same group. These were named "Baby," "Footless," and "Bobtail." Baby was a young rat about the age of the former lot but the other two were fully a year old. Footless had lost his left front leg and hobbled along on three, while Bobtail as his name implies had lost his tail close up to his body.

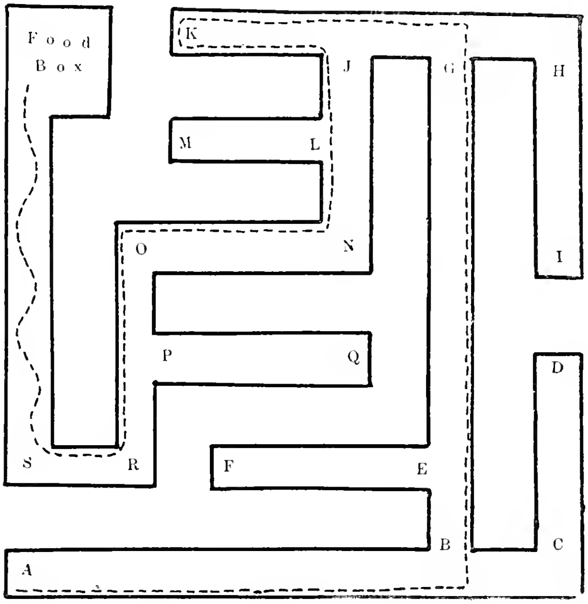

Fig. 5—Second trial of rat "6"—vibrissae cut on the left side.

Behavior:—These rats were much less timid than the other rats whose vibrissae had been cut but their behavior as a whole was very like that of the rats previously tried, except that from the first they kept close to edge of the walk, to the left when the vibrissae were cut upon the right and to the right when they were cut upon the left. As they ran out on the maze they one and all turned their vibrissae down, dragged them along the edge and scarcely ever ventured away from it. Now, as has frequently been pointed out, any maze can be learned by keeping constantly to the one side or to the other and that is what these rats did. The result of all this was that they learned the maze in the lowest time of any group of the series. It was interesting to watch them find their way at once around the maze and scarcely halt or hesitate.

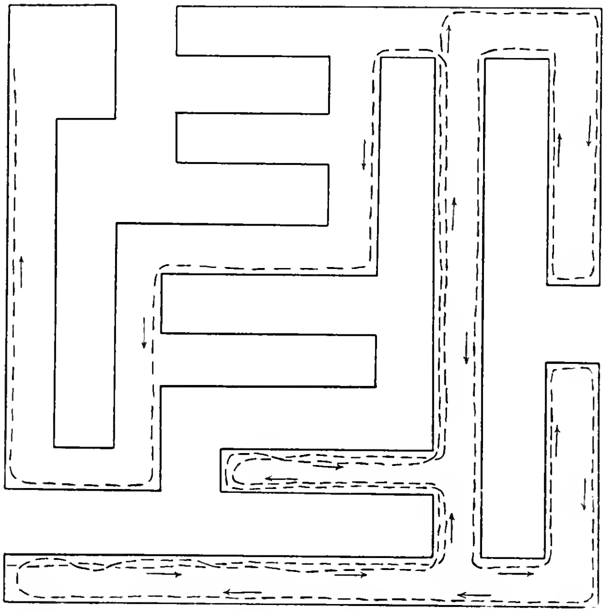

Fig. 6—Fourth trial of rat "3"—vibrissae cut on the right side.

An exact record was made of the first ten trials so that the path followed could be drawn but as six of the nine rats learned the maze in the first ten trials it seemed useless to continue this later.

Bobtail was incommoded by the loss of his tail and could not make as good time as the other rats did but he managed very well. Footless on the contrary had a hard time. His vibrissae were cut on the right and he perforce must keep to the left edge and it was his left fore foot which was gone. He did it, I had almost said manfully, in spite of falls, and was but little slower in learning the maze than any of the others in his group, succeeding in spite of his deformity. The females were slow and Baby as might have been expected was the quickest of the lot. Some of the rats abandoned the edge of the walk in the later trials but others followed it to the very last time. When they came to the entrance to a *cul de sac* they crossed over but continued, on the other side of the alley, to go along the edge which they had been following.

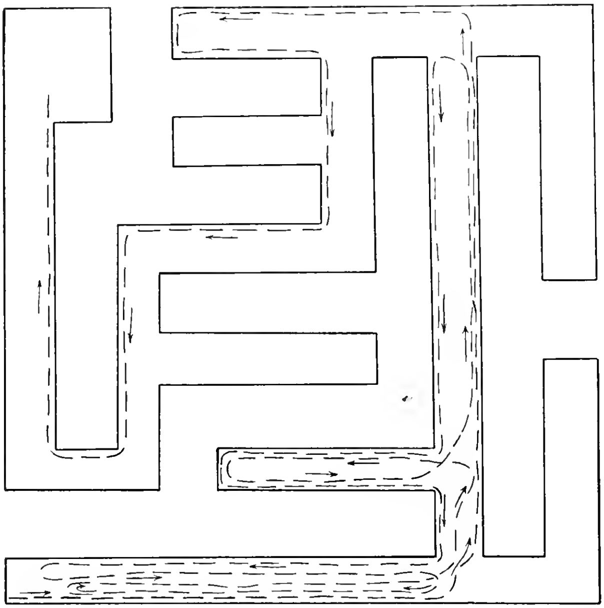

Fig. 7—Fifth trial of rat " 5 "—vibrissae cut on the left side.

The detailed path of some of these runs has been mapped and appears in figs. 4, 5, 6 and 7 the learning curves in figs. 8 and 9.

Summary of Experiment IV.

Five rats in maze—vibrissae cut on the right side.

Average errors in the first twenty-five trials	41.
Average errors in the first trial	4.4
Average time of learning ....(trial)	10.6
Average time of the last ten trials in learning	36.6 sec.
Average time of the last of these trials	18. "
Slips and falls in the first twenty-five trials ......(avg.)	2.8

Summary of Experiment V.

Four rats in maze—vibrissae cut on the left side.
Average errors in the first twenty-five trials........... 39.
Average errors in the first trial...................... 13.
Average time of learning.....................(trial) 18.

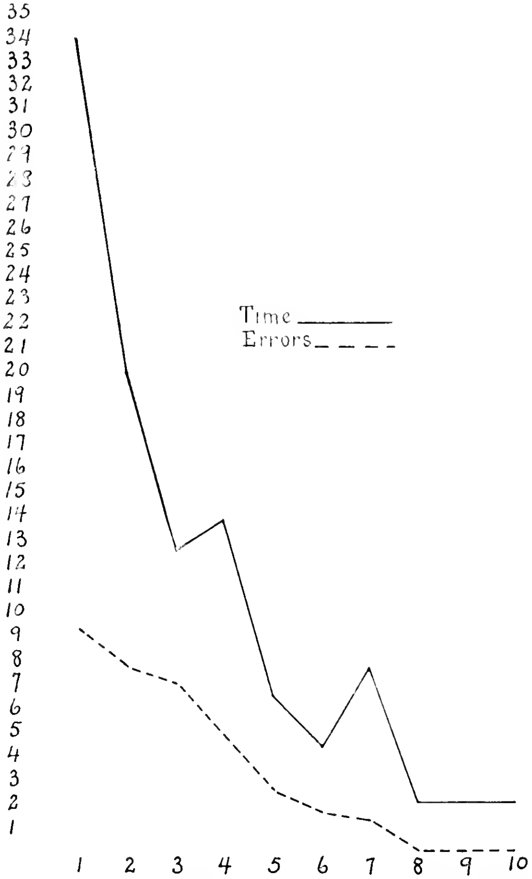

Fig. 8—Learning curves, time and error, of rats with vibrissae cut on the right side.

Average time of the last ten trials in learning......... 17.8 sec.
Average time of the last of these trials............... 10.2 "
Slips and falls in the first twenty-five trials......(avg.) 10.2

These summaries speak for themselves. There are still a great number of slips and there is still the characteristic behavior but the time of learning in spite of this is decreased. Comparing the two it is seen that when the vibrissae were cut on the right side forcing the animal to the left where there were fewer blind alleys the errors were greatly decreased at first and the time of learning much less. On the other hand the total number of errors was almost the same in the two groups but the curves show radical differences. Where the cut had been made on the right the error curve begins lower and there is an almost uniform descent and the last fifth represents a practical automatism.

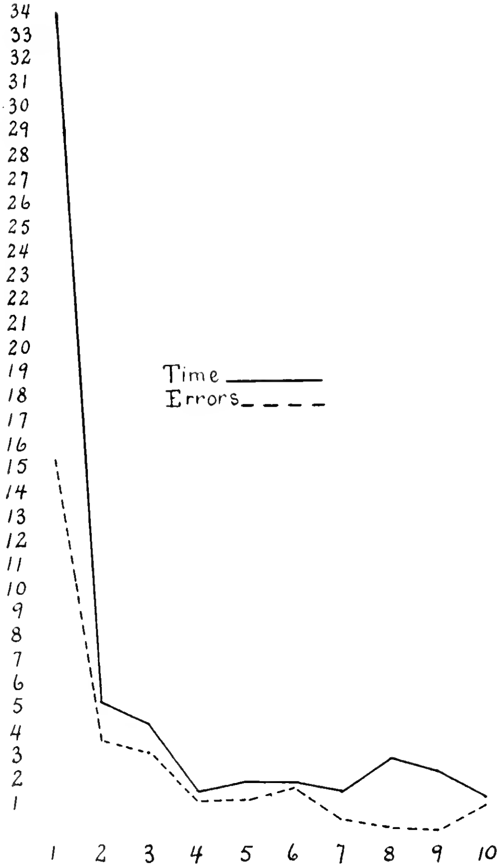

Fig. 9—Learning curves, time and error, of rats with vibrissae cut on the left side.

The error curve when the cut had been made on the left drops more rapidly but does not in the entire distance become uniform. The time curves begin at about the same level but the one where the cut has been made on the right—the more favorable—side shows extreme irregularity as compared with the other although unlike the other there is uniformity in the last fifth of the curve.

One is puzzled to account for some of these differences. The higher time curve for the more favorable side no doubt comes from a closer following of the edge a procedure which on that side is tolerably successful. The big drops in this time curve are possibly due to the dropping out of some of the by-ways into which this habit of following the edges led the animal. The following of the right edge although it took the animals around the maze was not so successful as a whole and was earlier abandoned. But there was more of it to abandon and the cutting out of errors did not occur so quickly although the time dropped more rapidly.

Rats can evidently make use of their vibrissae in solving their problems. The long side hairs touch vertical surfaces, the short curved ones, nearest the nares, the floor or ground as they run. Or the animals can turn the long hairs down and follow along edges and the act saves them many a slip and fall as the record shows.

If a rat runs out into the open it runs close against the sides of house, wall, or walk. It does this instinctively, supposedly from fear. From recent work upon animals we may conclude that the vision of the white rat is poor. May not this habit of keeping close to vertical surfaces be due to the fact that the vibrissae of the rat serve much as a blind man's hands serve him in a room or as his cane as he walks about the street. If a blind man had lost his right hand he would naturally keep to the left of the walk. A rat does not need his vibrissae to tell him the size of holes, his ordinary cutaneous sensations are sufficient. I have seen one of these rats squeeze through a hole an inch and a quarter in width while the vibrissae of this same rat from side to side including the head measured five inches.

The animals in Experiment II were seen to make more use of their vibrissae than under some other conditions but the two edges of the narrow path were exactly alike and they went from one to the other indifferently. If the edges were made unlike, if a low rail for instance, were put along one side, the behavior of the rats might be affected in much the same way as by the removal of the tactile hairs on one side.

Experiment VI. Anosmic rats with and without vibrissae. These rats were males whose olfactory lobes had been removed the last week in August. They were put in the maze the first week in October 1910. The vibrissae were removed from three of them but were intact in two.

The behavior of these animals as observed added nothing new for the real purpose of this work. They were used merely as controls since in the observation of the use of the nose it is impossible to tell whether it is being used as a tactile organ or for smell.

The records showed that the average time of the last ten trials was as low as any set tried while the errors were about the same as in the normal maze. A comparison of the rats with and without vibrissae showed the usual thing. The time of those where the vibrissae had been removed was one-half more for the last ten trials and the number of trials taken in learning was two-thirds greater. These rats, also suffered ten times as many slips and falls as those which had their vibrissae intact.

The curve showed a learning process which differed essentially from some of the others. The error curve was disproportionally high and almost entirely above the time curve. The curve drawn from the figures of the rats without vibrissae was very different from that drawn from those whose vibrissae were uncut.

Shall we say this—smell is in all likelihood the intellectual sense of these animals. When they are deprived of this, probably their whole remaining sense reactions are somewhat lowered in consequence. If the animals are in good condition otherwise, there is no reason why their speed may not be as great as the other animals, but they will make more errors in learning.

Experiment VII. Rats with infra-orbital nerve cut on maze without sides. In this group there were nine females. They were operated upon the first week in May, 1911, brought up to the laboratory May 14, fed in the maze May 21 to 24 inclusive and put in the maze to run May 25.

The infra-orbital branch of the fifth nerve was cut just before it anastomoses with the seventh so that presumably the tactile hair could mediate no sensation. The tip of the nose was made insensitive as well. For description of the operation and tests of sensitivity see appendix.

The behavior of these rats showed in an exaggerated form all that has been mentioned in connection with the rats whose vibrissae had been removed. One feature which did not appear in any of the others was a squealing at the end of blind alleys, or when a slip was made. They did not use their noses so much but seemed to depend more upon their feet. Perhaps an actual record of some of the notes will show better than any other way the nature of the behavior. Reference to the plan of the maze will show the course to which the letters refer. (See fig. 7.)

May 25, Rat 1, 1st trial.—Starts off cautiously; stays between A and B 10 sec.; falls; head over the side as if looking at the floor; on to B; makes much use of feet; toes are curling over edge; squeals; washes; on to E; head over edge; on to G walking edges; on to I; the body is elongated and flattened; washes; head over edge; falls; on G, H, G, H, N, O, N, O, on to end. 47 min.

Rat 2, May 25, 1st trial.—A to B walking edges; back to A; washes; on to B, head over, still walking sides; head in E; back to B; on to F; back to B; on to F. (This rat has a new way of going, he walks with his hind feet on the path and his fore feet feeling the edge in front of him.) D, slips; C; D; F; falls; D; G; still walking close to edges; turns around two or three times; back to B; on to F; E; F; B; G; C; G; R; bad slip; on to end. 24 min. 30 sec.

Here are some bits taken at random from the records of different rats and at different trials: Walks close to edge all the way; nose against floor; sniffs as if smelling; walks edges; body much flattened and lengthened; sniffing; slips; squeals as if afraid of falling when she gets to the end of an alley; running now; nose down; jumps from A to S; put back; when resting these rats hang on by their toes; if touched they squeal; they give every sign of seeing and smelling; up on hind feet sniffing; halts at almost every turn with head over edge; a cautious run; tries hard to get from A to S; tries to jump at K; up on hind legs time and again: staggers as if dizzy; carefully walking edges, etc. (See fig. 17, Plate III.)

Summary of results of Experiment VII.

Average number of errors in the first twenty-five trials	74.	
Average number of errors in the first trial	11.1	
Average number of trials in learning	28.5	
Average time of the last ten trials in learning	25.	sec.
Average time of the last trials	12.	"
Slips and falls	74, avg. 6.7	

It will be noticed here that the average number of errors in the first twenty-five trials exceed those of any other group thus far reported and the time of learning is longer. The average time of the last ten trials is high and the slips and falls are many. In the previous cases the slips and falls were confined to the early part of the learning period, but in this they persisted all the way through, far beyond the twenty-five trials quoted, making the total average about the same as for the rats with the vibrissae cut from birth, but with the errors differently distributed. There was a disproportion between the time and the error curve and the height of the time curve in the beginning was unlike anything seen. Evidently these rats were more unfavorably situated for learning the maze than any animals tried up to this time.

Experiment VIII. Blind rats with vibrissae; the maze without sides. This group consisted of six blind rats, females, whose eyes were removed August 3d. They seemed to be little the worse for the operation, were climbing all over the cage in an hour or so and there were no ill after effects. They were fed in the maze five days and were put in to run Aug. 21.

They really seemed to run more freely at first than rats with vision. They did not have the peculiar gait nor flattened, lengthened bodies which characterized the others.

In the beginning they ran to the extreme end of each path. They never turned until they were obliged to. Thus they always found it difficult to take the right way at B and even when they had fully learned the maze they were still forced to slow up here and feel for the turn. This was one of the last errors to be cut out and the next was K. Here they apparently found it easier to go to the end and then return than to accommodate themselves to the turn at J. There was a great deal of " nosing " and rising on hind feet and sniffing as if smelling. They tried to jump in the usual places A, K, and M.

Their early runs were most cautious ones, so very cautious that five of the six rats did not make a single slip or fall in the first five days' trials. About the fourth day they began to increase in speed yet the total time of a run was long because of the increase in errors. They ran rather rapidly, cut corners, fairly jumped some, and were more reckless every way than some animals with eyes intact which were on the maze at the same time.

One saw more of the learning of the maze in sections, the typical retracing of paths than in any other group used on this maze.

They kept close to the edge and their chief error lay in going past the turn and the next most common one in following an edge with their vibrissae which led them into a blind alley. One could always see in these rats their use of vibrissae on floor and edge of path even in rather rapid running. (Fig. 13.)

As the path was learned the kinaesthetic elements were very prominent. One could invariably tell which way a rat was going to turn before he came to the place of turning for after he had passed one turn his body was bent for the next. The direction of the turn seemed a much easier thing for them to compass than the position: i.e. the distance of one turn from another.

Summary of the results of Experiment VIII.

Average number of errors in the first twenty-five trials	68.	
Average number of errors in the first trial	20.6	
Average time of learning (trials)	33.	
Average time of the last ten trials in learning	17.	sec.
Average time of the last trial	14.	
Average slips and falls in the first twenty-five trials	3.	

A comparison of this summary with that for Experiment II, shows that with these blind animals, all other conditions being the same so far as known, the average number of errors for the first twenty-five trials as well as for the first trial were doubled, the average time of learning was doubled, and the average time for the last ten trials.

How shall we explain the slight difference in the number of slips and falls? The loss of sight, it cannot be doubted, is a real loss in this problem. The animals became unusually cautious so that in the early learning period there were few slips and falls. But the learning period was prolonged far beyond the twenty-fifth trial and whereas the other animals had for the most part eliminated such accidents before the twenty-fifth trial these animals had more falls after this time than before: a total of twenty-eight as against nineteen.

Still one might have expected a greater number than this on such a maze and under such conditions. But the nose and vibrissae seem to be of more help than eyes to a rat in such cases and as these had to rely almost entirely upon the form of sensory control best adapted to the situation, they were, doubtless, saved many an accident.

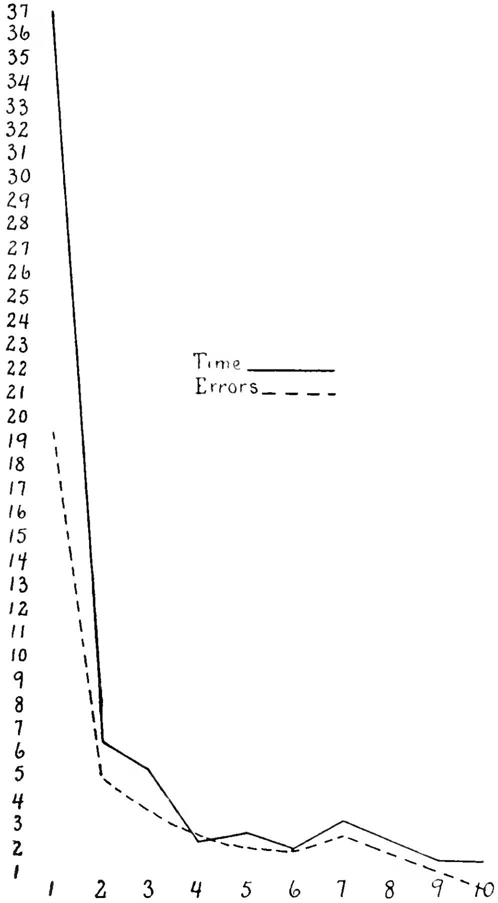

Fig. 10—Learning curves, time and error, of blind rats with vibrissae.

Strangely enough the curve plotted for these rats (fig. 10) resembles no curve so much as the curve plotted for the normal rats in the same maze with sides up in Experiment I. In general outlines they are nearly the same and also in the relation of the time and error curves. The time curve for the blind rats is more irregular but this is probably due to the necessity of avoiding accidents in a maze without sides. Why does not the error curve possess the same irregularities which that plotted for the normal rats in the same maze has (Exp. II)? As has been said before these rats must have been thrown back almost entirely upon the cutaneous and kinaesthetic sensations for control. Even the contact sensations are greatly lessened in a maze like this. There is no contact from the sides or from above and the only contact sensations they get are those coming from the floor through their feet, noses and vibrissae. Hence the curve partakes more of the nature of the curve for Exp. I, where the type of maze used was that which, as has been proved by others, is chiefly learned through kinaesthetic sensations. This curve is more irregular and longer in reaching its level because of the more difficult conditions.

Experiment IX. Blind rats without vibrissae; maze without sides. Five blind rats whose vibrissae had been removed were next put upon the maze. These rats were taken at random from the group of blind rats and were in just as good condition as the other blind rats with vibrissae which we were using at the same time on the maze.

These rats were put on the maze Aug. 26, and were kept at the problem until Oct. 18. They had then been given over 150 trials, ten times as many as the normal rats needed and five times as many as the other blind rats required on the average to learn the maze. None of these rats had learned it at this time and although one of them seemed to be cutting our errors and probably all would eventually have conquered the coördination the work was discontinued with them. Our interest lay not so much in the actual time taken to learn the maze as in the comparative difficulty of learning it under these conditions. (Fig. 11.)

The curve is not plotted as the others, that was impossible, but an error curve is made by averaging the errors by groups of twenty-five in order to show the slight lessening of errors after the first fall.

Although we were satisfied that these were not exceptional animals we now cut the vibrissae of three blind animals which had been used on a problem box previously. They were of the same age and sex and came originally from the same group. They had the advantage of previous training although of a different kind and had also played on the maze all the time that they were learning the other problem: that is they were put on the maze to play and taken from it one by one over to the problem box. They played here daily from Aug. 25, to Oct. 9, forty-six days, from an hour to an hour and a half a day. The maze was turned 90 degrees at the time but they were always put on at D which was the point nearest to their cage and made their way from here as they chose around to the food box where enough of the odor of food remained from the preceding experiment to attract them. From here they were taken to the box upon which they were working. Thus in reality they had been upon the maze as many days as the others up to this point, only for far longer periods and in a perfectly free fashion. When put upon the maze they always found their way immediately around to the food box and from here ran out on the maze in every direction. It might have been supposed that they would have learned it from every conceivable position.

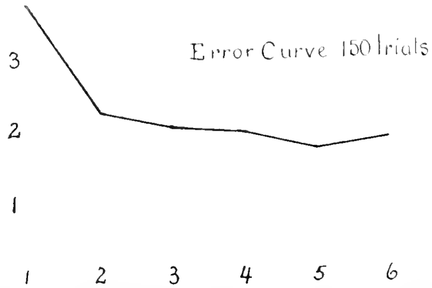

Fig. 11—Error curve for blind rats without vibrissae—plotted for groups of 25 trials.

These animals were now given fifty trials on the maze in its original position and only one could run it successfully at this time. This one learned to keep to the left and did so by curling his toes down over the edge of the path, sometimes dragging one whole foot along the edge and by keeping the pacing gait. (Fig. 16, Plate II.)

Behavior:—The behavior of the first three rats was different from any of the others put on. They were sluggish, had to be driven to their work by blows. When put upon the maze they flattened themselves out, clung sometimes by all four feet to the edges of the walk and refused to budge. It required several sharp raps with a long pencil to start them off and then they went most unwillingly. Hunger was an unavailing stimulus in this situation. After crawling along a little way they settled down again. If the delay proved unbearable another blow with a pencil might be necessary or any sharp noise or jar often startled them into going a bit further. This reluctant hesitancy continued with some to the very last. The slips and falls in the first twenty-five trials were not more than those of some other groups but the number did not lessen greatly in the succeeding trials. The errors were excessive with a fairly constant ratio. It seemed impossible for these rats to find the turns at B and J and it was only by feeling with feet and nose around these angles that they succeeded in taking these paths. Suppose the body, as we have often seen it in the blind rats especially, were set for a left turn after leaving A, but for safety the middle of the path, or for guidance the right edge of the path, was followed: then the turn would be made at C which was wrong. Now if rightness and leftness is the criterion of a turn when the animal comes out of this cul de sac and reaches B, the turn has become a right turn instead of a left turn. So far as any one could see the only hope of these rats in making this turn lay in their feet hitting the angle at B in some way as they ran down from A, but it seemed very easy to step over and miss. The only way to get it was to run along the left edge in the beginning and that meant many slips and falls.

The direction of the turn seems a much easier thing to compass than the position or place of the turn. It was striking to see the helplessness of these animals on this maze, the lack of tonicity, the slow crawling movement, the quivering flattened body.

Why did they find this problem so difficult to learn? The first reason has already been given: the inability to get the position of the turn and thus making it too early or too late. In other mazes with sides there are usually corners or projecting partitions which mark such turning points. Even man finds it difficult to carry distance in other than visual terms. One estimates distance by the fatigue produced in achieving it, in terms of time, or the units taken to cover it, i.e. steps. But all these prove more or less inexact. The precise point to be attained has to be marked by some visual or tactual object.

Second, it may be that if such problems are learned in sections and largely through kinaesthetic factors, that too great an interval of time must not elapse between the sections in order for them to be synthesized into a whole. That is, in this case the sluggishness of the animal may have prevented any entire organization of the series.

Third, and this is probably an important factor, the disturbances of equilibrium brought about by loss of both sight and vibrissae render the acquiring of any such coöordination by these animals almost impossible.

Figs, 15, 16, 17, 18 and Plates II and III, show characteristic positions of the animals in some of these experiments. The normal rat keeps to the middle of the path as a rule. The blind rats follow edges with vibrissae and use feet and toes much over the edges. The picture of the blind rat without vibrissae shows the way they use noses also The rat whose nerve is cut stands with feet far apart for balance and head up—a characteristic pose.

II. Summary of Labyrinth Experiments with Conclusions

Experiment I showed that so far as concerns mazes, this one was entirely comparable with others of its kind and the results with normal animals were typical results. In Experiment II, and all the other labyrinth experiments, the same maze was used with no sides to the runways. A very different type of behavior was revealed; but the results showed, as had been suspected, that although entirely open it was still a maze to the rats and the difficulties were not lessened. The next, Experiment III, with rats with no vibrissae was made under greater difficulties. There was increase in errors, decrease in speed, slightly lengthened learning period and a great number of slips and falls with much incoördination in the whole behavior. When Experiments IV and V were reached where the vibrissae are cut on one side it was found that a condition was produced which was actually helpful in this problem. The animals followed the edges of the paths with their vibrissae and being forced to keep to one side learned the maze in less time than any other

SUMMARY OF NUMERICAL RESULTS OF EXPERIMENTATION ON MAZE

	Average number errors first 25 trials	Average number errors first trial	Number of trials in learning.	Average time of last 10 trials in learning	Average time of last trial in learning	Slips and falls (25 trials) average
*Maze with sides up.........	41	18.	16.5	11. sec.	8.5 sec.	none
Rats with vibrissae..........	35	9.5	16.5	11.8 sec.	8.8 sec.	2.5
Vibrissae cut...............	44	8.	22.	18.5 sec.	7.5 sec.	12.
Vibrissae cut on right........	41	4.4	10.6	36.6 sec.	18. sec.	2.8
Vibrissae cut on left.........	39	13.	18.	17.8 sec.	19.3 sec.	10.2
Sensory nerve cut...........	74	11.1	28.5	25. sec.	12. sec.	6.7
Blind with vibrissae..........	68	20.6	33.	17. sec.	14. sec.	3.
Blind without vibrissae.......	97	15.	....	Average time of the last 150 trials, 31 sec.	....	7.

* With the exception of this first group all of the experiments were made on the maze with sides down.

group. Experiment VI gave the olfactory control and VII increased the tactual, contact difficulties without adding anything really new. When, however, Experiments VIII and IX were finished, it was seen that sight and contact may serve together or interchangeably for some problems, although the loss of either raises difficulties, but that the loss of both, or rather the efficient means of using both, makes difficulties almost too great to be overcome.

Previous histological and structural studies had shown that the tactile hair is a powerful tactile organ and that this is due:—

(a) To its great innervation.

(b) To the leverage which magnifies the stimulus.

(c) To the vibratory nature of the stimulus which is the only adequate stimulus for some reflexes, which summates subliminal stimuli, which prolongs the initial stimulus.

(d) To its muscular connections which transmit stimulus over large areas.

(e) To its haemostatic apparatus which permits free vibration of the hair to the depth of the follicle, which perhaps increases or modifies the pressure, which may raise or lower the nervous threshhold and which may possibly have some chemical significance.

The studies here reported prove:—

1. That these hairs have several important functions in the acquisition of such coördinations.

2. That these have not been observed in the ordinary maze because its mode of construction safe-guarded the animal at the very points where these sense organs are most efficient.

3. Open running, especially where footing is difficult, reveals different behavior.

4. Extending as they do sometimes two inches beyond the head, the hairs become in this sense "distance sense" organs whose office is probably chiefly protective.

5. Those curved hairs most anterior sweep the surface upon which the animal runs and the constant sensations thus aroused probably contribute largely to the "sense of support."

6. The failure of these sensations is warning of a void and throws into action powerful reflexes which save the animal from danger of falls.

7. The hairs projecting from the side also mediate guiding sensations as they sweep a vertical surface or are turned down against an edge as an animal runs. They keep it in the safe path.

8. They are, presumably, an important external element in rightness and leftness and hence closely associated with those kinaesthetic sensations which control an animal's turning.

9. As exquisitely sensitive mobile organs they are an effective aid to those kinaesthetic sensations functioning in locomotion by giving exactness to the place of the turn.

10. They are so evolved in this animal to supplement an exceedingly defective vision.

11. So long as an animal's efforts are engrossingly engaged in maintaining its own equilibrium all efforts to acquire other coördinations will be rendered increasingly difficult.

I. The Sense of Equilibrium

One of the most significant things revealed in the course of this study was the number and distribution of the slips and falls of the animals. To our surprise they were not nearly so many as we had expected from the narrow, elevated, unprotected runways. The maze was low, and what falls there were did not seem to affect the animals seriously. They were always picked up, put on the maze at the point from which they fell and for the most part at once began to run anew and often finished the run without error. The time lost was so brief it was not even counted out in the records.

As was remarked before, these slips and falls were made from both the sides and the open ends of the runways but in far greater numbers from the sides. The normal rats had few accidents but those with the nerve cut and those whose vibrissae were cut from birth had five times as many. The blind animals were only at a slight disadvantage in this respect. It might be concluded, therefore, that the vibrissae are of much more importance to the rat in such a situation like this than vision. But when we look at the record of the rats without either vision or vibrissae we infer that one of these sense organs at least is necessary for the acquiring of this coördination.

Such accidents as have been described might have different causes. First, they might come from rapid or careless running. In the normal rats so far as could be seen this was the case.

There was little trouble in the beginning and falls only began to occur as the rat increased in speed. In other animals, particularly those without vibrissae, this was not seen in anything like the same degree. There was extreme caution and fewer falls in the first trial or two but falls occurred when the speed was slow.

Second, these accidents may have been brought about by the incoördination resulting from the emotional conditions which were produced by the first fall. If this were the cause, why were not all groups affected equally and why were other signs of such disturbance not more evident?

Third, they may have been due to vertigo. Vertigo may come from labyrinthine, optical, or Weil says,[17] tactile disturbances. Labyrinthine trouble must be excluded as it would scarcely affect whole groups of animals and there are no signs of it in the natural and free climbing of these animals, vision is scarcely good enough to function in any such signal way and finally there were no known tactile disturbances except those brought about by the cutting of the vibrissae.

Fourth, they may have been due to the insufficient data for equilibration—what Bastian calls "guiding sensations." [18] Vision plays a leading role in human locomotion and it may be supposed that it has important functions in animal locomotion. The rat then with its poor sight is at a disadvantage of which the records of the blind rats may be a fairly accurate measure. The only other deficient sense of which we are cognizant in these rats was the lessened tactile sensations coming from the mouth caused by the removal of the vibrissae. This will be referred to again in a moment.

It happened at this time that Dr. J. G. Wilson was engaged in some research upon the semicircular canals and animals, including white rats, were available for observation with one or both labyrinths destroyed. A rat with one labyrinth destroyed revolves to the side of the lesion and in walking tends to circle to that side. When both labyrinths are destroyed it lies flattened with limbs extended, clutching support. It cannot maintain itself on a narrow support by clasping it with its limbs as normal animals do. This ability returns about the same

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[17] Weil 2: Des Vertiges, Paris, 1886, Quoted by Morat, Physiol. p. 612.

[18] Bastian, H. C.: The Brain as an Organ of Mind, 1891, p. 543.

time as the power of locomotion but in regaining this ability to walk it is very slow, much slower than a dog. This is mentioned because it has been noted before in the experimental work that the equilibrium of the rat seems unstable.

The day after the operation if the animal were placed on its back, a proceeding which it resisted forcibly, when released it righted itself with a spring which was machine-like in its quickness and perfection: in other words it was an unimpeded reflex. The normal animal rights itself but its movements show more variation in control. This animal's feet were now anaesthetized with ethyl chloride and it was again placed upon its back, where it remained unresisting until the effect of the anaesthetic had passed off. It is known that a frog from which the cerebral hemispheres have been removed can maintain its usual attitude so long as the afferent impulses from its feet are unaffected but if these be abolished it falls at once. A part of the disturbance in equilibrium in locomotor ataxia is said to be due to the loss of tactile sensations from the feet.

One more illustration. Among these rats was a blind rat whose labyrinth had been destroyed. It moved about as easily as those that saw but circled to the side opposite the injury. The only explanation which can be offered of this behavior is that as the seventh nerve was cut in the operation and therefore the vibrissae, although sensitive, were motionless on the injured side, the blind animal, which relied more on these organs as guides in locomotion, turned naturally to the side where they were more efficient.

Afferent impulses from the skin of the feet and the vibrissae of the head seem to be important elements in equilibrium and locomotion. They function as a constant factor in preserving posture and any break or change in these impulses is the stimulus to quick reflexes which serve to regain the attitude or stable position. Over these impulses the labyrinth appears to exert a controlling, inhibiting effect as is shown in the machine-like movements of the animal when cut off from this influence, but if now the afferent stimulus be abolished by anaesthetics the reflex fails. The stimulus to the righting movements of the rat without labyrinths comes from cutaneous impulses from the feet and not from the stimulation of the nerve endings in the back upon which it is laid or from the stimulation of the endings in the muscles and joints which results from the unusual body position.

It is easy to see, if we take Sherrington's view of the cerebellum as the head ganglion of the proprio-ceptive system with the labyrinthine centers as the most important ones, how by means of the large cerebellar tracts in the cord connections with the periphery are established. The cerebellar connections of the fifth nerve can be seen: but Sherrington and others consider the peripheral elements centering here to be those coming from muscles and joints, which being phylogenetically very old and dealing with constant habitual states, function in an unconscious way in maintaining skeletal tonus and bodily attitude. To these other kinaesthetic components must be added the cutaneous. Sherrington would say, probably, that the cutaneous element was only the precursor and not a real part of the proprio-ceptive reflex. Others would say that these cutaneous elements are on the same level as the kinaesthetic and for the most part are only physiologically sensory, not consciously so, and need involve no cortical connection.

Sherrington says of these reflexes, "It is difficult to see how a steady mechanical stimulus can continue to elicit a reflex constantly for long periods. . . . . . . If a weak agent is to stimulate, its application must be abrupt. But in the tonic reflexes whose source lies at the proprio-ceptors a weak stimulus, although apparently unchanging, seems to be an effective stimulus." Thus these reflexes differ very much from other reflexes in the threshold value of the stimulus, fatigueability, and in the time factor: but when the afferent element fails or changes quickly, as in the illustration of the running rat, there come instant, quick, preserving reflexes, which usually involve the other systems also. In the case given of anaesthesia of the feet, any cortical control was impossible and the peripheral end of the lower arc was cut off. It was not merely that sensation was lacking or changed but that the end organ was incapable of functioning.

Whatever may prove to be the cause of the many slips and falls, white rats, even in their natural conditions, have a very unstable equilibrium. The most common pathological condition which one sees among them is a twisting of the head and upper part of the body to one side so that the animal in running moves in a circle. If this disturbance increases the head is finally pulled back so that in resting it is turned toward the hind part of the body while its fore legs are extended forward in a characteristic fashion as if to brace the animal. If stimulated now the animal rolls, it can no longer walk. If picked up by the tail it revolves on its long axis. Whether this trouble is due to internal ear or to cerebellar trouble I do not know, nor whether it has one or several causes.

If a rat falls from the maze or from the table as frequently happens, it begins to whirl. This may continue for only a brief period or it may last half an hour, but it is the common effect of a blow or fall of any kind. The reason for this is for pathologists to determine but the facts are as stated.

Wesley Mills and others have made much of what they are pleased to call the "sense of support" in animals. They do not mean, as I understand them, a distinct sense, but a fundamental complex of muscle and joint senses with stereognostic senses which function in certain definite ways and which may be observed chiefly through its disturbance. Mills says, speaking of the behavior of young puppies the day of birth:—"It would seem that there is no more urgent psychical necessity to young mammals than this sense of being supported. All their ancestral experiences have been associated with terra firma so that it is not very surprising that when terra firma seems about to be removed they are so much disturbed." [19]

Mr. Yerkes later made this the subject of some experimentation in space perception and concludes from some tests when blindfolded that vision is the important factor in the space perception of tortoises. He found the same hesitancy at the edges of elevated surfaces which increased from strictly water forms to land forms. The hesitation also appeared at much less height for land forms than for water forms. When blindfolded the water forms usually ventured from any height without hesitation, apparently having no tactual-kinaesthetic sensations from skin, muscles and joints strong enough to cause an inhibition of the movement. The land-water forms on the contrary turned back from the edge and would not leave a board from which they would have flung themselves under

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[19] Mills, W.: The Psychic Development of Young Animals and Its Physical Correlate, *Trans. Roy. Soc. Canada*, 1894, sec. IV, p. 50.

other conditions. The strictly land forms were inactive and evidently more dependent upon vision for locomotion.[20]

Thus Mr. Mills observations were confirmed. This sense of support in the land animals is a strong fundamental sense from whose control, under the necessities of self preservation, vision has, in a way, partly freed it by associating with it perception of space which renders inoperative within certain limits the inhibitory influence.

These are not the only observations on the subject. Small[21] found the same hesitancy in young white rats, Miss Allen[22] none in the guinea pig, while Thorndike's chicks,[23] four days old, jumped at ten inches, hesitated at twenty-two and did not attempt thirty-nine.

We are very apt to think of sensory endings as organs for knowledge, for reflecting the exterior environment and to forget that a large part of our sensory experience arises within the body itself and is concerned immediately with the primal needs of the organism.

A water animal supported by the fluid in which it lives does not have the double problem in locomotion which a land animal has. The escape from the water and the acquirement of swift locomotion has been the slow process of ages. An immense increase in muscular power was made necessary by this change. To the sensory control in this task all of the existing sense organs contributed but they were modified by the need of definite orientation, and of swift locomotion for the preservation of the race and the species under new and difficult conditions. The modification of the ear has already been spoken of, the eye changed from monocular to binocular, from peripheral to foveal vision,[24] and in muscles and joints, in sinews and extremities sensory nerves multiplied to furnish control for the difficult equilibration necessary in locomotion.

Not only in phylogeny but in ontogeny as well is locomotion a difficulty to be conquered, a difficulty requiring the aid of

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[20] Yerkes, R. M.: Study of Space Perception, *Jour. Comp. Neur. & Psychol.*, 1904, vol. 14, p. 17.

[21] Small, W. S.: op cit., p. 305.

[22] Allen, Jessie: Association in the Guinea Pig, *Jour. Comp. Neur. & Psychol.*, 1904, vol. 14.

[23] Thorndike, E. L.: Animal Intelligence, p. 159.

[24] NOTE:—It is not to be understood that this development has no other functional correlates.

every sense and rendered increasingly hard by every defective sense.

In the rat, for instance, vision is poor and probably only serves to give it general orientation. Hearing, judging from observation is keen and has in it elements of both distance and direction.[25] Olfaction also has in it for animals in which the sense is keen that which may give both distance and direction and, in case of trails, marvelously supplement a defective vision in exact orientation.

The rat has another compensatory arrangement as this work has tried to show. It has about the mouth an exceedingly sensitive system of hairs.

Of these vibrissae those curved hairs nearest the nares drag along the surface of the ground and floor and in incessant vibration give immediate stereognostic sensations of contact and support. Projecting slightly in front of the body the failure of this sensory report seems to warn the animal of a void. The longer hairs arising from the side of the lip may be turned down against the edge of a surface so that the rat may follow it, an act for which poor vision would be ineffective, or these same hairs may graze the side of a vertical surface and furnish evidence of protection and guidance as an animal runs. In other words the vibrissae serve these creatures much as a blind man's hands or cane serve him in difficult or unfavorable situations. A rat does not instinctively run along vertical walls and avoid open spaces from fear but instinctively takes the course for which it is best fitted by nature.

J. Appendix

Section of nerve. In order to satisfy outselves as to the exact sensory nerve supply to the follicle it was resolved to cut the branch of the trigeminus which innervates it. There was a further reason in that it was desired to use, in the animal experimentation, rats whose noses and vibrissae were entirely insensitive.

In order that the motor nerve might not be cut the section had to be made before the anastomosis with the facial. This was done with strict antiseptic precautions. The wounds healed readily and in two weeks the animals to be used in the experi-

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[25] NOTE:—A blind rat can be called around a simple maze almost without error.

mentation were ready for use and save for a thinness of fur over the nose they could not be told from the others which were used at the same time as controls.

Three of these rats were afterward killed and by dissection and by tissue stained by the Marchi method we were furnished with proofs of section as well as of the certain distribution of this nerve.

Trophic functions. In view of the fact that trophic function of nerves is much discussed at present there may be some interest felt in the following phenomena. About ten days after the section of the nerve the vibrissae were noticed to be curling and splitting and breaking. They felt rough and dry to the touch and appeared rough and uneven on close inspection. They pulled out easily, the animal showing no apparent signs of pain and many of them were more brittle and broke far more easily than ordinarily. The animals washed their faces as diligently as ever so that this condition could not have resulted from lack of care. As old hairs sometimes persist in the follicle for a year after they are really dead, even while the new ones are growing up beside them, the rats were at no time without these appendages but they were noticeably shortened in length and fewer in number. It may be argued that the effect upon the hair was due to the interference with the blood supply and not to the loss of innervation. The reply would be that while this may be true, the hemorrhage was slight, as was stated before, the follicles themselves were intact, the wound had healed and the dressing was off in two weeks while the effect upon the hairs was seen months later even after the nerves had begun to regenerate. Surely such prolonged effects could not be a result of the disturbance of the arterial supply in the course of the operation. The hairs lengthen very rapidly. I do not know how long it would take a new hair to grow from the follicle to its full size but in the use of rats upon the maze, where the hairs were kept clipped close they had to be cut twice a week to prevent their being dragged upon the path.

It might be, however, that the effect upon the hairs was caused by a vaso-motor derangement. It will be remembered that the trigeminus contains vaso-motor fibers which originate in the third, fourth and fifth roots of the spinal cord and which reach this nerve through the superior cervical and gasserian ganglions There are both dilator and constrictor fibers in this nerve and when one remembers the rich vascular supply to the follicle and the probability that the circulation may be either by way of the sinus or not, one can see that the loss of vaso-motor regulation might be functionally serious. But whatever the cause, seven months later when to all appearances from gross dissection the nerve was regenerating and the blood supply normal the vibrissae were still scanty, broken and split.

Proof of regeneration. All of the animals used in the experimentation were killed and carefully dissected after the experimentation was over. The time between the operation and this examination ranged from four to seven months. In every instance the nerve had regenerated, but in many cases the number and size of the nerve bundles had decreased. In only one animal did the tactile hairs appear entirely normal. The notes taken of the last three examinations, seven months after the operation, are indicative of the appearance of the dissection.

Rat 3, male. Vibrissae long and strong, a total of 30 with 13 long hairs on the right side, a total of 34 with 12 long hairs on the left side. The nerves on both sides were well regenerated so far as one could tell by inspection.

Rat 8, female. The vibrissae are almost lacking on the left side. Only a few scanty hairs remain. There are about 20 on the right side, six of which are long. The nerve on the right side has regenerated but is not of the size of a normal nerve. The nerve on the left side is still more imperfectly regenerated. It has only four small bundles and one large bundle of fibers before the anastomosis with the facial.

Rat 5, female. Vibrissae scanty. On the right there is a total of 18 hairs with eight long and on the left a total of 12 hairs with five long. On both sides the nerves have regenerated. The right shows a broad clear white band of fibers, the left nerve is more broken with gaps in its width.

Tests for sensitivity. In connection with the experimentation tests were made to discover whether the animals retained any sensitivity in the upper lip or tip of nose, to learn what particular kinds of sensitivity if any remained, to find out what orders of sensitivity were connected with the functioning of the hair and in what order they regenerated. Needless to say all of these things were not established but in testing these points were kept in view.

For stimulation the point of a dissecting needle, of a pencil, the heated end of a blunt probe and ice were used. It was soon found that the animal's eyes must be kept covered in order to be certain that it was not reacting through vision. As a rule the rats, which were thoroughly tame, were held in one hand so that the fingers covered the eyes and the other hand was used in testing. The conclusions of the experimentator were checked up by those of others in the laboratory.

No animal tests of this kind can have the value possessed by human tests but they are interesting by way of comparison and necessary in this case as a control for the behavior experimentation. The following notes are those of a typical animal to which are appended a few notes selected from those taken from the animals used in the discrimination tests.

Rats operated Tuesday, Sept. 12. Both infra-orbital nerves cut. Ten minutes later climbed out of the box. Tested an hour later—no sensitiveness in upper lip or nose.

Monday, Sep. 18. Tested again this morning. No apparent sensitiveness to pulling hair, brushing hair, or to touching upper lip or end of nose with point of a needle even if the needle were pushed into the skin but the animal flinched every time the interior of the nostril was touched or the lower lip. It also sometimes moved its head when the upper lip was touched but with a slow movement quite unlike the quick jerk given when the lower lip was touched and never made this movement when the eyes were covered. Did not react in any way to needle pricks on these parts when the eyes were covered although the point of the dissecting needle was pushed far in. Tried a heated probe, so hot that it blistered the finger but it produced no effect neither did ice.

Sept. 23, (11 days). Lips still insensitive to pain or touch by point of compass or from pulling of hairs. On the left side there are only four long hairs. Five are broken off short. The short hairs toward the tip of the snout are bent and curled as if dead and pull out very easily. On the right side there are 10 long hairs, two broken ones and the short hairs near the tip of the snout resemble those on the other side. Some of them are split on the end. Tested the lip with a hot point but got no reaction. The animal squealed every time it was touched posterior to the vibrissae.

Oct. 2, (20 days). Other hairs are now breaking and curling. There is no apparent sensitivity to pain, touch or warmth in the upper lip in the neighborhood of the vibrissae but the animal always winces when the under lip or interior of the nares is touched. He shows no sign of feeling deep pressure.

Oct. 14, (32 days). Still more hairs breaking and splitting. These hairs feel rough to the touch. Tested by pulling and pushing hairs, for light touch and deep pressure, for pain and for warmth and cold but found no signs of any sensitivity.

Oct. 24, (42 days). Same as Oct. 14. No signs of any sensation yet. Wound perfectly healed.

Nov. 23, (72 days). Tested with needle, pulling hairs, pressing cheek, and with hot points. There was some slight sensitivity on the upper part of the cheek. The upper row of hairs was still insensitive to pulling but the needle and hot point evoked reactions. The tip of the nose gave evidence of sensitivity occasionally but much less often than the parts mentioned. The reaction to the hot point was probably pain as the point was hot enough to be painful when tested on human skin and as it cooled there was no reaction perceptible. The normal animal objects to having these sensitive parts of his body touched and nearly always responds by a quick jerk but these animals have permitted themselves to be tested freely and are only now objecting. There is no way to know whether they are responding to touch or to temperature unless they react to the one when they do not to the other. In this case it is only the extremes of temperature to which they respond and to pain with the possibility that the heat reaction may also be pain.

Dec. 9, (12 weeks). Reacts to heat (probably pain), and to cold in the two upper rows of vibrissae. Seems to be hypersensitive to hard pressure. The right side is more sensitive than the left.

Dec. 20, (14 weeks). Same as above. The point must be hot to get the reaction and in using ice it was fully 30 seconds before the flinching was seen. There is hypersensitiveness to deep pressure and to needle prick. In most cases the animal does not show any signs of feeling when a hair is pulled out.

These hairs are probably dead but occasionally there is a hair which causes a squeal when pulled.

Here are some more notes taken from those of the animals which were used in the discrimination tests. They are reported here because the behavior seems significant.

July 22, (11 weeks). Rats tested again today. Lip still insensitive. There is one thing noticeable for the last week or so. If they are taken up in the hand they root with their snouts like little pigs. The act is quite unlike the dainty touches which they usually give with their noses and vibrissae. Differences in the vibrissae are still to be seen but they are not so marked. Many of the old hairs have fallen and new ones are coming in.

Aug. 7, (13 weeks). There appears to be a little sensitivity among the outer vibrissae, not when pulled or touched but the skin about them seems to be a little sensitive. There is still the same rooting action with the snout.

Aug. 17, (15 weeks). The animals are refusing to open the swinging doors of the box which they have before pushed open easily with a blow of the nose. They come up to the door, sit before it and wait for it to be opened for them. There appears to be no reason for this unless their noses are growing hypersensitive. The doors swing freely from above, are very light and have caused no trouble previously but if they are not pushed with sufficient force they sometimes swing back before the animal gets through and strike the nose or head. The normal animal does not mind this but these seem to. The behavior is becoming very marked in all.

PART II. TACTUAL DISCRIMINATION

DIVISION I. EXPERIMENTATION,

to determine whether the vibrissae of the white rat aid in the discrimination of roughness of surface

While the work of the animals on the maze showed conclusively the effectiveness of the vibrissae in such representative situations, there was still left the open problem as to whether these organs could function in other tactual ways, whether they could mediate sensations of roughness or discriminate inequalities of surface. That they had a part in the regulation of equilibrium we know; that they contributed "guiding sensations" in the control of locomotion; that they were closely linked up with the kinaesthetic system in determining sequences of turns, "rightness" and "leftness;" but could they or did they, in the animal's experience, serve as agents for those other tactual qualities, contact values, of surface.

The experimentation which is reported in Part II was undertaken to determine this point. In the course of it, however, the general problem of discrimination arose in such a characteristic way that there has been added a brief discussion of some of the features of the act as a whole, in the light of the specific behavior observed in this problem.

A. Description of Apparatus

The box used in this experiment (see fig. 12 p. 54 and fig. 19. Plate IV), was made of three-quarter inch stuff and its dimensions were 5 ft. x 2½ ft. Two cross pieces were set one foot from either end, dividing its length into three parts, the entrance, the runways, and the food box. The runways, each four inches in width, were formed by six partitions set lengthwise in the middle of the box. These dividing walls measured 3 ft. x 5 in. and one side of each was lined with zinc. Two had corrugated and four had plain linings and the partitions were set in grooves so that they could be lifted and interchanged and thus the corrugated runway could be in any one of the three positions. The whole box, including the walls and linings was painted black. From the entrance there were free openings into the alleys A, B, and C, but at the end of these alleys in the cross piece doors were hung from above which could easily be pushed open by the animal's nose from the runways but which could not be opened by it from the food box. A button secured the doors when it was desired to have them closed. Later, when it became necessary, copper plates nine inches in length were screwed to the floor of the alleys at the food box end and connected by wires across the top of the food box with key, induction coil and batteries. The box had a glass cover in two parts but as the animals became more accustomed to the experiment it was not needed.

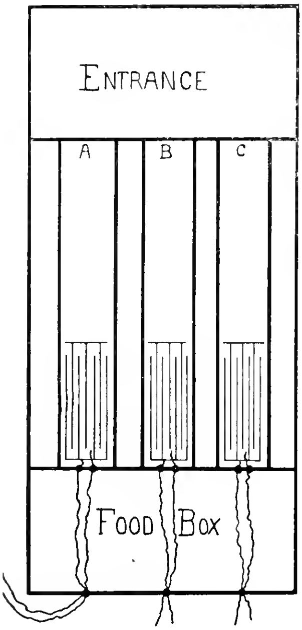

Fig. 12—Top view of problem box. The wiring is arranged so that the current may be turned on to any two of the plates leaving the third one safe.

B. General Conduct of the Experimentation

The box was kept thoroughly clean, was washed with disinfectants to exclude odor and, in order to prevent choice by position, the partitions were changed so that the corrugated pathway recurred regularly in the following serial order:—C, B, C, A, B, C, A, C, B, A, B, B, C, C, A, A, B, A, A, C, A, B, C, C, B, B, A, B, C.

The rats were put in the center of the entrance box with their faces away from the openings of the alleys so that they had to turn to see them. The problem was to choose the corrugated pathway. The animals were given three trials a day in the beginning but later the number was increased to five and they always ran under the stimulus of a healthy, normal hunger. The records showed the number and distribution of the errors, the time taken from the moment they were put in the box, and general observations of their behavior. It was determined that as only three choices were offered the percentage of right choices must be high, that the perfect runs must reach 75% of the whole, and that this standard must be maintained for a period of five days or 25 trials. As a matter of fact in most cases where the problem was learned a proficiency of 80% was reached.

The first set of animals used consisted of three groups, (a) animals with vibrissae, (b) animals without vibrissae, and (c) anosmic animals. Several months later a second set of animals was used which was composed of four groups, (d) rats with the infra-orbital branch of the fifth nerve cut, (e) blind rats, and (f and g) normal controls for each of the above groups.

The behavior of the animals in the box will first be described as a whole and then with the statement of the results of the experiments only those features will be emphasized in which one particular group differs characteristically from the others. No excuses will be offered for describing the behavior in such detail since it is believed that in such experimentation this careful observation of behavior is the important thing, far more important than pages of tabulations either of time or error records.

The experiment was complicated by several factors: First, the animal had three possible choices instead of the usual two; but as the interest lay in positive signs of discrimination, not in establishing records, it was felt that such signs would be more clearly observable with three possibilities than with two. For example, if an animal tries one pathway without success, when there are only two, he may take the other simply because it is the only other and not because of any sense quality which attracts him—there is no other alternative.

A further matter which materially lengthened the time of learning was the fact that the problem was not considered learned until the animal stopped at the entrance to the wrong runway: it was not sufficient to make the discrimination at the plate, it must be made before running down. In reality many, indeed most of the animals, had to be thus held up at the plate before they learned to seek the stimulus associated with the safe way or perchance negatively with the punishment. In one group where records of punishment were carefully kept a rat which took 195 trials to learn the problem in the way indicated, was only punished 10 times in the last 100 trials. In other words, if the problem had been considered learned when he made the discrimination at the plate this rat would have accomplished the task by the 95th trial. The insistence upon the carrying back of the discriminating act to the entrance of the runway, however, made it far more definite and easy to observe and freed it from many of the emotional elements which obscured it when it was made at the plate. Often incipient fear or excitement was aroused at the plate in such a way as to block an association which was really formed and deter an animal from crossing a perfectly safe plate, or else the nearness to the door and the smell of food stirred impulses too strong to be inhibited and led an animal over a live plate to try a closed door. In any case movements were increased at the plate and difficult of interpretation.

C. General Behavior of Animals in the First Series

These animals at first wandered about "nosing" everything and blundered finally down the right alley and into the food box. It took but a trial or two to show that they were really seeking food: they had made that association. In the activity preceding success they "nosed" the entrances, the sides of the wall as they ran down the alleys, the floor and sometimes the glass cover; but for awhile there was no evidence of the seeking of any particular sense stimulus. Rat "A," group (a) was the first to show such signs and from that time on, he time and again turned from the wrong pathway to seek the right. He usually "nosed" the entrances, while most of the other rats got their contact experiences with the sides of the path after they had entered.

There was much individuality in the reactions of the different rats. If a rat happened to take one of the side paths first, when it came out of this it followed the sides of the entrance box and took the path on the opposite side. This was rather characteristic of all the rats and might be repeated many times if the true path chanced to be the middle one. But at the same time each rat had peculiar ways of its own: some usually turned to the right first, some to the left; the more active rats like "H," group (a), dashed off immediately into any opening, while others always hesitated.

Habit was most marked as a sort of circular reaction and in many cases, like those governed by position, was easily established. "A's" 11th trial for instance, was one where he went back and forth as fast as possible from one alley to another, the adjacent one, as if he were wound up and literally could not get away. This was repeated 22 times before he finally took the third alley which was the right one.

The first choice made on a given day was likely to be a persistent one. The path which was the right one previously had some attractive power. This was more noticeable in the trials of a single day than from one day to another; yet in some instances, a successful association seemed to be carried over and influenced the first choices of the following day.

There was little difference in action between animals with vibrissae and animals without. The latter, however, "nosed" the floor more and kept closer to the sides where they could use their noses.

Errors dropped out little by little, the time decreased even for animals in which you could observe no signs of discrimination, and the percentage of right choices was very soon above the others; but after 150 trials although the errors and time had steadily decreased, so that an animal often ran several days without error, this behavior was not a consistent one and could not be extended to five days. Most of the animals gave clear evidence, so far as observation could show, that the difference in the pathways was sensed in some way but they did not make any consistent use of the power. In reality they could run in and out of two alleys and get in at a third in less time than they could do so by stopping to discriminate. From a human point of view there was no reason why they should. The electric apparatus was then put in and the rats were given a shock if they went to the end of the wrong pathway. Most of the animals could have made 60% instead of 33% of right choices before the electricity was used but the active signs of discrimination were lacking. The disturbance caused by the punishment made a break in the series but it lasted only for a day or two. When a rat is hungry he dashes off immediately, probably chiefly under the guidance of his olfactory sense. Here we had hungry rats, but we had produced a situation which not only called for sense discrimination but also for an initial inhibition of this instinctive impulse to run for food. In this particular set of animals the case was made harder because in the 150 previous trials fixed habits of reaction had been formed.

Although the shock was slight, one experience was enough to establish an association and to check the impulse in its complete working out. There was a great difference among the animals in this respect. Some had to reach the plate before it was effective, others stopped at the entrance; some could not carry the association over from one day to another, some from one trial to another; and some rats lay at the entrance quivering all over, not from fear as they often ventured on a live plate without showing anything like this behavior, but apparently with excitement as though the restraint put upon the impulse to run had caught all other impulses in a leash and produced an emotional condition which at first was inhibitory of all action.

"F," a rat in group (b), which had made one of the best records previously, when put in the box always ran straightway down some pathway as chance directed, but he never made but one error per trial for after this punishment he always stopped to "nose" at the next entrance. He was the last of his group to learn the box, but in the last 100 trials he never made but one error per trial. He had to have the shock before the first impulse to run could be blocked. On the contrary "A," group (a), whose records had been good previously immediately made the required per cent of correct choices.

When this halt came, most animals developed activities which tended to multiply the sense stimuli, particularly the cutaneous and the olfactory. Heads were put in pathways before venturing in, the sides of the partitions were brushed by noses and vibrissae in running down a path, the whole body was often pressed hard against the side. As a result, animals began more and more to turn away from or turn back in the wrong pathways, after such activities and seek other roads to success. It was significant that they almost never turned away from or back in the right pathway.

We noticed before that, previous to the introduction of punishment, many animals that still showed few outward signs of discrimination, were making what seemed an undue proportion of right trials. There was an air of increased confidence in their reactions in the right pathway, they more often and more unhesitatingly went to the end of it. There was nothing which would make one think of choice or prevision, but if chance or habit led them to this right path they took it and while sometimes they hesitated or wandered away from other paths, there was nothing which looked like conscious avoidance.

This sense of familiarity, if we may call it such, due to assimilation, facilitation, call it what you will, had in it probably no discriminated sense elements; yet it was powerful enough, in my judgment, to account for 60% of the right choices, as large a per cent as some experimentation shows where the results are attributed to some definite sense-discrimination. The behavior differed essentially from that which supervened later in the learning process when the animal after seeking a stimulus reacted to it in an immediate, definite, clear-cut way.

After these rats had really learned the path they scarcely noticed the plate. Some learned to jump it. They always received a shock at the end if it proved the wrong one, but still they jumped. Others learned to get two feet between the partition and get over by means of one foot on the plate. They had to let themselves down in order to open the door and thus could be punished, but a few animals continued this to the end even in the true path where it was unnecessary.

D. General Behavior of Animals in Second Series

These animals were put in the box and allowed to run through freely at first with all doors into the food box open, then with two of them closed and after five days the regular experimentation was begun with the use of punishment; hence this set had no break in the course of the experimentation as did the others. Although the behavior was very similar it may be well, in view of the discussion which follows, to emphasize some phases of it.

First, there was the usual lessening of errors and increasingly frequent choice of the right path with, however, no sensible evidence of discrimination.

Second, some rats found it exceedingly difficult to inhibit the first impulse to run and for many trials had to be punished before they would stop to discriminate, yet the first choice after such punishment was almost invariably right. One normal rat, a very active fellow, never could get farther than this. He was the only one of the 33 rats used that failed to learn the problem with the exception of those with the nerve to nose and vibrissae cut.

Third, so far as anyone could see every sense the animal possessed was used in the box but at first in a very random and exploratory way. Every bit of the box, every corner, side and edge was "nosed" over and over again. From this activity, thermal, tactual and olfactory experiences were obtained. There was every opportunity to use the eyes so far as a limited vision permitted.

Fourth, there was great individuality in the way in which the roughness of the surface was sensed. Some animals touched the sides lightly with the vibrissae at the entrance or all the way down as the case might be, some used noses in addition to the vibrissae, and some pressed the whole body closely against the walls of the passage as they ran.

Fifth, positive preferences, repeated series and the effect of the preceding right choice upon the succeeding ones were common observations with all.

Sixth, it became more and more noticeable that the sense experience described was being actively sought, more immediately in connection with the plate, but also down the entire passage and at the entrance, and finally was carried back entirely to the latter place.

Seventh, with some individuals the roughness of the sides became an immediate stimulus to enter a path whether this right pathway was the first, second or third attempted.

Eighth, others, e.g., rat "A," group (e), always tried at least two pathways. If they reached the wrong alley first, they rejected it, and went on until they came to the right one; but if they came to the right one first, after testing it, they went on to another and then back to the right. There were several rats of which this was true; rats in which the discrimination evidently depended upon the contrast between the two experiences. This is quite a different thing from the case where one contact experience became a stimulus to enter and another possessing no such power was simply neglected.

Ninth, in the end choice was clear-cut and direct, the animal going from one to another pathway until he found the right one and then confidently down and through.

E. Records of Experiments of First Series—Nov. 27, 1910 to Feb. 8, 1911

(a) Rats with vibrissae—(3 males):
  Average number of trials in learning, 165.
  Average time of the last ten trials, 28.7 sec.
(b) Rats without vibrissae—(4 males):
  Average number of trials in learning, 195.
  Average time of the last ten trials, 168.1 sec.
(c) Anosmic rats:
  (1) Rats with vibrissae—(2 males):
    Average number of trials in learning, 204.
    Average time of the last ten trials, 156.5 sec.
  (2) Rats without vibrissae—(3 males):
    Average number of trials in learning, 190.
    Average time of the last ten trials, 179.2 sec.

F. Discussion of the Results of the Experiments of the First Series

It will be seen by a comparison of these results that evidently the vibrissae are an aid in the learning of such a problem. It not only took the normal rat without vibrissae 30 trials longer to learn the box but the average time taken per trial was five times as long. Vibrissae seem to be an aid in the discrimination of inequalities of surface. It may be said that time and error records do not show discrimination and this is true. But the records help to establish and verify the observations of the behavior reported. Of the discriminating act we will speak later.

The anosmic rats were used simply as controls so that we might be able to say that certain behavior was not due to the use of the olfactory sense. The number of these animals was too small to claim anything positively on the basis of their records. They had been on the problem longer than the normal rats when the electricity was introduced, and thus had 20 more trials to their credit. In order to make the records comparable 20 should probably be subtracted from each of the average number of trials in learning. If this were done, there would be but little difference between the normal and the anosmic groups. There is also little difference between the anosmic animals with vibrissae and those without, so far as the number of trials goes, but there is a marked difference in the average time per trial and here they also compare unfavorably with the normal animals.

The anosmic animals were much less active than the normal animals. They tended to grow heavier and the muscular tonus had sensibly decreased. One can easily see therefore why the time per trial was lengthened; but as the rats were always kept at the problem until they succeeded in entering the food box there was no reason why these rats should not have learned the problem, as they did.

Olfaction, no doubt, is the guiding sense of rats in seeking food, the sense which excites, quickens and controls such an activity. Take this away and there remains a less active, more inert animal whose initiative in this respect is at a lower level.

As has been said before, the entire purpose of a sense is not to give knowledge. Indeed, one may easily conceive, in the lower animals particularly, that this is the lesser function. Sensation is a stimulus to activity, not necessarily to a particular activity but to general activity. The functioning of one sense may be entirely dependent upon the results of the activity of other senses, so intimately are their neural systems correlated.

If olfaction is the keenest of the higher senses of this animal, its loss would probably affect even the strength of the sensation of hunger by depriving it of those elements of odor which precede all satisfaction of the appetite and give food most of its flavor, in other words by robbing food of its strongest and most intimate associations.

We should expect then, not that the anosmic animal might not learn this problem, but that lacking the incentive of certain strong associates, lacking the initiating peripheral stimulus to this particular act, and feeling the loss of general excitation caused by the cutting off of a mass of sensuous stimuli, response would be more slow—and slower still in animals which were further crippled by the loss of their vibrissae than in those where these aids to learning were still intact.

G. Records of the Experiments of Second Series—June 11 to Oct. 18, 1911

(e) Normal rats with vibrissae—(5 rats):
Average number of trials in learning, 161.
Average time of the last ten trials, 22.1 sec.

(f) Blind rats with vibrissae—(5 females):
Average number of trials in learning, 188.
Average time of the last ten trials, 45.8 sec.

(g) Rats with the infra-orbital branch of the fifth nerve cut—(6 females):
Number of trials, 441.
Average number of errors per trial at close, 1.7.
Average time of the last ten trials, 11.3 sec.

H. Report of Special Behavior of Animals of the Second Series

(a) Rats with infra-orbital branch of the fifth nerve cut.—The mode of cutting this nerve and the tests of sensitivity which extended over a period of seven months have been fully described in another section of this paper. The noses and vibrissae were entirely insensitive so far as we could see when this experiment began, six weeks after the operation. These animals had been used on the maze experimentation and were in a sense trained animals as were all the other animals used in the box. Some actual excerpts from the daily notes may serve as well as anything else to indicate the behavior.

June 11. The behavior of these rats is very like that of those used before, etc.

June 15. These rats are not so active as some of the others. They "nose" all about the box, however. They use their feet on the upper edge of the partition and may get some cue in this way. They made the association with the plate the first time.

June 26. Rat "1" went as rapidly as possible from C to A to B and to the very end of each runway without any "nosing." Rats "4" and "5" after a few trials and failures, sat for a quarter of an hour at a time without moving. Every 15 minutes they were lifted from the entrance where they lingered, given a sniff of food and put back in the box. There was then a brief activity and then quiet again. This conduct continued for three hours when they finally entered the food box.

June 29. Thus far the rats are showing no signs of discrimination. They sniff entrances to be sure but far less than the normal rats. Like other rats they take the side paths in the great majority of cases, going from one to the other around the sides of the entrance box or directly across as the case may be. Today they had two trials each and in both trials the true path was the middle path "B." "A" was entered 39 times, "C" 29 times, and "B" only nine times.

July 10. These rats are still slow. They are not "nosing" as much as the other rats, they are just blundering in.

July 19. This rat, (rat 2) is exploring systematically—"nosing" entrances.

July 22. Rat "2" appears to be learning some way, just how it is difficult to say. She has only made two errors in the last six trials.

July 27. Rat "2" made one error in five trials. In the second trial she "nosed" the entrances several times over. In the third trial she tried the entrances of C, B, A, B, C, and B, and finally went unhesitatingly down A. In the fifth trial she remained at the entrance to C for a time and then went over to B and down. I have discovered how she does it. She puts her nose over the upper edge of the partition far enough to get contact with her under lip. This contact sensation would be unusually strong when she draws her lip down between the corrugations on the true pathway. This rat was the only one of the group to learn the problem and this was the way she did it.

This group like the others began with a general mode of behavior which resulted in a gradual dropping out of errors, shortening of time, and falling out of the many extraneous activities. But the others from this kind of a reaction developed characteristic discriminative types of action which solved the situation, a thing this group was unable to do. The experiment covered a period from June 11 to Oct. 7, 1911, and in this time the greatest number of trials for any rat was 441. At the end of the four months the nerves were regenerating, sensitivity was returning and no doubt the rats would eventually have learned the secret of the box as the normal animals did but it seemed useless to continue the work further.

The graph which follows (fig. 13,) is made from the totals of the daily averages taken in groups of 25. It shows that the errors had not materially decreased since the first initial drop. It will be seen that the entire series closes with an average of 1.7 errors per trial. This point was reached in the third, fifth, tenth, sixteenth, and eighteenth average taken. Five times it fell slightly below this point but never below one error per trial. The variation per animal was not great.

Little has been said of time because it is very difficult to make time a criterion in discrimination tests. We can put an animal in a maze and take the time from the moment he begins to run and this time has significance, but we have no way of knowing when an animal begins to discriminate.

The other experiments had shown the influence of the vibrissae in such a problem, this by the elimination of all tactile sensibility in nose and upper lip reduced the animal to a condition where its ordinary conduct could not define the situation.

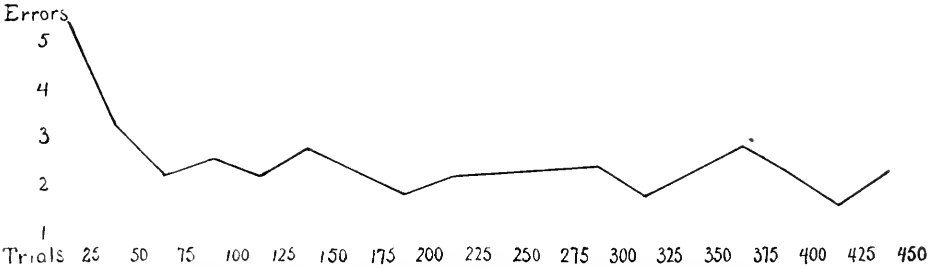

Fig. 13—Error curve of rats with infra-orbital nerve cut.

(b) Blind rats.—The general conduct of all of the blind rats differed less than had been expected from that of the groups which had preceded. It was first noticed that they were more active in the use of noses and vibrissae than the others and it was thought that forced as they were to depend entirely upon the olfactory and cutaneous senses for guidance in this situation they would learn the problem sooner. They had the initial stimulus of odor to start them off and they had the only other senses of any avail here undisturbed by any visual distractions. The results did not justify our expectations. The average number of trials in learning was somewhat greater but the average time per trial, if it is significant at all, was twice the normal average. How is this to be explained? We would not think that the loss of vision so slight as that of the rat's would be a very great hindrance in such a situation as this. But while these rats used their noses and vibrissae actively they did not move about so rapidly nor so confidently as the normal animals. Yerkes says, "It is claimed by those who have experimented with blind dancers that the loss of sight decreases the amount and rapidity of movement and the ability of the animals to avoid obstacles."[26]

It is quite possible that vision has a tonic, stimulating effect upon all movements. The loss of it, however, was shown in other ways than in mere decrease of movement. From the first it was noticeable that the movements of these rats were more indefinite and inaccurate. For instance they could not easily and quickly come to an entrance. Then, too, they often confined their explorations to two pathways or to the same one over and over again. The quick attempt at the third path way, when two had proved closed, was lacking for a long time. They developed a line of conduct, after some signs of discrimination had appeared, of going inevitably down the second pathway after one discrimination. They learned, of course, later to complete the act but the immediate possibility of more than two pathways, the quick trial of the whole series seemed to be largely the gift of vision.[27]

Besides the general stimulating effect and the possibility of the spatial series, vision seemed to lend to objects at a distance, i.e , entrances, ru ways, etc., an attractive power which led the normal animal in certain definite directions, which constantly tempted it on, kept it going, and enticed it here, there and everywhere. It made possible a wider experience and brought the animal more quickly and more surely into that intimate contact with surfaces which was necessary to this particular bit of learning.

Thus we may probably say that the blind rat's longer learning period as well as the slowness of its reactions, were the result of the slower and more indefinite movements due to the loss of sight.

These blind rats were not really needed in the problem but

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[26] Yerkes, R. M.: The Dancing Mouse, 1907, p. 179.

[27] NOTE:—Some of the blind rats that were being used were in a cage with several normal rats. It was possible to close one's eyes and separate the blind rats from the others by means of the general softness and flabbiness of the body due to loss of tonus. I have tried it many times.

we were curious to see whether by any possibility vision played a part in the discrimination of such surfaces as we were dealing with here.

There is one other matter of some interest, however. The plate with the other rats at once acquired vital associations and it did also with these but in a different way. The discussion of the possible associations will be left till later and here will be described only the excitement which was aroused as the rat approached the plate. The writer has not in mind those rushes across the plate which landed a rat in the food box or against a closed door, or the jumping of the plate or going over on one foot, etc. These might all have been, however acquired, incorporated as parts of one entire reaction and recur regularly without any specific sense appeal or control. The peculiar actions which were observed were different. They consisted of a hesitating approach, of many returns to the entrance, of little rushes to the plate and back, of testing it first with one foot and then with another, of withdrawing the foot from a perfectly safe plate with every appearance of shock, and sometimes of a spring of the entire animal back. This action differed from one trial to another and looked extremely like prevision.

The point to be made here is simply this, that this conduct was almost entirely lacking in the blind rats. The brightness of the copper plate had apparently become, to animals with vision, a warning signal. The blind rats were upon the plate before they knew it. They nearly always went on and tried the door even over live plates. They went more quickly it is true, but never showed, when on the plates or when approaching them, the characteristic excitement of the others. This may have been due to the general lessening of activity mentioned before but the differences of conduct seem too essential for that. In animals with vision associations were aroused which resulted in the excited state before the actual experience and as this preliminary warning failed with the blind animals there was none of this rise of excitement and they reacted to the plate immediately. Sherrington says, in discussing the distance receptors, "The ability on the part of an organism to react to an object when still distant from it allows an interval for preparatory reactive steps which can go far to influence the success of the attempt either to obtain actual contact or to avoid actual contact.

. . . . . By associative memory a tinge of the affective tone of the consummatory reaction may suffuse the anticipatory. The latter becomes indirectly a pleasure-pain reaction." [28]

Anatomical considerations as well as the experiments upon the maze had seemed to show that the sense of sight was very weak and imperfect in the rat.[29] It may seem that the course of this discussion would imply a reversal of this conclusion but such an implication would be erroneous. The first statement and previous work had shown wherein the sense was deficient, these experiments together with those of others show in what ways it is efficient. Sharp outlines, form, minute details, etc., no doubt are lacking in the visual experiences of a rat; but some degree of brightness, shadowy outlines, vague extent of surfaces are also undoubtedly a part of that experience. The copper plates, which it has been inferred entered as a visual factor into the reactions of the normal rats, were bright polished interlacing plates screwed upon the dead black surface of the floor of the box. Directly above them, not quite three feet distant was an electric light. These animals were used at night and if brightness discrimination is possible at all it must surely have been so here.

It may be said in view of this discussion that vision, though not the necessary sense to the accomplishing of this task, excites activities, arouses impulses, permits the formation of associations which make success easier of attainment. It may also be concluded with reason, and what is said here is only in the light of this problem, that the loss of vision does not make the tactile sense more keen but only more necessary and that vision, even poor as it is in rats, is an inestimable boon in the life of any animal. It is the sense which, because of its general exciting and tonic effect, spurs it on; by extending the environment, leads it out in new ways; guides it, however inaccurately, to places where it would never go; and warns it of danger while there is still time for escape.

(c) The normal rats.—The behavior of these rats was so similar to that of those used before that it is not necessary to go into it here. A comparison of the records of the normal rats of the two series shows that the numerical results are almost iden-

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[28] Sherrington, C. S.: Integrative Action of the Nervous System, 1906, p. 326.

[29] Vincent, S. B.: The Mammalian Eye, *Jour. Animal Behavior*, 1912, vol. 2, no. 4.

tical although the animals were used in three groups by two experimentors, and one group was separated from the others by an interval of eight months.[30]

Summary

This part of the experimentation was undertaken to discover whether the tactile hairs had any part in the discrimination of surfaces. The results show that they do. Not only is the number of trials in learning greatly increased by their removal but the time per trial is greatly lengthened. The work also seemed to show that the power of discrimination which remained after the removal of the vibrissae lay in the very sensitive nose since the blind rats and the anosmic rats could make the discrimination while rats with insensitive noses as well as vibrissae failed. The experimental work seemed to show as well that in such a problem as this the chief use of olfaction and vision is in initiating action and by a tonic effect sustaining it. These hairs then as the whole work shows are delicate tactile organs, which function in equilibrium, locomotion, and the discrimination of surfaces in distinct ways which have been described and the inference is drawn that the great innervation and fine mobility to which the increased sensitivity of these organs in rodents is due has arisen in compensation for an exceedingly poor vision.

DIVISION II. GENERAL DISCUSSION

There are always points of interest in any experiment which do not directly concern the main problem. A few of these in connection with this work have already been mentioned but some of the more general phases of the act of discrimination seem worth while considering now. The discussion is related to the discriminative process in general but is based upon the observations and experimental results which have been reported.

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[30] NOTE:—There were two normal animals belonging to group three whose records are not included in the averages. One rat, a female, had some trouble, perhaps in the vestibular tract, which pulled her over to one side, made her revolve in circles and rendered locomotion difficult. This came upon her soon after the experimentation began but her work was continued and she learned the problem at the 278th trial. It seemed unfair to class this animal with the normal ones. The other rat was the one spoken of before that never succeeded in learning the problem although given 460 trials covering a period of 95 days.

Miss Mothershead ran one of these groups of normal rats and I am greatly indebted to her for her records and observations.

A. The Value of the Use of Contact Senses in the Study of Discrimination

The greater part, indeed almost all, of the "so-called" discrimination experiments with higher animals has been made with the help of the distance senses. This is also true of the experiments in imitation and association which involve discrimination. The contact senses always play some part, to be sure, but the distance sense is the one which is being tried out and usually this sense is vision. It is not singular, therefore, that in the use of a sense so late in phylogenetic development, and in many animals so weak, there should be such conflicting opinions as to the process of discrimination itself in animals.

The contact senses are probably of far greater value in the lives of the lower animals than we realize and we are very apt on the other hand to over-emphasize the importance of the higher senses. The associations also, in the experiments using visual cues, have not been native vital ones. It is doubtful whether visual discrimination is ever the direct stimulus to a rat's quest for food, yet in experiments it has been made to serve this purpose. The lights, colors, etc., which have been used have been stationary yet it is well recognized that moving objects are those to which animals respond most quickly.[31]

For students of animal behavior the advantage of the use of other senses is great. If psychic processes are to be inferred from behavior there must be behavior to observe and there is very little of this in the reactions to visual and auditory stimuli. As a rule only the final act is seen and all the intervening steps are hidden. Yet the discussions of animal intelligence are based, for the most part, entirely on such experiments. The conclusions are not fair to the animal. On the other hand, when contact senses are employed, there is a far greater amount of observable activity—activity which reveals stages of development, which changes from day to day and from trial to trial, and which gives our inferences far more justification as well as plausibility.

No one can tell when an animal sits and looks at two lights or two colors and then responds with certain conduct what has happened in the preliminary interval. Of course the inference is equally impossible in regard to some of the other senses to

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[31] Yerkes, R. M.: The Discrimination Method, *Jour. Animal Behavior*, 1912, vol. 2, no. 2.

which we appeal and in a certain degree it is true of the contact senses but the behavior involved in the latter reveals much more to us. In these experiments, for example, nothing could be said with certainty as to how much or what the animal saw, but every movement which was made, every part of the box which was nosed, could be described. It cannot be known in any way when an animal begins to sense differences in color or brightness but it was always possible to see when these animals began to seek contact experiences in definite places. Nothing can be said as to whether any process of comparison goes on when an animal is in the presence of two colors but when it goes from one runway to another trying the sides of both, when it cannot choose a corrugated pathway until it has tested a plain one, it may be inferred that something like comparison, something like discrimination is present. So far as behavior can show the whole process is open in the use of the tactile senses but when the distance senses are used we see as a rule only the consummatory reaction and the developing of the same, the perfecting of a crude reaction is hidden.

This is a plea for more experimentation involving the cutaneous senses and a protest against the conclusiveness of the analyses of the mental processes of animals when based upon investigations which require the use of the weakest and most defective sense.

There are rather constant differences between discriminations involving the distance senses, particularly vision, and those which are made through the contact senses. In the one the stimulus must be presented and in the other it must be actively sought. There is therefore a greater degree of activity in the one case than the other. The greater self activity thus aroused in the animal is probably a factor in favor of this latter form of discrimination. In the experimental work employing vision, the colors, forms, etc., to be discriminated have usually been presented simultaneously, or if successively, with only a very brief interval between. When the contact senses are used the sensory cues are of necessity successive and therefore time and place are greater factors in this form. If there is any comparison in the case of simultaneous visual presentation it may be made directly, at least the effect of contrast is direct; but in tactile discrimination some form of mental content must be carried over from one point of stimulation to another. In either case there may be direct association with the object, either positive or negative to which the animal reacts, but in the first instance there need be but one such association since both possibilities were present in the same moment, in the second there must be both forms for the experiences are more widely separated in time and order.[32] The affective and emotional tone probably differs and influences the corresponding reactions. The hunger stimulus is most closely associated with the contact senses while protective reactions from danger are likely to be associated with the distant senses of sight or hearing and these facts will affect the reactions. Experiments and conclusions drawn from them should recognize these differences.

B. The Sense of Familiarity

One of the simplest forms of cognitive experience is known as the sense of familiarity. The conduct which seems to be based on familiarity has been mentioned. It occurs in every form of animal experimentation and is characterized by decrease in errors, in useless activities and in time, yet it gives no evidence of real sensory discrimination. The subject will have to be discussed first from the human standpoint and then carried over to the animal field.

If we take the position that the activity comes first, or rather that sensory discrimination arises out of the reaction or as a result of it, we shall have put ourselves right in the beginning. The response is originally to an entire situation, a whole, out of which as yet no sense qualities have arisen: they are all fused. But close observation shows that the reaction is being influenced by these very sense qualities and that it changes with their change although the introspective evidence in man and the discriminative action in animals is lacking. How shall we explain it?

One explanation is that the reaction occurs too quickly for any sense element to stand out and that there must be delay or impediment for this to happen and yet that the reaction was different because of these elements and in a general way was sensed as such.

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[32] NOTE:—This description does not apply, of course, in all of its details to experimentation involving sound.

It has been said that these qualities are in the fringe, margin of consciousness yet influence the reaction just as the different backgrounds unconsciously influence the visual perceptual experience. This is of course a statement of fact and not an explanation.

There have been efforts to account for the state by postulating slight increments of sensation too feeble for consciousness but which summate, so to speak, in discriminated elements. These weak elements are, as Miss Washburn says, physiologically sensory but not introspectively so. Miss Washburn herself would try to refer the phenomena to fusion of certain sensations in cortical cells and trace it back to phylogenetically old attitudes.[33]

Others believe with Wundt that the sense feeling or feeling tone, which accompanies all sensation yet is distinct from it and which also has a qualitative range, is responsible for this state which is suffused by a friendly, familiar feeling.

Recent work of Head gives evidence in man of a lower conscious center than the cortex—of a thalamic consciousness. According to Head this consciousness is non-discriminative and the sensory elements are visceral, thermal and certain forms of contact sensations all of which produce strongly affective reactions. He says, "Under normal circumstances the thalamic element in contact sensibility rarely if ever reaches consciousness, which is dominated by discriminative sensations of touch and it only becomes a conscious factor when the influence of the cortex is removed. Thus we believe that the essential organ of the optic thalamus is the center for consciousness for certain elements of sensation. It responds to all stimuli capable of evoking either pleasure or discomfort, or consciousness of a change in state." [34]

The controlling nervous mechanism from being chiefly segmental has been steadily pushed higher and delegated to central organs in the leading segments as all work in comparative neurology shows. From animals whose segmental autonomy is practically complete, the development can be traced step by step till man is reached whose activities are so pre-eminently dominated by cortical influence. Yet animals like these, which have

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[33] Washburn, M. R.: The Physiological Basis of the Relational Processes, *Psychol. Bull.*, 1909, vol. 6, p. 369.

[34] Head, H.: Sensory Disturbances from Cerebral Lesions, *Brain*, 1911, vol. 34. Pts. II and III, p. 181.

been discussed, no doubt live for the most part on the lower, more primitive, thalamic level whose perfect reflexes and low grade consciousness serve most of their needs.

In man with his highly developed distance senses and great correlation and association centers built over them, the cortical center has become the controlling and important one and the peripheral scarcely comes into consciousness in revival. With some animals this may not be so: the early revival may largely be effective in the periphery and function in action and attitude as an immediate reinforcement of present sense stimuli, as a certain pure sense or feeling of familiarity, lending steadiness and a certain degree of control to movements, but finally becoming elaborated, when higher connections have grown stronger with repeated use, even in such animals as these, into a cortical control based upon discriminated sense elements.

C. The Emotional Element

The action at the plate has been rather fully described. Can we analyze it? Here a check arose in the midst of an habitual activity. There is but one general response to a painful cutaneous stimulus and that is a movement away from it, a movement protective, instinctive. The shock was slight, but it came as a surprise and the animal rushed off the plate. This happened several times. Then the pain became associated with the sight of the plate and the activity was aroused in advance of the actual cause. The plate became a warning signal, "Keep off." The quest for food urged the animal on but all the activities were also present which were associated with danger. The conflict between the impulses resulted in an exaggerated activity and the emotion grew. He rushed up. He rushed back. He tested with one foot a perfectly safe plate, pulled it back quickly as if burned and washed it with his tongue. He danced about, quivered, and finally made a wild dash in or out.

The blind animals were upon the plate before they knew it. The shock was only a stimulus to action. They either tried the door or ran off. It could not be said that they showed no signs of emotion or that there were no associations in their case with the plate; they did give evidence of some emotional activity but this was very feeble in comparison with that exhibited by the others. There was no preparatory interval, no warning in advance so that revived attitudes, renewed activities could function. The situation was upon them before they knew it and they reacted immediately to the present stimulus. It was as though the immediate potent stimulus destroyed, precluded, any incipient emotional activities which may have been present. One is reminded of the remarks often heard from those who have been in some sudden accident or danger. When asked if they were frightened they replied, "No, I had no time to be."

The biological conception that the chief value of the distance senses is to allow a preparatory interval for adjustment before the final consummatory act is a familiar one. Physiologists say that the reaction to contact stimulation is immediate and that the response even though it involve a series of acts may be regarded as consummatory. Psychologists recognize the short reaction time for touch. Sanford says, "Touch, active and passive together is pre-eminently the sense of closest motor connection. This also has its important meaning in psychological life in general." [35]

Sherrington elaborates the idea that contact stimulation results in definite movements of particular members or parts of an organism while to the stimulation affecting the distance senses the organism reacts as a whole[36] and Head would explain these two types of activity as arising from thalamic and cortical influence respectively.

The explanation of the emotional activity which it may be conceived Head would offer is this: The thalamic response to the stimulus at the plate would be an instinctive one, immediate and direct. Such a response the blind animals exhibited. In the normal animals, however, the cortical centers for vision were in active function and discharging downward upon the thalamus inhibited this instinctive thalamic response. During this inhibition the affective and emotional tone which is characteristic of this level had time to develop and was finally released, as Dr. Herrick says, in a spasmodic reaction. Head says, "All stimuli which appeal to the thalamic centers have a high threshold. They must reach a high intensity before they can enter consciousness, but once they have risen above the

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[35] Sanford, E. C.: The Function of the Several Senses in Mental Life, *Am. Jour. Psychol.*, 1912, vol. 23, no. I. p. 60.

[36] Op. cit. p. 343 et seq.

threshold they tend to produce a change of excessive amount and duration, and this it is the business of the cortical mechanism to control. The low intensity of the stimuli that can arouse the sensory cortex and its quick reaction period, enable it to control the activity of the cumbersome mechanism of the thalamic center." [37]

In the case of the blind animals where the cortical control through the visual centers was lacking the intrinsic thalamic response was the one observed and the emotional elements which had no time to develop were lacking.

Whether this explanation prove the true one or not, we know that the motor connections are close and the cutaneous reactions are immediate while the distance senses permit exactly this preparatory interval during which the conflicting impulses can be adjusted, the sensory experiences of the past brought to the aid of the present, new lines of conduct struck out, danger avoided and success won. The emotional condition which was the reflection of this conduct was stronger, naturally, in the normal animals where the distance sense involved was functioning than in the blind animals.

D. Association and Discrimination

A common tendency in discussions of association, especially in connection with animal behavior, is to try to establish evidence of a certain serial order—stimulus A, act B, act C, etc. If this problem showed any one thing more clearly than another it was the fact that at first there was a general intensive type of activity, that every possible sense was actively at work on the situation, that out of this general behavior was differentiated specific acts and out of general sensory stimuli definite sense experiences. Of course this is inference but so far as could be seen the activity, sensory stimulation, and discrimination were mutually dependent. The bodily activity about the box was gradually eliminated from the entrances, carried down into the runways, to the doors, then to the plate, and finally back to the entrance of the runways. The sensory activity followed the same course. The point to be made is this, acts A, B, and C are all bound up in the activity as a whole and even here in fragmentary undeveloped form and grow out of this general

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[37] Op. cit. p. 191.

activity in their perfected associated forms just as the sensory factors are elements which are split off, discriminated from the general sensory situation. The following description then holds with the understanding that all these connections were originally inherent in the situation as a whole.

The associations which were formed in the learning of this coördination were various, if we may trust our observations, and inessential as well as essential in character. First, certainly, the animals learned to associate the whole situation with food and the obtaining of food with the preceding activities. Second, this activity was associated with definite parts of the box. Third, the successful activity was associated with an open door and the unsuccessful with a closed door. Fourth, the plate was associated with pain. These early associations were made quickly and generally but from here on there were marked individual differences. The open door should have been associated with a safe plate and the closed door with a shock. It took the animals a long time to make this association. Some rats would go over a live plate time and again to try a closed door and even return upon the plate after a lengthened attempt would appear to have ruled it out.

The problem was to make the association of the corrugations with the open door but as will be readily seen this association might be made with the open door and not with the safe plate. Many rats really failed in this respect. They never, judging by their actions, reacted to a safe plate, and although the association between the corrugations and the open door or food was strong enough to lead them over it, they went on one foot, or jumped, or shrank, or showed signs of fear in some way. Some animals never learned to eliminate the plate from the coördination even when the whole process had become more or less automatic. It was always from this point on, roughness, plate, open door, the plate being safe or not as the case might be; while others later learned to go from surface contact on over the plate with no evidence of any sensory or affective reaction to it. Before the learning was said to be complete they had to make the rough surface association at the very entrance to the runways.

There were a few animals as we have said that always had to interpolate in their series, in whatever order made, experiences from one or both of the wrong runways. In the end many of the unnecessary associations dropped out and those which remained became more and more automatic in character.

In this discussion there has been an effort made to preserve the distinction, which some forget, between the acquisition of the act and the perfected reaction and the associations have been treated in such detail in order to show the real complexity of the problem and the great individuality of the reactions. Perhaps sufficient emphasis has not been laid on the rejected associations or at least those which finally sloughed off, as those of position, preferential or associated with previous successes, and the differing degrees of ability to carry the controlling association back regularly in time and space from the door to the plate, from the plate to the surface of the walls and from the walls near the plate to the walls at the entrance.

Just what mental stuff this associative memory process is carried on with it is difficult to say. Granting that the sense experience is somewhat similar, an argument from structure of course, why not admit it to be comparable to such very simple human experiences. We may well rebel against the idea that rats possess visual images such as ours when they have such very poor visual organs, or against ideas in the human sense; but something certainly is carried over here which is not incorporated directly in the stimulus. Perhaps in our efforts not to become anthropomorphic we have swung too far the other way. There seems to be evidence of comparison, there seems to be memory of distinct sense experience. A belief which is shared by many is that all human imagery has in it real sensory elements and that revival involves periphery as well as center, the whole arc in other words, although we fully realize that our present knowledge of neurological structure does not confirm this. There are, however, some facts which might seem to support the contention.

The perfection of neurological technique is giving us increasing knowledge of the variety of functional fibers in the nerve trunks and makes us feel that there are still unknown possibilities in these. The centrifugal fibers which are found in some of the afferent nerve trunks, the optic for example, are thought by the biologists Cajal,[38] Duval, Lenhossek, Roux and others

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[38] Ramon, y Cajal, S.: Histologie du Systeme Nerveux, 1911, p. 366.

to function either in the reinforcement of stimulation, or in the setting of the synapse in more exact adaptation, or in secondary sensation, or in giving higher intensity under attention; while the psychologists Külpe,[39] Wundt[40] and others explain after images, secondary sensations, and memory images correlated with peripheral sensations by the same fibers. Much of the recent work on imagery, particularly that of the Wurzburg school, has failed to show that degree of clearness of imagery in the thought processes which had previously been supposed to be there and has forced a re-examination of the elements involved in reflective thought. The theory of peripheral sensations centrally initiated which function in control in some simple form has some foundation in fact.

Why should not, therefore, some such simple sense elements, far more representative of sensations than perceptions, call them images if you will, we will not quibble over words, function in the life of animals? Stripped of the rich associations which human thought adds to them and the rich variety and complexity which human sense experience would give them, they must be very meager indeed, yet distinct enough to form a part of the meaning which the past has given, and memory preserved, and to which the animal reacts so typically.

It is not insisted that the completed act may not follow, when learned, from direct stimulation at the entrance to the runways or that the association may not in most cases be between activities. What is insisted is the fact that in a situation where the stimulus which is the cue must be actively sought, where space conditions are constantly changed, there is strong presumptive evidence that the sensory experience is a discriminated one. Not that such experience is ever entirely separate from the act, that could not be, but that it arises as a result of it and in turn sets up a new series of activities. This presumption is further strengthened by observations of activities in which this sensory stimulus only proves effective when in contrast with its opposite, when an animal must always have the two experiences before the final act occurs. Then there is the behavior at the plate. Here there was pain associated with contact followed by excessive activity. Later the activity was

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[39] Külpe, Oswald: Outlines of Psychology (Eng. trans. 1893), pp. 83, 183.

[40] Wundt, Wm.: Principles of Physiological Psychology, (Eng. trans. 1904), vol. 1, p. 182 et seq.

aroused in advance of the contact experience, presumably through vision. Not only was the activity revived but also, judging from the essential character of the activity, the sensory experience itself in some form. The behavior in all of its details lends credence to the above assumption.

This emotional condition is not so marked in all discriminative acts as in this but one well wonders, after watching this process day after day, if on this lower level and in their inception all such acts do not have this emotional setting. According to Head, the discrimination would be the unusual, the more exact, the quick cortical control, imposed upon the slower, more instinctive, habitual, less exact, sensory and affective thalamic. But whether emotion does or does not play a vital part in all such acts, it did in this and therefore has been described as it occurred.

The general stages then of this act of discrimination are as follows:—The sense of familiarity marks the first stage. In the problem which has been reported the use of electricity really forced the next stage. The first effect of this punishment was an emotional condition which multiplied movements and therefore greatly increased the contact experiences through feet and sides of body but chiefly through vibrissae.

The pain caused by the shock became associated with the sight of the plate and probably also with its position. In this way the emotion was evoked in advance of its real cause and judging by the behavior was keener and more vivid when it appeared prospectively than when it was aroused directly.

The earlier stages of the process which was characterized only by the familiar feeling had led to 60% of the trials being made in the true pathway and hence experiences of inequalities of surface were far more numerous than experiences of plain surfaces for it must be remembered that the preliminary emotional condition occurred at the safe plate as well as at the others.

The experiences with the plain surfaces were closely connected in time with those of the rough and finally the very strength which had been developing in the latter set it off as different but in this it was helped by the contrast between the two.

The disassociation was also helped by the vital and different associations which belonged to each—pain, closed door, no food, with the one, and open door, food, pleasure with the other.

The practical use of the discrimination led to its formation and helped to perfect it.

As it grew in power it could be further separated in time and space from the place and moment of necessity. It also became more definite and accurate and showed active signs of the comparison which was at first probably only implicit in the act.

It can only be said in conclusion that the problem was solved by a series of discriminations and associations which varied with individuals and which had a regular course of development; that the process showed in certain stages what seemed like comparison and at the plate what seemed like revival and that this leads us to infer some form of stable psychological content, independent of fixed time and space conditions perhaps weakly analogous to human imagery. *

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* See Katzaroff's work on recognition for a description of the feeling of familiarity. He finds, in recognition, the two stages in human consciousness which this paper has attempted to describe in animal behavior. Katzaroff, D. : La Recognition, Archives de Psychologie, 1911, t.11, no. 41.

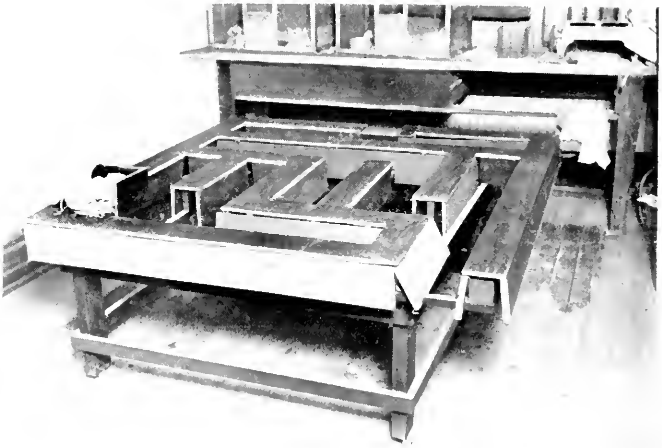

Fig.14—The maze as used with sides down.

Plate I

Fig. 15—Normal animal with vibrissae on maze without sides Notice the position in center of track, the way the feet are placed, the lifted head and body, the free movement, etc.

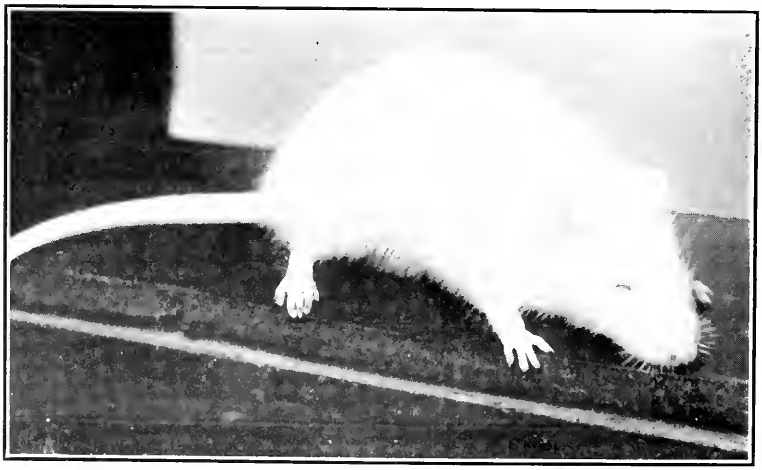

Fig. 16—Blind rat without vibrissae. Notice the flattened body and the use of toes and nose on the edge of maze.

Plate II

Fig. 17—Rat with infra-orbital nerve cut. Notice the extended limbs for equilibrium, the use of toes, etc.

Fig. 18—Blind rat with vibrissae. Notice use of toes and vibrissae on edge of maze.

Plate III

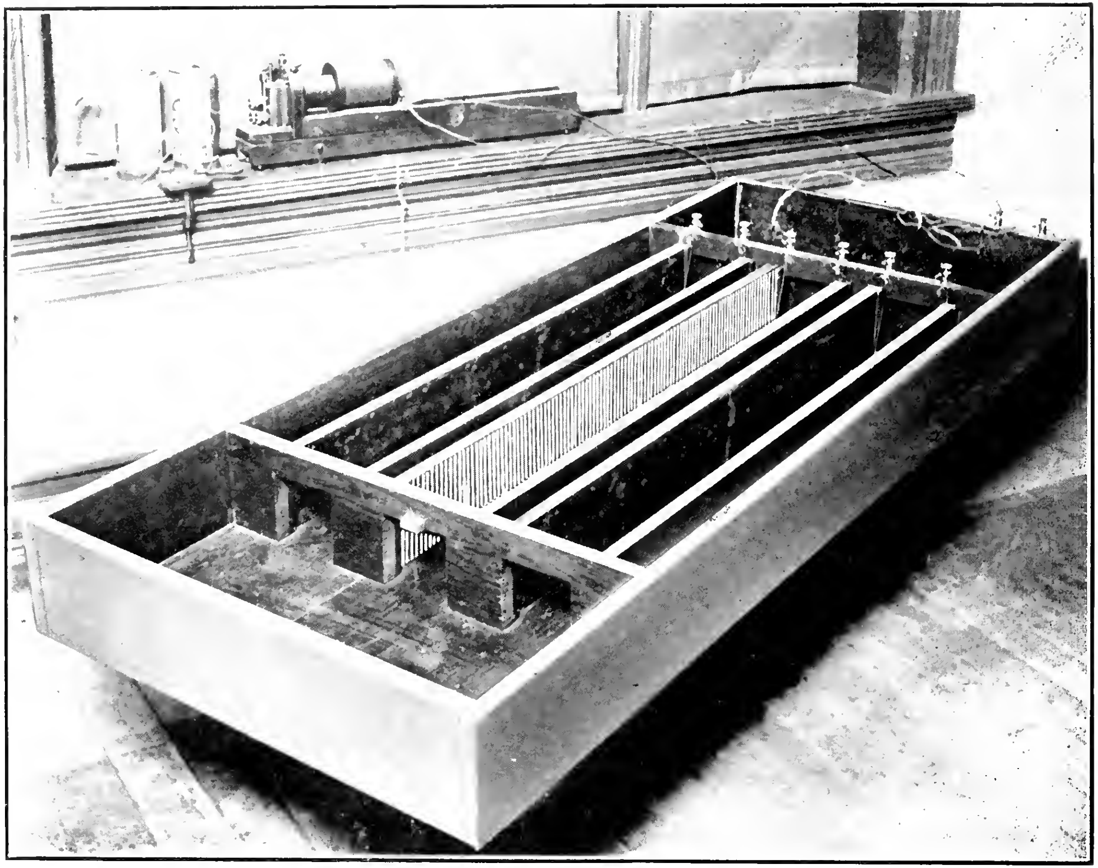

Fig. 19 - Problem box used in discrimination tests. The corrugated surface which seems lighter in the picture was really indistinguishable in color from the other partitions. The end of the box in front is the entrance. The copper plates in the floor at the farther end of the alleys are hidden, as are also the swinging doors which admit to the food box at the back.

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