THE JOURNAL

OF

ANIMAL BEHAVIOR

VOLUME 6, 1916

CONTENTS OF VOLUME 6, 1916

Number 1, January-February

Number 2, March-April

Number 3, May-June

/ / ι ᛫/ /�521

NUMBER 4, JULY-AUGUST

NUMBER 5, SEPTEMBER-OCTOBER

Number 6, November-December

Subject and Author Index

VOLUME 6

Original contributions are marked by an asterisk (*)

*Alcohol, effects on behavior of chicks, 103.

Allen, G. D. Reactions of *Planaria*, 375, 381.

Andrews, E. A. Behavior of *Folliculina*, 375, 381.

*Ant, marriage flight of, 70; literature on, 400.

*Ape, record of birth, 330.

Arey, L. B. Orientation in amphioxus, 411, 417.

*Arlitt, A. H. Behavior of chicks, 103.

Awati, P. R. The apple sucker, 386, 395.

Back, E. A. Fruit fly, 386, 395.

Baege, M. H. v. Animal psychology, 412, 417.

Banks, N. Distribution of insects, 392, 395.

Barnard. Feeding of butterfly, 395.

Barrows, W. Reactions of spider, 386, 395.

*Bees, behavior of solitary, 367.

*Beetle, habits of, 325.

*Behavior, of chicks from alcoholized eggs, 103; *analysis of, 150.

*Bingham, H. C. Reactions of bird dogs, 371.

*Bird, color vision of, 1; *effects of alcohol on, 103.

Bittner, L. H. Tropisms, 375, 381.

Blackman, M. W. Life history of *Pityogenes*, 383, 396.

Blair, K. G. Luminous insects. 386, 396.

Bonner, W. Wintering of ants, 400, 406.

*Brain weight, in relation to behavior, 267.

Bromley, S. W. Asilids, 388, 396.

Brün, R. The orientation of ants, 401, 406.

*Buddenbrock, W. v. The tropism theory, 341; function of statocyst, 376, 381; the tropism theory, 376, 381.

*Burtt, H. E. Behavior of white rat, 222.

Buttel-Reepen, H. Color sense of bees, 386, 396.

*Capon, behavior of, 319.

Carr, H. Donaldson's "The Rat," 419.

Carter, L. A. The cyst of amoeba, 376, 381.

Cary, L. R. Sense organs of jellyfish, 376, 381.

Chapman. R. N. Life history of *Agrillus*, 386, 396.

Chemical senses, literature on, 408.

*Chick, behavior of capon toward, 319; *vision in, 169, 189.

Child, C. M. Development of starfish, 377, 381; "Senescence and Rejuvenescence," 420; "Individuality in Organisms," 420.

*Chimpanzee, born in Cuba, 330.

*Churchill, E. P. Learning in gold fish, 247.

Cleare, L. D. Behavior of butterfly, 388, 396.

Coburn, C. A. Behavior of pig, 414, 418; behavior of crow, 416, 417.

Cole, L. W. Experiments with raccoons. 412, 417.

*Color vision, in birds, 1; literature on, 386.

Commensalism, literature on, 394.

*Cowan, E. A. Behavior of chicks, 103.

Coward, T. A. Behavior of blackbird, 412, 417.

Crawley, W. C. Marriage flight of ants, 401, 406.

Crozier, W. J. Reactions of sea cucumber, 377, 381.

Davis, W. T. An ant's nest, 401, 406.

*Death feigning in *Tychius*, 138.

Delayed reaction, 412, 413, 417, 418.

*Dermal senses of *Necturus*, 81.

De Voss, J. C. Color blindness of cats, 409, 417.

THE COLOR VISION OF BIRDS

I. The Spectrum of the Domestic Fowl

K. S. LASHLEY

Johns Hopkins University

Evidence bearing upon the color vision of birds has come, thus far, chiefly from three sources; tests for the Purkinje phenomenon, discrimination tests with pigments, and photo-electric studies of the retina. Hess ('07) advanced the first evidence for the Purkinje phenomenon in birds. He placed white rice grains on a matt-black background, illuminated them with a spectrum, and placed fowls before them. The birds, light adapted, pecked first from the region of the orange through the red to the limit of the human spectrum, then in the yellow to blue-green, never in the blue or violet. Dark adapted and with a spectrum of low intensity they began to peck in the region of the yellow or orange-yellow and reached somewhat farther into the blue-green but never into the blue. Similar behavior was observed in the pigeon. The point of greatest stimulating value seemed to shift from the longer to the shorter wave-lengths with darkness adaptation. These results also led Hess to conclude that the spectrum of the day-bird is shortened at the violet end. In view of Watson's proof ('15) that the spectrum of the fowl is fully as extensive as that of man the validity of such a method as that of Hess becomes questionable.

Katz and Révész ('07 and '09) reported experiments with color-papers and stained rice grains in which fowls, when dark adapted and in dim light pecked more frequently at grains reflecting the shorter wave-lengths than when light adapted and

in bright light. A somewhat more conclusive test was made by Hess ('08) in measurements of the pupillary opening. The maximum contraction of the iris was produced by longer light waves in light adaptation than in darkness adaptation. A preliminary report of the writer's experiments was given by Watson ('14). They are recorded at length in the following pages. Yerkes ('15) using a similar method, obtained evidence of the change in the relative brightness values of the red and green with change of adaptation in the ring-dove.

Students of color discrimination in birds have usually employed color-papers or dyes with no certain control of intensity or saturation. Porter ('06) records tests with the English sparrow and cow-bird in which red, yellow, green, blue, and two shades of gray paper were used. The birds learned very readily to distinguish between these. Rouse ('06) used almost identical methods with the pigeon and secured like results. Katz and Révész ('07) trained chicks to pick out colored rice grains from among gray ones. As Hess ('12, p. 21) points out for the work of Katz and Révész, all these results might have been obtained with completely color blind animals. Hess ('12) reports tests with rice grains stained to match the Seebeck-Holmgren wools. Fowls distinguished the reddish grains from the greens and grays of this series, which were confused by a red-green blind man. From this Hess concludes that the fowl is sensitive to the wave-length of the red and green rays. The uncertainty of conclusions as to the color vision of animals drawn from analogy with the condition of brightness vision in color blind men has been pointed out by Frisch ('14) and the evidence of Hess himself for a shortening of the fowl's spectrum in the blue-green tends to invalidate his evidence for color vision. The careful work of DeVoss and Ganson ('15) shows in a practical way the justice of the most severe criticisms that have been urged against the use of color-papers in the study of animal vision.

Rouse ('05), by recording the rate of respiration in the pigeon after stimulation with light, was able to show an increase in rate progressive with change from the longer to the shorter wave-lengths. He was not able to find like changes with alteration in the intensity of light of constant wave-length. The tests with wave-length and intensity were not carried out under

like conditions, however, and the results obtained are not comparable. Katz and Révész ('09) advanced evidence for color fatigue in the fowl after exposure to red which seems to prove some differential action of wave-length. Yerkes ('15) showed the ability of the ring-dove to distinguish spectral red from green but did not control the brightness of the lights.

Finally the study of the action currents of the retina gives evidence of differential sensitivity to wave-length in day birds, Kohlrausch and Brossa ('14) obtaining characteristic types of galvanometer deflection for different wave-lengths irrespective of intensity. The correlation between action currents and color vision has not been made however.

All this evidence offers good ground for the presumption of a true color vision in day birds, yet the results are in no case, absolutely conclusive. The question of the nature of the bird's spectrum, the number of primary colors, has not been approached experimentally. Hess describes the color vision of the fowl variously, as like that of a normal man, and as like that of a man looking through a piece of orange glass. He takes the latter view because of the supposed shortening of the spectrum at the violet end. Watson's data upon the threshold of the fowl make this view untenable. Beyond the probability that the bird is capable of some sort of reaction to wave-length, no definite conclusion can be drawn from the studies reviewed here. The details of spectral sensitivity, contrast, after images, color adaptation, and the rôle of color vision in the normal activities of birds are still open problems, promising to tax objective methods to the utmost.

The present paper offers further evidence for the existence of color vision in the fowl, in the form of data upon the relative stimulating effect of different wave-lengths upon the light and dark adapted eye, the ability of the fowl to react upon the basis of wave-length, and the appearance of relatively abrupt changes in the stimulating value of different parts of the spectrum. The experiments were begun in 1912, but, owing to delays incident to reorganizing the apparatus and to pressure of other work, they have progressed but slowly. The chief problem and the method of attack I owe to the suggestion of Professor J. B. Watson who has also given generously of his time in the readjustment and control of the apparatus. I am indebted,

likewise, to Dr. A. R. Middleton for assistance in equating the energies of the stimulus lights.

TECHNIQUE

Game Bantam cocks of somewhat impure breed have been used in all the tests, differential reaction to the stimuli being obtained by the Yerkes discrimination method with food, or food and punishment, as the stimulus to learning. Concerning the suitability of the fowls for experiments little more complimentary can be said than that they fit the apparatus. They show most of the peculiarities recorded by Yerkes for the dove and by Tugman for the sparrow, plus sexual reactions which sometimes make work impossible.

The Yerkes-Watson light apparatus, with some slight modifications for ease of manipulation, provided the visual stimuli. This apparatus gives two fairly pure monochromatic bands of which the wave-length, energy, and saturation are under accurate control (Yerkes and Watson, '11). These bands are reflected from similar plaster surfaces, 1 by 10 cm., exposed in the alleyways of the discrimination box. Three surfaces are used, one light being exposed constantly upon the middle surface, the other being shifted to the right or left in unison with lateral movements of the experiment box, thus effecting the interchange of the relative positions of the lights. This technique introduces a source of error which must be controlled carefully.

The primary distinction to be made in tests for color vision is between intensity and wave-length but reactions to other characters of the stimuli and experimental procedure must be guarded against. With the stimulus lights under complete control the discrimination method offers five other groups of stimuli which may lead to deceptive results. These are listed below together with the method of eliminating them in the final trials, in part as recommended by Yerkes and Watson (op. cit. p. 84 ff).

1. Cues from the movements of the experimenter.

    a. The experimenter was probably never visible to the birds, certainly not in control experiments.

    b. White lights were substituted for the monochromatic ones.

2. Cues from the noise and shifting position of the apparatus.

    a. White lights as above.
    b. Interchanging the monochromatic bands so that all movements of adjustment were reversed.
    c. Pretense of shifts during training.

3. Unequal illumination of the passages due to the reflection of the shorter wave-lengths from black surfaces.

    a. The apparatus was built to avoid this. (Yerkes and Watson l. c.)
    b. White light was substituted alternately for each of the monochromatic bands.

4. Differences in the pattern of the stimulus plates.

    a. Plates interchanged.
    b. Lights interchanged.
    c. White lights as above.

5. Light leakage in the apparatus and dark room.

    a. Tests under 2 above.
    b. The stimulus plates were illuminated directly by small Tungsten lamps, with and without interposed color filters.

These tests were all employed in the study of red-green discrimination and the more important also in all other tests except those upon the form of the spectrum. They gave always negative results: occasionally the chicks were detected in attempts to follow the movements of the experiment box, but they never learned to distinguish between a real shift in its position and the pretended shift which was made at every fourth or fifth trial. The results of the other controls limit the reactions definitely to the illumination of the stimulus plates in every important test. They will not be given in detail except where they bear upon brightness vision.

Adaptation was controlled in the following way. All tests were carried out in a completely darkened room with the experiment box enclosed in a black hood. When the chick made a correct choice a 4 ca. p. lamp 18 inches above the food dish was turned on until the chick picked up a bit of food, usually for less than one second. The chick was then returned to the starting box in darkness. Where light adaptation was desired, a 40-watt lamp with etched globe was held in the starting box for 30 seconds before each trial. That this produced a thorough brightness adaptation was shown by the following comparison

of the chick's time of reaction and the time required by the experimenter to adapt to the stimulus lights, 1/45 of the standard intensity. The experimenter's adaptation was always lighter than that produced by looking directly at the 40-watt lamp for 10 seconds.

Chick	Experimenter
22 seconds	20 seconds
14 "	16 "
4 "	6 "
18 "	10 "
6 "	4 "
14 "	20 "
2 "	3 "
6 "	2 "
3 "	3 "

When darkness adaptation was desired the chick was exposed to light for only the moment when he pecked at the food. Before the experiments he was kept in the dark for one hour, this being the time required for complete darkness adaptation (Hess '07).

THE PURKINJE PHENOMENON

Experiments were begun with two Bantam cocks, A and C. They were first tested with white light and were found to be markedly photopositive, invariably going to an illuminated plaster surface. Two white lights of different intensity were then introduced. The chicks showed a tendency to choose the brighter of the lights but their discrimination was very inaccurate and when the dimmer of the lights was well above their threshold they no longer selected the brighter: the reaction was evidently to the light as an object. An attempt was then made to increase the accuracy of their discrimination. Food was given at the brighter light and no food at the other. Training under these conditions was continued from October 23 until January 31 with ten trials per day.

During this time it was found impossible to get the chicks to distinguish accurately between white lights of relative intensities less than ten to one (absolute intensities of 18 and 1.8 ca. m.). They showed a slight preference for the brighter of two lights of intensities three to one (18.0 and 6.0 ca. m.) but never made ten successive reactions without error. I believe that the ratio of three to one represents very nearly the difference limen of the fowl under the conditions of these experiments. It is possible, however, that with a stronger

motive than hunger the apparent limen might be much lessened. The statements of other investigators imply that the chick is very strongly photo-positive and will choose the brighter of two lights of almost equal intensity. As this was found to be untrue, long training in brightness discrimination was necessary in order to prepare the animals for the following experiments upon the Purkinje phenomenon. The training was continued for 500 trials after fairly accurate brightness discrimination had been established. Many changes in the brightness of the lights, position of the experiment box, noise of rotating sectors, illumination of the experiment box, etc. were introduced to accustom the animals to changing experimental conditions.

When reactions to brightness had become automatic monochromatic lights were substituted for the white lights. Those first introduced were Red $650\mu\mu$ and Green $520\mu\mu$. The intensities of the two beams were equated with each other by the method and with the standard of Pfund[1] ('12, Yerkes and Watson, '11).

a. The fowls, light adapted, were offered a choice of the stimulus plates with these lights at standard intensity, food being given at every trial. They chose—

	Green	Red
Chick A	12	9
Chick C	19	11
Average	63%	37%

The green had perhaps the greater stimulating value under these conditions but the difference in brightness for the chick was evidently not very great.

b. The chicks were next dark adapted for one hour and the illumination of the stimulus plates was cut down to 1/90 of the standard intensity. Chick C was tested under these conditions. He chose—

Green	Red
13	1
93%	7%

At this energy the green had a much greater stimulating value.

---

[1] This standard has not been expressed in other terms. The stimulus patches illuminated at the standard energy have a luminosity which I estimate for 580 $u\mu$. at 2 candles per square meter. In the tests for the Purkinje phenomenon the lights were equated with the Pfund standard after reflection from the stimulus patches. In all other tests the energies of the beams were equated before reflection from the diffusing surface.

Control experiments indicated that the red was below the chick's threshold and that he was reacting to it as to darkness. The intensity of the lights was next increased to 1/45 of the standard and Chick A was offered a choice of them. He chose—

Green	Red
9	1
90%	10%

Furthermore, when offered a choice between the red and darkness he chose the red in 8 of 10 trials showing that the red was above his threshold. At low intensities the green has a much greater stimulating value than the red for the dark adapted chick.

c. With the energies of the beams at 1/90 standard, Chick A. light adapted, was introduced into the discrimination box. He chose—

Green	Red
10	0
100%	0%

As a control he was offered a choice between the red and darkness. He chose the red in 10 consecutive trials. The red used was below the threshold of the experimenter when light adapted and a record of the time of adaptation of the experimenter and the time of reaction of the chick shows that the chick also required a slight darkness adaptation before the red became visible to him. His accurate choice of the green at this energy was undoubtedly due to the fact that the choice was made before the red came above threshold.

d. The energies of the beams were increased to 1/9 of the standard. Chick A, dark adapted for one hour, chose—

Green	Red
5	5
50%	50%

The energies were immediately reduced to 1/18 and he chose—

Green	Red
3	3
50%	50%

Under the same conditions Chick C chose—

Green	Red
4	6
40%	60%

When the energy is as great as 1/18 of the Pfund standard

the greater stimulating value of the green is lost, irrespective of the degree of adaptation.

The results are thus far valuable only as illustrating sources of error in tests for the Purkinje phenomenon. In tests a and d no evidence for a greater stimulating effect of either light was obtained; in b and c the results are due, in all probability, to the reduction of the intensity of the red to threshold value and not to the process of adaptation. It seems probable that two factors may produce spurious evidence of the Purkinje phenomenon in experiments with animals. 1: While two lights of unequal energy may not produce a reaction upon the basis of brightness at high intensity, a reduction of their intensity may bring the weaker below threshold while the other is still visible. From data obtained during training with white lights it is clear that when two lights differing greatly in stimulating value are exposed together the reaction to the less intense may be lost while it still persists when this stimulus is exposed alone or with another of equal stimulating value. In work of this sort it seems necessary, then, to distinguish two types of threshold; a lower threshold determined by the absolute sensitivity of the eye, and a higher one, which might be termed the threshold of attention, due to the interference of the stimuli. 2: With lights of unequal intensity differing in brightness at high intensity by less than the limen of the animal the action of the Weber-Fechner law might produce a perceptible difference following a reduction of the intensity of the lights.

These factors, in all probability, would have produced the results obtained in all the recorded tests for the Purkinje phenomenon if a band of white light of properly graded intensity had been used instead of the spectrum. I am inclined to think that the methods of Hess, Katz and Révész, Yerkes, and my own recorded above are too crude to give a proof of the Purkinje effect and that the results obtained are due rather to one or other of these secondary phenomena. The records of the Purkinje effect in man are so conflicting that an analogy between man and other animals seems hardly profitable. The resemblance in the distribution of cones of the day bird's retina to the human fovea, where probably the phenomenon does not appear (Nagel '11), is sufficient, however, to demand extreme caution in interpreting results in this field.

With the uncertainty of the discrimination method it seems necessary either to introduce some technique which will eliminate fluctuations of attention or to test for the relative stimulating effects of monochromatic lights when the energy remains constant and only the state of adaptation changes. In testing for the Purkinje phenomenon I did not realize the necessity for avoiding threshold stimuli and so carried out only a few tests with constant light energies.

Contrary to the statements of Hess the red never seemed to have a greater stimulating value than the green of equal energy either for the light or for the dark adapted chick. (The energy of the red which he used was probably much greater than that of the green.) By a series of tests an energy relation was determined at which the red was just brighter than the green for the light adapted chick. This was at red 1/6, green 1/45 of the standard. When the energy of the red was decreased to 1/18 there was no choice, when it was increased to 2/9 it was chosen accurately and without hesitation. With red 650 $\mu\mu$, intensity 1/6, and green 520 $\mu\mu$, intensity 1/45, Chick C, light adapted, chose—

Red	Green
11	2
84%	16%

He was dark adapted for one hour, then chose—

Red	Green
4	6
40%	60%

Light adapted immediately he chose—

Red	' Green
3	1

Chick A under the same condition became erratic, developed a position habit, and gave no results that can be interpreted. The few records of Chick C indicate that there is a shift in the point of greatest stimulating value of the spectrum from the longer to the shorter wave-lengths with increasing darkness adaptation. The number of trials is too small for certainty.

As there was the danger of association of one or other color with food work with red and green was dropped at this point and the apparatus was arranged to give yellow 590 $\mu\mu$. and blue-green 500 $\mu\mu$. at equal energies. Both lights were cut

down to 1/90 of the standard; at this energy both are above the chick's light adapted threshold. Chick A, fully light adapted was placed in the experiment box. He chose—

Green	Yellow
7	7

Chick C was dark adapted for one hour, then offered the lights. He chose—

Green	Yellow
7	5

Light adapted immediately afterward, he chose—

Green	Yellow
4	5

At this intensity neither of the colors has a markedly greater stimulating value than the other. At the same energy the red drops below the light adapted threshold.

A point was determined at which the yellow was just brighter than the green for the light adapted chick. This was yellow 4/90, green 1/90. Light adapted, Chick A chose—

Green	Yellow
3	21

After dark adaptation he chose–

Green	Yellow
4	2

Chick C was tested in the same way but for some unexplained reason showed a complete breaking down of his reactions; even failing to choose between light and darkness. This lasted for several days and Chick A also became erratic so that the tests could not be continued without retraining for brightness. Such experiments, with food at every trial, make heavy demands upon the retention of earlier habits and it is surprising that the reaction persisted as well as it did. The apparent shift in brightness for the yellow and green, like the last test recorded for the red and green, indicates a Purkinje effect of adaptation.

The determination of energies of the monochromatic lights having equal brightness values for the chick (the brightness equation point) is of interest when compared with the respective thresholds for the same wave-lengths and is of primary importance for tests for color discrimination. The values that I

have determined are very rough but they indicate that the
relative stimulating value for the light adapted eye of mono-
chromatic bands of high intensity is proportional to the threshold
values of the same wave-lengths with light adaptation, as de-
termined by Watson ('15).

SENSITIVITY TO WAVE-LENGTH

As the primary object of these experiments was to determine
whether or not the chick is sensitive to differences of wave-
length and as six months had been consumed already in the
preliminary tests it was thought best to abandon the latter and
test for color discrimination. Red 650 $\mu\mu$. and green 520 $\mu\mu$.
at equal energies were used as stimuli. Preference tests were
of course impossible with chicks A and C.[2] Learning was
rapid and after 200 trials the chicks were judged ready for
control tests. The control tests described on page 5 limited
the reaction to the illumination of the stimulus plates. Tests
to distinguish between reaction to energy and to wave-length
were made by altering the brightness relations of the saturated
lights, and by diluting them. As determined in the Purkinje
tests the brightness equation point for 650 $\mu\mu$. and 520 $\mu\mu$ is some-
where near the energy relations of 8 to 1. The energy relation
of the stimulus lights was varied in both directions from this
ratio as described in table 1. Tests with the colors diluted
were made as indicated in table 2. The results of these tests,
summarized in table 3, show that a reversal of the brightness
values of the red and green did not seriously disturb the accuracy
of the discrimination. The errors made appeared when the
energy of the positive light was much reduced, irrespective of
whether this was red or green. The dilution tests give fairly
clear evidence of discrimination except in the case of Chick C
with dilute red.

---

[2] The behavior of some other birds in tests for color preference seems worth
recording. Training for red-green was begun with five hens but not completed.
Four of these showed no color preference for the lights at the brightness equation
point for light adaptation. The fifth under the same conditions chose the green
in preference to the red in 20 successive trials. This behavior suggests either an
acquired color preference or color-blindness. Unfortunately, this bird was killed
by rats before her vision could be tested.

TABLE 1

Tests for red-green discrimination with varied brightness relations of the stimulus lights. The energies at which the red was known to be brighter are printed in italics. In the remaining tests the brightness value of the green was equal to or greater than that of the red. Energies are expressed in decimals of the Pfund standard.

Chick A (*Positive to red*)				Chick C (*Positive to green*)			
Energies		No. of trials	No. of errors	Energies		No. of trials	No. of errors
Red	Green			Red	Green		
1.0	1.0	5	1	1.0	1.0	5	0
1.0	*.022*	5	0 .	*1.0*	*.022*	10	2
1.0	*.044*	5	0	*1.0*	*.044*	5	0
1.0	*.088*	5	0	*1.0*	*.088*	10	3
1.0	.177	5	0	1.0	.177	5	0
1.0	.355	5	0	1.0	.355	5	0
1.0	.500	5	0	1.0	.500	5	0
1.0	1.0	5	0	1.0	1.0	5	0
.022	1.0	9	3	.044	1.0	10	0
1.0	*.022*	6	0	*1.0*	*.022*	10	3
.022	1.0	10	3	.022	1.0	10	2
.088	1.0	10	0				

TABLE 2

TESTS FOR RED-GREEN DISCRIMINATION WITH VARIED SATURATION OF THE STIMULUS LIGHTS

Condition of stimuli	Chick A		Chick C	
	No. of trials	No. of errors	No. of trials	No. of errors
Both lights at standard energy............	5	0	5	0
Green much diluted......................	10	1	6	0
Bright white light substituted for green.....	5	3	5	1
Both lights at standard energy............	10	0	5	1
Red much diluted.......................	10	0	10	4
Red diluted until its quality was lost........	7	4	..	..
Both lights at standard energy............	5	0	5	0
White light of low intensity for red.........	8	0	12	4
Same white for green....................	10	1	6	0
White light of high intensity for red.......	5	0	6	3
Same white for green....................	10	3	5	0
Both lights at standard energy............	5	0	6	0
Two white lights of equal brightness........	10	5	10	2*

* A careful examination was made for secondary criteria which might account for this choice which tends to invalidate all the results obtained with Chick C. Nothing could be discovered by the dark adapted human eye. The test was repeated on the following day, when ten trials with five errors were obtained. The above record was probably a chance variation.

TABLE 3

SUMMARY OF FIRST TESTS FOR RED-GREEN DISCRIMINATION

Condition of stimuli	Chick A (*Positive to red*)		Chick C (*Positive to green*)	
	No. of trials	No. of errors	No. of trials	No. of errors
Red 1: Green 1........................	35	1	31	1
Red below 0.1: Green 1............... (green brighter)	29	6	20	3
Red 1: Green below 0.1................ (red brighter)	16	0	20	5
Green dilute: Red 1...................	10	1	6	0
Red dilute: Green 1...................	10	0	10	4
Red greatly diluted: Green 1...........	7	4	..	.
White light for red......................	13	0	18	7
White light for green...................	25	7	16	1
Controls				
White light of equal energy..............	20	13	20	7
Red 1: Darkness......................	5	To D. 0	15	To D. 5
Green 1: Darkness....................	10	To D. 4	10	To D. 1

The tests in which white light was substituted for each of the lights in turn are interesting as indicating the relative importance of the negative and positive stimuli in determining the reaction. Both chicks confused the white with the positive stimulus (table 3) and distinguished it readily from the negative. Punishment had been used in this case with the negative light which here appears to be most clearly recognized. In later experiments without punishment conditions appear to be reversed, the negative light being most frequently confused with the white. This is in accord with the view that punishment is the more efficient factor in learning. The tests also evidence either color discrimination or accurate perception of brightness. The use of the lights singly gives further evidence of the same sort, since darkness was chosen fewer times with the positive color than with the negative (table 3).

The work had to be dropped at this point. The tests recorded make it highly probable that the birds were reacting upon the basis of wave-length, but as the energies of both red and green were never altered simultaneously, the possibility that an extremely accurate perception of absolute brightness furnished the basis for reaction was not completely eliminated. It seemed

advisable therefore to repeat the experiment using still more thorough controls.

After a long delay, while smoked wedges were substituted for the Aubert diaphragms used in equating light energies, the work was resumed. Three cocks, A (now three years old), and two younger ones, D and E, were trained for discrimination with red 650 $\mu\mu$. and green 520 $\mu\mu$. uncalibrated, just as given by the carbon arc spectrum. Chick D was trained to avoid the red (middle stimulus plate) and choose the green; Chicks A and E to choose the red. After about 400 trials the chicks began to react perfectly. They were given an additional hundred trials to make the reaction more nearly automatic—then, as the lights could not be equated immediately, a series of rough control tests for brightness and secondary criteria was begun, partly to accustom the chicks to a changing problem and partly as a test of their sensitivity to wave-length. Three types of tests were employed to distinguish between brightness and wave-length; 1, first one, then the other light was reduced to threshold intensity while the other remained at the full energy of the spectrum; 2, a white light of constant intensity was substituted for each of the colored lights in turn; 3, each light was exposed alone with one passage completely dark. Table 4 shows the records of the chicks in the first of these tests. It will be noted in the results of this experiment that reduction of the intensity of the negative color produced no disturbance of the reaction while reaction of the positive color led to many errors. Had the reaction been due to the relative brightness of the stimulus patches Chick D should have been disturbed when the red was reduced, as were A and E, since this must then have represented the condition in which the difference in brightness approached threshold. Instead of this, however, Chick D reacted inaccurately only under conditions where A and E remained undisturbed. This seems to limit the effective stimulus either to the wave-length or to the absolute intensity of the positive stimulus patch.

TABLE 4

REACTIONS TO RED AND GREEN LIGHTS OF ESTIMATED THRESHOLD VALUE

	Intensity of lights		Chose	
	Red	Green	R.	G.
Chick A. (*Positive to red*)	Just above threshold Well above threshold Full intensity	Full intensity Full intensity Just above threshold	47 20 10	18 0 0
Chick E. (*Positive to red*)	Just above threshold Well above threshold Full intensity	Full intensity Full intensity Just above threshold	35 14 15	10 1 0
Chick D. (*Positive to green*)	Just above threshold Full intensity	Full intensity Just above threshold	0 23	9 12

The second group of tests, made with Chicks D and E gives · additional evidence against a reaction to the relative brightness of the stimulus patches. A very intense white light (the image of a Nernst glower directed upon the stimulus patch by a 2-inch lens of 6-inch focus) was first substituted for the red light, the green light being left at full intensity somewhat diluted by light reflected from the white stimulus patch. Under these conditions Chick E (*positive to red*) chose—

White	Green
11	1

Chick D (*positive to green*) chose—

White	Green
3	13

The white was then substituted for the green and the red was restored at full energy. The records of the birds were—

	White	Red
Chick E............	1	9
Chick D............	4	1

The intensity of the white light was many times that of the monochromatic so that the brightness relations of the stimulus patches were certainly reversed in the two tests. The probability of reaction to absolute brightness is also reduced by the dilution of the monochromatic lights by light reflected from the white patch. For me this reflected light had greater brightness than either of the monochromatic lights.

To avoid a reaction to secondary criteria given by the shifting

of the lights and experiment box the monochromatic lights were arranged so that both could be projected upon the same stimulus patch. They were exposed in irregular order with the other patch illuminated with the intense white light. Under these conditions Chick E chose—

Red	6	White	6	when r and w were exposed together.
Green	1	White	5	when g and w were exposed together.

Chick D chose—

Red	2	White	4	
Green	5	White	0	under the same conditions.

The white light was immediately reduced to threshold intensity and the tests repeated.
Chick E chose—

Red	8	White	1
Green	3	White	8

Chick D chose—

Red	2	White	5
Green	5	White	0

The change in the intensity of the white light with the resultant change in the dilution of the monochromatic points to a sensitivity to wave-length. The complete change in the technique eliminates a reaction to secondary criteria.

The conclusions from the third set of tests are based upon the time of reaction to a single monochromatic light: the time required for the chick to go from the door of the starting box to the food dish, a distance of 3 feet. The results of the tests with the three chicks are given in table 5. During these tests the intensity of the lights was varied from 1/18 to the full energy of the spectrum. The birds, although instinctively photopositive, showed a marked delay in advancing to the negative light, irrespective of its intensity. Unless the brightness differences of the monochromatic lights for the chicks are extremely great this experiment is sufficient to eliminate reaction to the absolute intensity of the light.

These tests are given in some detail as illustrating a fairly satisfactory technique when the energy and brightness values of the stimulus lights are unknown. Such methods have the disadvantage of introducing many disturbing elements; in such tests the animals ultimately become confused and give conflicting results.

TABLE 5

Time of reaction to one light alone. The time is that required by the chicks to go from the door of the starting box to the food dish, a distance of three feet.

Red light alone at varied intensity	No. of trials	Average time	No. of errors (Darkness chosen)
Chick A. (*Positive to red*)..............	8	1.45 sec.	0
Chick E. (*Positive to red*).............	12	2.12 sec.	0
Chick D. (*Positive to green*)...........	5	30.60 sec.	4
Green light alone at varied intensity			
Chick A........................... (Refused to advance in three trials)	8	7.25 sec.	3
Chick E...........................	8	16.37 sec.	2
Chick D...........................	14	5.60 sec.	0

At the end of these tests the lights were equated in energy, the chicks were retrained for a few days to increase the accuracy of their reactions and then tested with the lights under accurate control. The energies of the lights were varied widely in both directions from the brightness equation point and were likewise varied in absolute intensity at different brightness ratios. The results of the tests with the three chicks are given in table 6. At the end of the experiments the chicks were offered two white

TABLE 6

Tests for red-green discrimination with varied brightness relations of the stimulating lights. Arranged as table 1.

Chick A. (*Positive to red*)		No. of trials	No. of errors	Chick E. (*Positive to red*)		No. of trials	No. of errors	Chick D. (*Positive to green*)		No. of trials	No. of errors
R	G			R	G			R	G		
2.0	1.0	15	1	2.0	1.0	20	0	2.0	1.0	20	1
1.0	1.0	68	8	1.0	1.0	20	4	1.0	1.0	20	1
1.0	.5	10	0	.5	1.0	5	0	.5	1.0	10	1
1.0	.25	10	0	.5	.11	10	0	*2.0*	*.11*	12	1
1.0	*.10*	10	1	.25	.5	10	1	Injured by Chick E.			
1.0	*.05*	10	0	.25	.11	20	2				
2.0	*.05*	10	1	.11	1.0	15	0				
2.0	*.08*	5	0	.11	.11	9	1				
2.0	.15	10	0	*2.0*	*.11*	15	0				
.44	1.0	15	0	*2.0*	*.08*	10	0				
.22	1.0	20	2								
.22	.22	10	1								

lights of equal intensity exposed under the same conditions as the monochromatic. Chick A chose the stimulus patch to which he usually reacted positively 7 times, the other 8 times. Chick E chose the central patch 6 times, the other 4. Chick D could not be tested. A was further offered a choice of two white lights of relative intensities 1 to 90. He chose the brighter 7 times, the other 3, an accuracy less than that with any intensity of monochromatic lights. These tests, with the other controls mentioned in the discussion of technique limit the efficient stimulus to the illumination of the stimulus plates. Summarizing table 6 we find that with the red certainly brighter than the green the chicks made 3 errors in 72 trials or 4.1 per cent. error. In 325 trials with the green brighter or equal to the red in brightness they made 23 errors or 7.7 per cent. Further, in trials where the intensity of both lights was greatly altered there was no reduction in the accuracy of choice, so that the possibility of reaction to the absolute brightness of either stimulus is eliminated. As between brightness and wavelength, then, these experiments speak conclusively for the latter. The possibility of other characters of the stimulus lights themselves furnishing the basis of discrimination will be considered after the work with yellow and blue light has been recorded (page 20).

The same three fowls were trained with yellow at 588 $\mu\mu$. and blue-green at 500 $\mu\mu$. with energies equal. Chicks A and E were trained to choose yellow, D to choose green in order to take advantage of the previous training. Strangely enough the chicks were confused by the green at 500 $\mu\mu$, not greatly different from 520 $\mu\mu$. to my eyes, and failed to discriminate in the first trials. They had previously reacted to 520 $\mu\mu$ when white light, darkness, or yellow were substituted for the red. However, after 120 trials they gave less than ten per cent. error and were considered ready for control tests. Tests for the Purkinje effect had previously shown that the following brightness values held for these wave-lengths for the moderately light adapted eye of the fowl.

Yellow	Green	
4	1	yellow brighter.
2	1	yellow perhaps brighter.
1	1	neither brighter.
1	45	green *certainly* brighter.

Tests at these values were carried out with the results shown in table 7. The ratio of 45 to 1 gives uncertain results owing

TABLE 7

Tests for yellow-green vision with varied brightness relations of the stimulus lights. Figures in italics show where the yellow is brighter for the chick.

Energies		Chick A.		Chick D.	
Yellow	Green	Trials	Errors	Trials	Errors
1.0	1.0	14	2	20	4
.01	1.0	20	2	20	2
.11	2.2	14	1		
.05	1.0			10	0
2.0	*1.0*	29	6	12	1
1.0	1.0			10	1

to difficulty with the apparatus: a reduction of the yellow below .1 of the standard brings it near the chick's threshold[3] and a greater energy of the green than 2.2 could not be obtained with the present arrangement. The tests are therefore not as extensive as I desired. However, chicks long trained to brightness discrimination failed to distinguish this red and green even at the energies of 1 to 1 and the tests with variations in both directions from this ratio seem adequate to eliminate a reaction to brightness. As in the case of red and green the effective stimulus is restricted to wave-length.

The evidence for color vision thus far presented seems to prove that the chick can distinguish between monochromatic lights of any intensity between threshold and the Pfund standard, irrespective of the brightness or saturation. The effective stimulus is the wave-length. The question remains, is the discrimination based upon retinal sensitivity to differences of wave-length or upon some entoptic phenomenon.

The difference in visual acuity in light of different wave-length is well known, and, though it seems to be largely a matter of relative brightness it may furnish a basis for discrimination. Whether a like variation in acuity occurs in the color blind I cannot discover from the literature. Allied to this phenomenon is that of diffraction or dispersion within the eye. At low intensities the red and yellow stimulus patches have for me sharp outlines while the green of equal brightness lacks sharpness

[3] The absolute intensities of the lights in this experiment are not comparable with those of the Purkinje tests. The introduction of the smoked wedges cut down the energy of the spectrum so that the equation of the lights with the Pfund standard had to be made before they were reflected from the plaster surfaces instead of afterward as in the first experiment.

and seems to be surrounded by a luminous halo. It seemed possible that the birds were reacting upon the basis of the sharpness of the visual objects rather than upon their color, either as a result of diffraction or of serious chromatic aberration.

Tests were made at different times during the experiments with a view to controling these factors and gave the following results.

1. Wide variations in the size and shape of the stimulus plates were without effect.

2. High intensities and dilutions, reducing the apparent diffraction of the shorter wave-lengths and giving sharp outlines for me to both stimulus plates did not effect the reaction of the birds.

3. Intense white light with imperfect color filters, completely altering the secondary phenomena for me, were discriminated as promptly as the spectral lights.

4. The evidence given in the following section for abrupt changes in the reaction value of the spectrum is difficult to explain by these phenomena.

The visual acuity of the fowl determined by Johnson ('14) seems to eliminate the question of any great chromatic aberration in the chick, and the foregoing tests make a reaction upon any other basis than retinal sensitivity highly improbable.

THE CHARACTER OF THE SPECTRUM

With the establishment of sensitivity to differences of wavelength the problem of the difference limen for wave-length in different parts of the spectrum at once suggests itself. A thorough solution of this problem would require months of training with careful controls of brightness at every stage. The Yerkes-Watson apparatus is not well adapted for such experiments as it cannot be arranged readily to give lights from adjacent parts of the spectrum. The following tests, serve to give a clue to the form of the spectrum of the bird, particularly with reference to the existence of regions of widely different reaction value separated by relatively short intervals of the spectrum.

Chick A, positive to 650 $\mu\mu$. and negative to 520 $\mu\mu$. was offered red 650 and yellow 580 $\mu\mu$. He chose the red six times in seven trials and showed little confusion. The red was evi-

dently different in reaction value from the yellow. The element of intensity was not eliminated here but since the chicks had been reacting so well to wave-length and not at all to brightness differences I think it unlikely that the discrimination was made here or in the following tests upon the basis of brightness.

Chick E, trained like Chick A, was given 7 trials with 650 $\mu\mu$. and 520 $\mu\mu$, making no error. The red was then shifted toward the shorter wave-lengths with the following results.

Wave-length, $\mu\mu$.		Chose		Character of longer waves for the human eye
"Red"	Green	"Red"	Green	
650	520	7	0	Red.
610	520	5	0	Red-orange.
600	520	6	0	Orange-yellow.
580	520	3	3	Yellow. Position habit.
590	520	3	0	Yellow-orange. Secondary evidence of discrimination.

This indicates that there is a change in the reaction value of the spectrum between 580 and 590 $\mu\mu$. This is the region in which the yellow assumes an orange quality for man.

Chick D, positive to green, was first given 5 trials with the red and green as in training, making no error. The test was continued as follows:

Wave-length, $\mu\mu$		Chose		
Red	"Green"	Red	"Green"	
650	520	0	5	
650	600	0	5	Reactions prompt.
650	630			Position habit developed at once.

This indicates a change in the reaction value of the spectrum between 600 and 630 $\mu\mu$. This is the region of the transition from red to orange for man.

Chick A was given the following tests.

Wave-length, $\mu\mu$.		Chose	
"Red"	Green	"Red"	Green
650	520	5	0
610-590	520	5	0
590-565	520	5	1

(The reaction here with green and yellow was given upon the basis of the green as negative color, the chick going to darkness in preference to green.)

550-530	520	2	2	Refused to advance.

This suggests a change in the character of the light between 530 and 565 $\mu\mu$, corresponding roughly to the change from yellow to green for man.

After training with yellow and blue-green Chick D was given the following tests.

Wave-length, $\mu\mu$.		Chose	
"Yellow"	Green	"Yellow"	Green
580	500	1	6
535	500	Right position habit.	
565	500	0	5
565	500	0	3
(1/18 standard)			

There is a change between 535 and 565 $\mu\mu$. This agrees with the results obtained from A. The change in the energy of the yellow was made as a slight control of the brightness element.

Chick A was offered green 530, violet 460 $\overline{\mu\mu}$. The use of the yellow-green was due to the difficulty of obtaining lights nearer together in the spectrum. In an earlier experiment after training with red and green Chick A had been offered a choice between white and red, white and blue, and red and blue (impure color filters). He chose accurately red and blue in preference to white, red in preference to blue and all in preference to green 500 $\mu\mu$. I expected him to choose the violet in preference to the green and refused him food at the latter. Instead, however, he chose the green five times in succession, then, getting no food, developed a position habit. He was then fed at the green and immediately chose it five times in quick succession.

Chick D was offered a choice between 500 and 460 $\mu\mu$. He showed no choice and developed a position habit immediately.

It is rather difficult to interpret the results of these two tests with the assumption of identical color divisions for the chick and man. In the beginning of training with yellow and blue the shift from 520 to 500 $\overline{\mu\mu}$. seemed to confuse the chicks (page 19). If we suppose that there is a marked change in the reaction value of the spectrum between these wave-lengths, there seems to be a general agreement in the results; for Chick A 530 $\mu\mu$ and 580 $\mu\mu$. resembled each other more than they did 500 $\mu\mu$, and 460 $\mu\mu$ perhaps resembled 500 $\mu\mu$; for Chick D 500 $\mu\mu$ and 460 $\mu\mu$ were more nearly alike than the original 580 $\mu\mu$ and 500 $\mu\mu$. The accord of the animal's behavior with this interpretation justifies the assumption, pending more accu-

rate investigation, that there is a marked change in the reac-
tion value of the spectrum between 500 and 530 $\mu\mu$ with no
marked change between 500 and 460 $\mu\mu$, i. e., the region corre-
sponding to the blue and violet for man begins at a longer wave-
length for the chick.

To summarize this part of the work, the accuracy of the
discrimination of the fowls is affected by changes in the position
of the stimulus lights through the following intervals and it
is suggested that the wave-lengths lying between each pair of
these intervals, which are probably shorter than the tests indicate
have a fairly uniform reaction value.

$$\begin{align}
630 &- 600 \ \mu\mu. \\
590 &- 580 \ " \\
\{ 565 &- 550 \ " \\
\{ 565 &- 535 \ " \\
\{ 520 &- 500 \ " \\
\{ 540 &- 470 \ "
\end{align}$$

THE RELATIVE REACTION VALUE OF INTENSITY
AND WAVE-LENGTH

In field studies of animals where the conditions of illumination
are not under control it is difficult to determine whether the
animal, even if known to have color vision, is reacting to color
or to brightness. The distinction is of importance in many
biological problems where the necessity for natural conditions
makes an actual test of the efficient stimulus impossible. The
only clue to it in such cases is given by the relative ease with
which habits of reaction to the two attributes of the light stim-
ulus are formed. The data upon the rate of learning in my
experiments gives some indication of the relative efficiency of
wave-length and intensity in light stimuli.

a. Birds already trained in brightness discrimination, when
trained with red and green of different brightness values for
them (red 650, green 520 $\mu\mu$. at equal energies) changed quickly
to reaction upon the basis of wave-length, *without any alteration
in the brightness values of the lights which might have destroyed
the habit of reacting to brightness.* After training with colors
the association with wave-length was dominant even when the
brightness values of the stimuli were so greatly different as to
call out the instinctive brightness preference in untrained birds.

b. The conditions under which training for brightness and
color discrimination have been carried out are not strictly

comparable, but some unrecorded experiments by Dr. Middleton and myself upon the fowl's difference limen for brightness indicate that where threshold intensities are not involved habits of reaction to brightness are established with much greater difficulty than are those of reaction to wave-length.

From the evidence even of a. alone I believe that the field experimenter may feel confident that, if the birds show a differential reaction to colored objects not differing enormously in brightness for him, their reactions are made upon the basis of wave-length.

DISCUSSION

One fact the experiments seem to have brought out clearly: The fowl is sensitive to differences of wave-length irrespective of intensity and its sensitivity is greater than, or at least different from, that of any form of partial color blindness in man. Less certainly it appears that for the fowl the spectrum is divided into areas of widely different reaction value, of which there are not less than five, probably more. It is not probable that all these occupy areas of the spectrum corresponding to the more conspicuous divisions for man. There is also some slight evidence for a Purkinje effect but this needs verification.

The proof of color vision in the fowl should make possible the more ready correlation of the so-called physiological methods of studying sensitivity with other behavior methods. The probability that the specific action-currents of the retina following stimulation with different wave-lengths are an index to a more general color sensitivity is increased. The lack of such specific action-currents in night birds furnishes a final test of the interpretation of retinal action currents. Experiments upon the color vision of owls are in progress. The value of such methods as those of Rouse and Bàbàk is also enhanced by a verification of some of their results by other methods. The reflex responses offer an index of sensitivity more accurate and convenient than the discrimination method, but they must be correlated with other activities of the animal before they can furnish a basis for attack upon more general problems.

The probability of a high degree of sensitivity to wave-length in other day birds suggests anew the problems of organic and sexual selection in birds, problems which have largely fallen into disrepute of late. The prominent rôle played by sensitivity

to wave-length as compared to brightness offers the possibility of field and experimental studies of these much discussed questions where the experimenter may feel reasonably confident that his results are due to color perception.

The conclusion of Katz and Révész that the Purkinje phenomenon cannot be explained by the process of adaptation in the rods does not seem to be justified since neither the Purkinje phenomenon nor the absence of visual purple has been established for birds. It seems too early yet for a satisfactory correlation of structure and function. Further studies of adaptation upon birds with different retinal composition will doubtless help to clear up the question of the function of the retinal elements.

LITERATURE CITED

DeVoss, J. C. and Ganson, Rose. Color Blindness of Cats. *Journal Animal*
1915. *Behavior*, **5**, 115-139.
Hess, C. Ueber Dunkeladaptation und Sehpurpur bei Hühnere und Tauben.
1907. *Arch. f., Augenheilk.*, **57**, 298-316.
1907. Untersuchungen über den Lichtsinn und Farbensinn bei Tagvögeln.
Ibid., **57**, 317-327.
1908. Untersuchungen über das Sehen und über die Pupillenreaktion von
Tag und von Nachtvögeln. *Ibid.*, **59**, 143-167.
1912. Vergleichende Physiologie des Gesichtssinnes. *Winterstein's Handbuch
der vergleichenden Physiologie.* Bd., **4**, Jena.
Johnson, H. M. Visual Pattern Discrimination in Vertebrates. *Journal Animal*
1914. *Behavior*, **4**, 340-361.
Katz, D. and Révész, G. Ein Beitrag zur Kenntnis des Lichtsinns der Hühner.
1907. *Nachr. d. K. Ges. d. Wiss. zu Göttingen, Math.-physik.* K1, 406-409.
1909. Experimentelle-psychologische Untersuchungen mit Hühnern. *Zeitschr.
f. Psychologie.* Abt. 1., **50**, 93-116.
Kohlrausch, A. and Brossa, A. Die Photoelektrische Reaktion der Tag- und
1914. Nachtvogelnetzhaut auf Licht verschiedener Wellenlänge. *Arch. f.
Physiol.*, **5**, 421-431.
Nagel, W. Helmholtz. *Handbuch der physiologische Optik.* Bd. **2**, 207. Leipzig.
1911.
Pfund, A. H. Application of the Selenium Cell to Photometry. *Physical Review,*
1912. **34**, 370-380.
Porter, J. P. A preliminary Study of the Psychology of the English Sparrow.
1904. *Amer. Jour. Psych.* **15**, 248-271.
1906. Further Study of the English Sparrow and other Birds. *Ibid.* **17**
248-271.
Rouse, J. E. Respiration and Emotion in Pigeons. *Jour. Comp. Neurol. Psychol.*
1905. 1 *5ᵛ* 494-513.
Watson, J. B. *Behavior.* Holt, New York.
1914.
1915. The Spectral Sensitivity of Birds. Papers from the Tortugas Laboratory. *Carnegie Inst. Pub.* 211.
Yerkes, R. M., assisted by Eisenberg, A. M. Preliminaries to a Study of Color-
1915. vision in the Ring-dove, *Tutor risorius. Jour. Animal Behav.* **5**,
25-44.
Yerkes, R. M. and Watson, J. B. Methods of Studying Vision in Animals.
1911. *Behav. Monographs.* Vol. 1, No. 2, iv+90.

THE BIOLOGY OF THE MUD-DAUBING WASPS AS REVEALED BY THE CONTENTS OF THEIR NESTS

PHIL RAU AND NELLIE RAU
Saint Louis, Mo.

With five plates

This paper is primarily a study of the contents of the nests of three species of mud-daubing wasps. Before entering upon a discussion of how the nests are provisioned and how the young fare in their struggle against adversities and enemies, it will be well to become familiar with the nests themselves, their structure, their sites, decorations, etc.

Fossorial Hymenoptera are roughly classified, according to their habits, in four groups: 1. Those which build no special receptacles for their young but are either parasitic or subparasitic, or take advantage of the abodes of other insects, holes, etc.; 2. Builders of cells in the form of pottery constructed of clay mixed with water or saliva and dried; 3. Excavators of burrows in the ground; 4. Makers of tunnels in wood or the stems of plants.[1]

The three species of Fossorial wasps herein dealt with belong to the second group of this classification, those wasps which construct cells of clay or mud as receptacles for their young and its provisions. The mothers themselves do not use these structures for their own shelter, but go elsewhere for the night. All three of these species are spider ravagers.

First we have the pipe-organ type of mud nests (see figs. 1, 2, 5) built by *Trypoxylon albitarsis* Fab., the shiny black wasp with beautiful white toe-tips. Then we have the familiar mud nests which at first sight look like a clod of earth; these are made by two species belonging to the subfamily Sceliphroninae, *Sceliphron (Pelopoeus) caementarium* Drury, a pretty black wasp trimmed up in yellow (this wasp is commonly known by the boys in my neighborhood as "yellow-legs"), and the beautiful steel-blue wasp, *Chalybion caeruleum* Linné. The nests of these

---

[1] Sharp, D. Insects, Pt. II. *Cambridge Nat. Hist.*, p. 90.

two species are so similar as to be indistinguishable (figs. 3, 4, 6, 18).

Some authors have placed these two wasps in the same genus, probably chiefly because of their similar habits of nesting, but I have found that there is some difference in the spinning of the pupal case by the larvae of the two species, and Mr. Rohwer writes to me that he believes that the two species "should be retained in different genera for besides a difference in coloring there is a shortening of the petiole in *C. caeruleum* and certain other differences which indicate that it is of a different group." Thus we have convergence of habit of nest-building in three distinct genera.

NIDIFICATION OF *S. CAEMENTARIUM* AND *C. CAERULEUM*

During the sunny days of summer one may see many of these mud-daubers coming to the edges of streams and puddles, critically selecting mud of exactly the right consistency and literally standing on their heads biting out chunks of it and carrying it to some distant shelter. There they fashion it into the familiar cells illustrated in figs. 3, 4, 6, 18. The size and shape of these pellets which they carry may be seen in fig. 13. These were dropped by insects taken at such sources, and are exact size. The smaller ones however are probably incomplete balls dropped by wasps which were interrupted during the gathering. It is generally thought, and all the treatises (excepting the Peckhams'[2]) state that this mud is mixed with the saliva in the mouth of the insect. I do not wish to discredit this statement, for I have no proof to the contrary, but since it is generally made on supposition, I think it would be permissible for us here to suppose also that the amount of saliva used by an insect in a day would be many times the size of the little body producing it, especially when the wasp sometimes constructs a whole cell in an hour and a half, or on other occasions when she is building incessantly, whole days at a time, or reinforcing the nest, as shown by the thick walls in figs. 7, 9 and 10.

In these two species and in *T. albitarsis* as well, the young from eggs deposited in the early fall feed and go through their metamorphosis during the winter and emerge as adults the next

[2] Instincts and Habits of Solitary Wasps, p. 178: "The wasp adds nothing to the mud, depending upon its drying for the necessary firmness, and if by some accident the rain strikes it the whole becomes soft and falls to pieces."

PLATE I
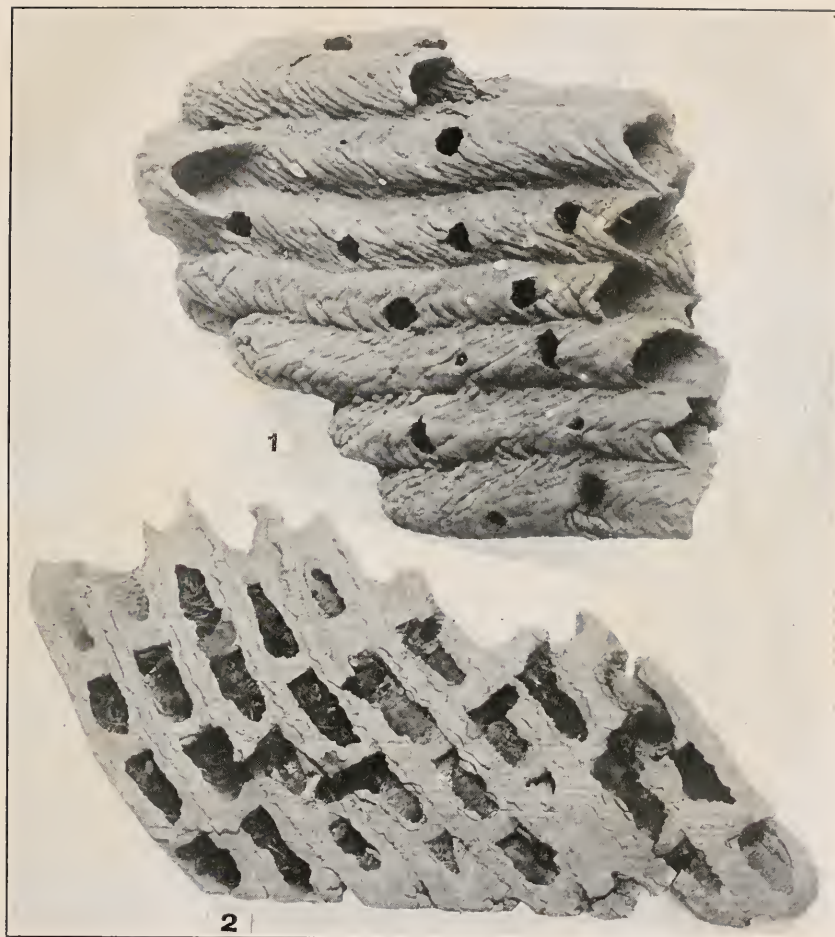
FIG. 1. Pipe-organ nest of *T. albitarsis*. Reduced.
FIG. 2. Same, back view. Reduced.

May or June.   Here at St. Louis we have both summer and winter broods, and I have a faint suspicion that those nests which harbor the winter brood of *S. caementarium* and *C. caeruleum* are built more massive than the summer cells.   This question is worth investigation to determine whether the wasps are endowed with the instinctive power of apprehending the approaching season.   When one sees the enormous thickness of some of the walls (*e.g.*, figs. 7, 9 or 10) in contrast with the thin walls and partitions often found in the summer nests (fig. 20), one is almost tempted to attribute this to something other than individual traits, although we have found an enormous amount of individuality expressed in the work of *S. caementarium*.   One finds, for instance, much variation in the careful or slipshod manner in which load after load of mud is applied to the nest. Fig. 4 shows how precisely each mouthful is sometimes applied to form half a ring on the cell, while fig. 8 reveals the careless way in which another mother applied her plaster, without any regard for size, shape or security.   I am sure that a nest made as loosely as this would be an easy mark for Hymenopterous parasites of the genus *Melittobia*[3] or even *Anthrenus* larvae when minute, had not this mother made up for her carelessness by thickly daubing mud over the outside of the nest.   This photograph shows the details of the contours after the loose reinforcement was carefully scraped off.   The nests of *S. caementarium* and *C. caeruleum* usually have additional mud daubed over the outside, no doubt for the purpose of strengthening the structure and increasing its warmth.   Some are decorated on top of this with whole pellets stuck here and there over the surface—not flattened or spread as usual (figs. 3, 18).   This serves no utilitarian purpose, so far as we can see, and is not generally done, but the very fact that it is sometimes done, shows that individual differences in manipulation exist, and to account for the origin of this difference leads one into fanciful speculation.   It certainly seems farfetched to say that some females have developed an aesthetic taste.   Better would it be to say that this habit of decorating is a vestige from the time when one or both species, living in milder climate, made a crude nest entirely of small round pellets carelessly stuck together. Later when climatic changes or migration northward occurred,

[3] They can pass through holes .013-inch in diameter.

those few individuals which builded strong survived, until now only this vestige remains of what may have been a former habit.

An idea of the amount of effort expended in the construction of a nest can be gained by examining the cross-sections illustrated in figs. 7 and 9, and the longitudinal section in fig. 10.

The material used in the nest is usually native clay, gray, red or various shades of brown, or even black loam. The Peckhams describe several cells made of white plaster, and I have several nests taken from the walls of a brick-yard stable which have some cells made of brick-dust and the remainder of black mud. Sometimes even the pellets of mud, which make up a single cell are clearly from different sources.

The favorite nesting-place of these species is the rafters of barns or sheds, especially when they are high and well out of reach of intruders. In areas untouched by man the overhanging rocks and bluffs are favorite nesting-places. One also finds the mud nests on the back of torn or hanging wall-paper, in the folds of horse-blankets, old carpet or grain-sacks hanging in out-buildings, in the sleeves and folds of hanging coats, on old umbrella ribs, on strands of hay or corn-husks or in small spaces between the rafters, but in every such case the nest conforms to its immediate surroundings. It frequently happens that the nests built in close quarters are very beautiful, since the builder cannot obliterate her art here by daubing mud promiscuously all over it. The nests built in folds of cloth or on strands of hay are usually more asymmetrical than those built flat upon a board or an overhanging rock, and conform to the folds of the drapery.

It was once my good fortune to gather a bushel of mud nests from some freight cars side-tracked in the city. This suggests a mode of the dissemination of the species not heretofore considered, and may well be a large factor in their distribution, since the Peckhams and others think that the wasps do not usually migrate far from the place of their birth.

On one occasion, when searching for mud nests, I was taken to a farm-house where the nests were abundant in the upstairs rooms. The house had not been occupied for the two years previous to that summer and insects had made themselves at home in it. The nests were abundant upon the walls and window-casings of the upper rooms and many wasps were busily

PLATE II
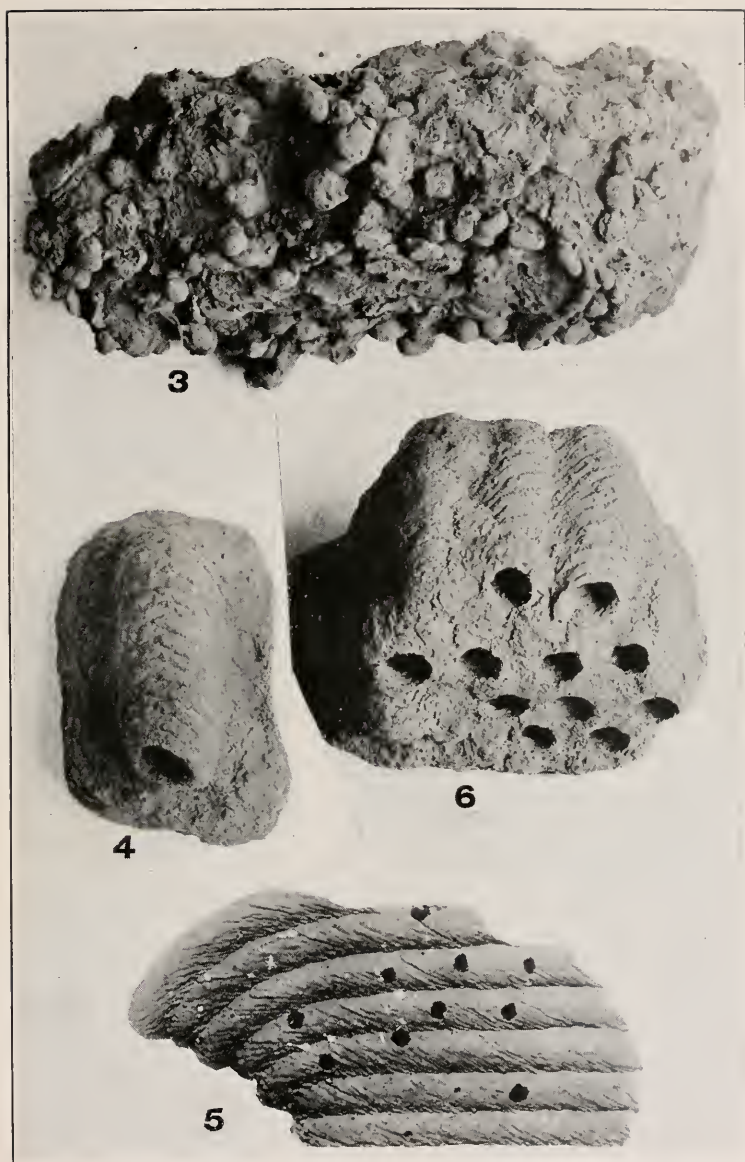
FIG. 3.   Nests of *S. caementarium* or *C. caeruleum*, with decorations of
  mud pellets.   Natural size.
FIG. 4.   One-celled nest of mud-dauber.   Natural size.
FIG. 5.   Pipe-organ nest of *T. albitarsis*.   Reduced.
FIG. 6.   A common form of nest of *S. caementarium* or *C. caeruleum*.
  Natural size.

coming and going.   But when I proceeded to gather them, they all proved to be cells from previous years, and I found that the good new nests were only on the ceiling, just out of reach.   It seems that the wasps built their nests wherever their fancy dictated so long as they were unmolested, but when people occasionally moved about in the room they promptly chose sites higher up, out of the range of disturbance.

The two species of wasps, *Sceliphron caementarium* and *Chalybion caeruleum* make mud nests which are very similar in appearance.   The species of the builder is ascertained with accuracy only by finding the dead pupae or adults in the cells or by noting the species of the adults as they emerge.   Occasionally the nests of both are decorated with pellets.   The only constant distinction which I have been able to discover lies in the difference in the structure of the cocoon; that of *S. caementarium* is smooth, glossy and brittle while that of *C. caeruleum* is the same but covered with a webby mesh.[4]   The occasional occurrence of both species of wasps emerging from one colony of cells does not necessarily mean that an erring mother has deposited her egg in the wrong nest, although it would seem to us almost impossible for a mother to find her own nest among hundreds of others as we sometimes see them massed in the lofts of large barns.   (In our barn, 643 were gathered and about three times as many remained).   The phenomenon is easily explained by the fact that the mud-dauber's nest occasionally occurs on top or along side of the pipe-organ nests, and on several occasions we have found them plastered to paper wasps' nests.   In fact one curiosity which we have is the nest of these two species of mud-dauber and a pipe-organ nest all subjoining a large paper nest.   We can see that probably the mother seldom commits the error of laying her egg in another's nest, but when choosing a site on which to build she sometimes regards the architecture of her sisters the same as the side of a barn.

NIDIFICATION OF *T. ALBITARSIS*

Trypoxylon albitarsis makes the Pipes of Pan, or as they are more frequently called the pipe-organ nests.   Fig. 5 shows the nest as it usually occurs; the short tier is in course of construction.   *T. albitarsis* does not daub the nest all over with

[4] Details in *Psyche*, Vol. XXII, p. 62-63.

mud when it is completed, thereby hiding its artistic architecture, but it, like the other two species, smooths the interior of each cell carefully. The holes at regular intervals in the nest are made by the emerging adults, and the white spots are the hardened chalky substance which the insects emit from their bodies immediately after they emerge. This white substance is emitted by *S. caementarium* and *C. caeruleum* also, but in the form of many minute pellets discharged before emergence.

The larva of *T. albitarsis* spins a very light web about the walls of its cell; just inside this it constructs its cocoon, black very strong and brittle. This it probably makes of the excrement which it clears from its alimentary tract after feeding is completed, and utilizes for a cocoon by throwing it all over itself. This is then kneaded into shape by dextrous movements of the body; it then hardens and makes a very comfortable abode.[5]

These nests are usually built against some flat surface; sometimes the back side is lined with mud, and sometimes the board on which it is plastered serves as a back wall. Here in fig. 2, we have a view from the rear of one such nest built without a back wall, showing cells, partitions, pupal cases, spiders, empty cells and two cells in course of construction. In this nest are three instances of the emerging insect opening its way into an adjoining cell instead of to the outside; if the adult belonging in the latter cell had already emerged, this wasp could leave by its exit, but if not it must certainly die imprisoned, because instinctively the insects can open their way through only one wall.

In contrast to this flat form I have seen about a dozen nests built on hanging corn-husks. Here without a substantial foundation the cells attained a perfectly cylindrical shape, as thick on the back as on the front. They afforded sufficient protection in all respects, however, for they normally brought forth healthy adults.

On only one occasion have I been able closely to observe the details of the building operations of *T. albitarsis* in progress.

[5] I have tried to observe this process by placing larvae about to pupate in vials. But it seemed they were unable to work on the smooth glass, for they produced only thick ribbons of the black material, but no pupal case.

PLATE III
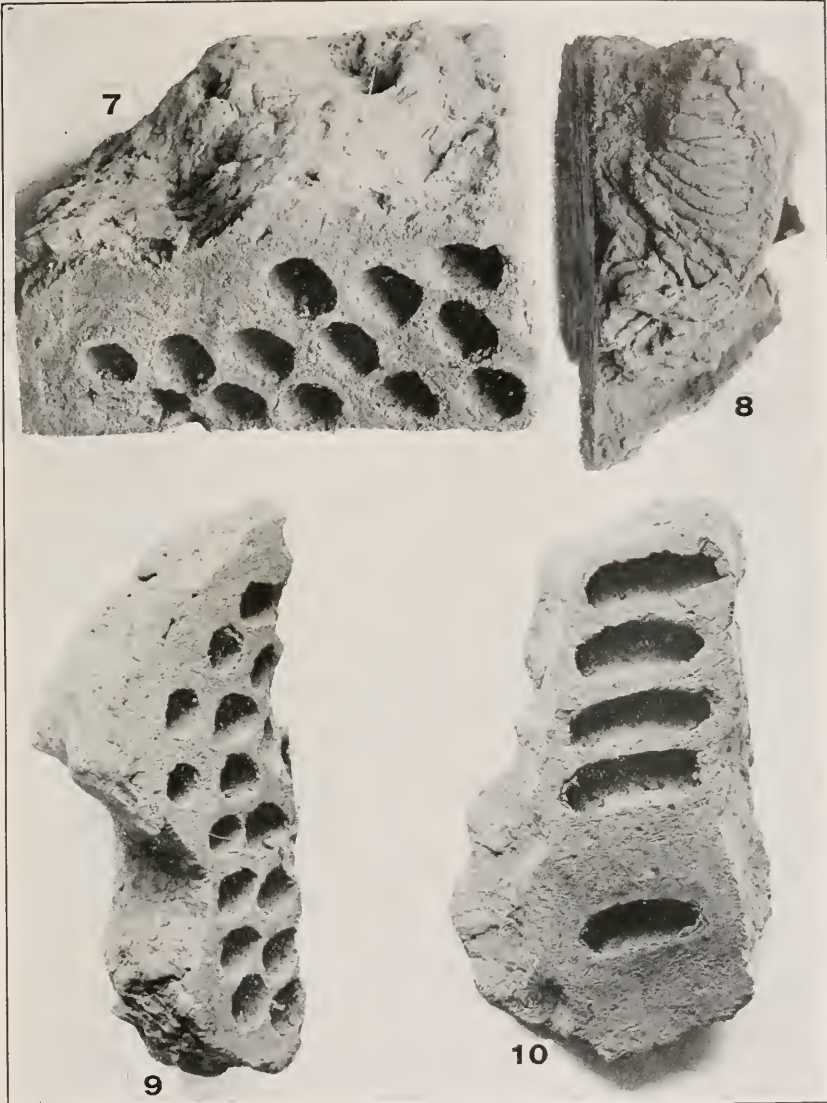
FIG. 7. Cross section of mud-dauber's nest showing the thickness of the walls and the relative position of the cells. Natural size.

FIG. 8. Nest of mud-dauber, showing the details of the architecture after the reenforcing layers of mud had been removed. Natural size.

FIG. 9. Cross section of nest. Slightly reduced.

FIG. 10. Longitudinal section of the mud-dauber's nest, showing the size of the cells and the thickness of the walls. Slightly reduced.

This nest that I was so fortunate to discover in course of construction was in an accessible position so one could easily watch the methods of building. It contained two complete tiers and the third was being added. The wasp returned with a mouthful of mud, but our presence disturbed her and she flew away. Only on her fourth return was she content to settle down to her work without heeding our presence. She would remove the load of mud from her mandibles to her front legs and apply it to the structure in its proper place and then smooth and work it down with her head. Her mud puddle could not have been far off, for she required only from one to three minutes to make the round trip and bring her load of mortar.

As usual, the male remained in the tube that was being constructed while the female brought the mud and continued the building. The male sometimes poked his head out of the cell to meet or greet his spouse, in a way very similar to the habit which we have seen in the smaller species of Trypoxylon (*T. clavatum*). A long pipe was first constructed. This was then filled for a certain distance with spiders and an egg laid with them and a partition put in, making a cell out of this section of the pipe. This process was repeated until the entire pipe was divided into cells, and then a second tier was made beside it. Since most of these nests are built vertically, with the openings downward, one wonders what prevents the spiders falling out while the cell is being filled, the egg laid and the mud applied for the partition. I have wondered whether the male did not in some way perform this office. It was soon necessary for me to leave, so we captured the female and took down the nest. We found the male 'way up in the topmost corner of the unfinished tier. The two older tiers were complete in every way, properly partitioned and sealed, and each cell contained spiders and a young wasp.

Dr. William H. Ashmead[6] says:"Walsh was the first to record the habits of *Trypoxylon albitarsis*, which usually selects the deserted cells of a mud-dauber (*Pelopoeus*) in which to nidificate, provisioning its cells with spiders. I can confirm this statement of Walsh's from personal observations, as I have not only obtained them from the old cells of *Pelopoeus* but also from those of *Chalybion caeruleum*. I have also bred *T. clavatum* from the same mud-dauber's cell."

[6] The Habits of Aculeate Hymenoptera, II., *Psyche*, Vol. VII. p. 45.

While I can agree with Mr. Ashmead in regard to obtaining adults of *T. clavatum* from the nests of *Pelopoeus* or *Chalybion*, I cannot agree to the statement of both himself and Mr. Walsh that *T. albitarsis* uses the old cells of both these species. Many hundreds of adults have emerged from pipe-organ cells in my possession. In addition I have invariably seen these wasps at work on these nests, so I can hardly think of them as using old cells of other wasps.

One often finds nests parts of which, and especially the middle parts, are two, three or even four tiers high, one built on top of the other, as shown in fig. 1, where two layers exist and a third is being commenced. Whether one mother constructs tier upon tier, or whether a second mother builds her nest on top of the first I do not know. This condition occurs almost too frequently to be attributed to mere accident. Nevertheless the occurrence of nests in this form brings out an interesting point in the instinct of the emerging wasp.

Fabre[7] carried on some experiments with the mason-bee *Chalicodoma muraria*, in which he found that instinctively the animal could bore out of only one earthen covering, and while apparently it had the physical ability to emerge from an extra covering it would rather die in its prison-house than make the extra exertion to escape. But how fares it with these wasps whose mothers or aunts build tier upon tier, making it necessary for the emerging wasp to bite through more than one wall before gaining its freedom ? It is interesting here to note that the insects seem to have some faculty of discerning the front side of their cells, just as the larva of the blue wasp or the yellow-legs has the faculty of righting itself about in its cell as it reaches maturity so that it always pupates with its head toward the exit. In *T. albitarsis* nests of only one layer of cells, one seldom sees an error in choosing the proper side for exit. It has been my good fortune to obtain a few nests which were two or more layers deep, and to study their contents to learn whether these wasps did plod faithfully on until they gained their freedom, or gave up at the first defeat. I have little doubt that there is sufficient strength in those mandibles to penetrate several walls, so the question is merely one of instinct. One nest of two layers was placed flat upon a table so that the emerging insects

[7] The Mason-Bees. Tr. by A. T. De Mattos. Chap. II.

PLATE IV
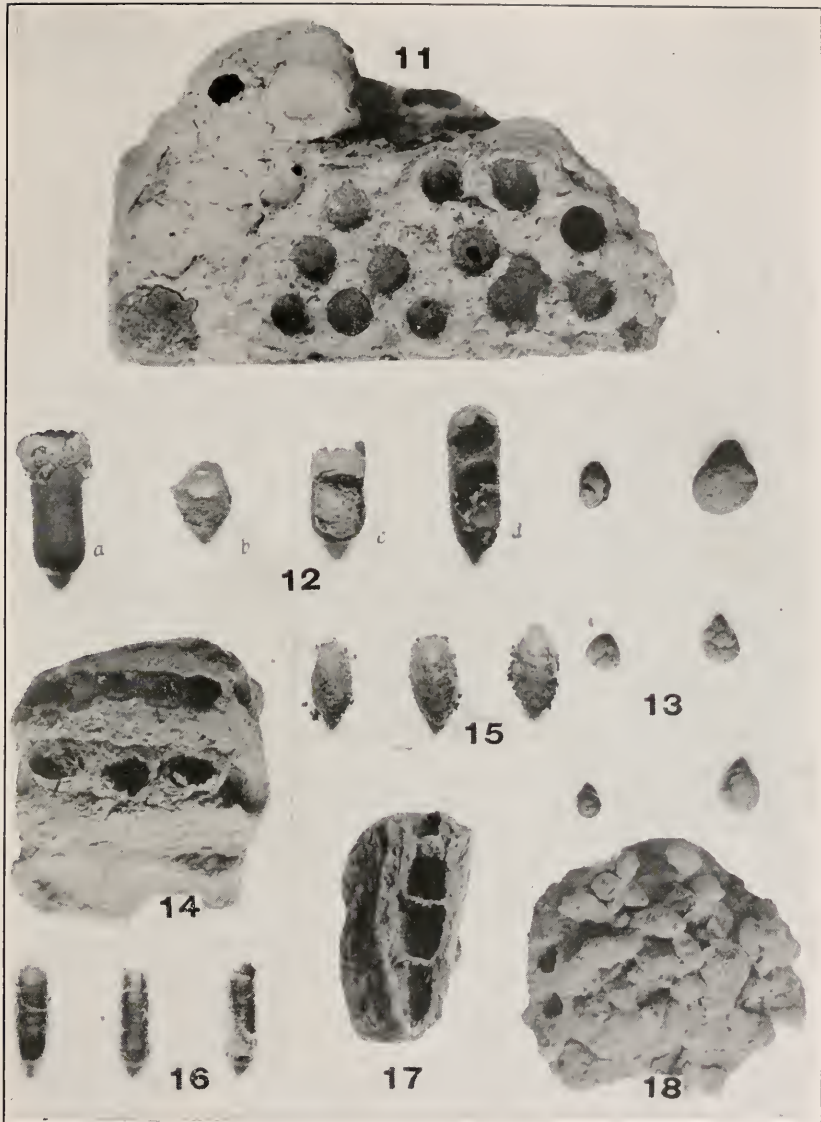
FIG. 11.   A deserted mud-dauber's nest, the cells used by *O. cordata* and the openings resealed with waxy material.   Natural size.

FIG. 12.   Pupal cocoons of *T. albitarsis* after having been used by *O. cordata; a,* complete pupal case with old opening resealed with wax; *b,* waxy plug removed, showing hole made by emerging *O. cordata; c,* part of cell opened to show pupal case of *O. cordata; d,* cell of *T. albitarsis* opened to show partitions and plug of waxy substance.   Natural size.

FIG. 13.   Mud balls taken from the mandibles of mud-daubing wasps.

FIG. 14.   Longitudinal section of mud-dauber's nest showing the pupal cases of *O. cordata* between the waxy partitions.   Natural size.

FIG. 15.   Pupal cases of *O. cordata* taken from deserted cells of mud-daubers' nests.

FIG. 16.   Pupal cases of *T. clavatum.*

FIG. 17.   Old nest of mud-dauber, with two mud partitions, and mud plug in old opening made by *O. lignaria.*

FIG. 18.   Nest of mud-dauber, showing decorations of mud pellets.   Reduced one-half.

could not gain their freedom by way of the under side, which was partly open; the table merely replaced the board wall upon which it had been built.   Fourteen wasps escaped in the normal way from the top layer and the periphery of the lower layer. Seven adults in the central cells could not escape, but each one bored through the wall and entered the adjacent cell, where they were found dead.   They followed no special direction in boring out of these lower cells; one had bored through the front wall, and the other borings were equally divided on either side. In one such dungeon three dead prisoners were found, the original inmate of the cell and the neighbor from either side. Had each one of these seven mature insects had the instinctive courage or energy to push on through one more wall, all would have escaped.   In another nest we found where this same in- ability had brought death to one insect, the only one in the nest that was so situated that its exit led into another cell.   In a third nest the same was true for two insects.   We cannot call this defective instinct, but only simple instinct, for in the insects' normal experience they should have but one wall to penetrate in order to gain their freedom.

One would like to say at least that it is wonderful that the emerging wasp knows how to direct its exit towards the light, but even this is not always the case.   I have another record of an eight-celled, one-story nest in which three individuals had bored through the side-wall into their neighbor's cell and died there, instead of breaking through their own roof to free- dom.   So even this instinct of working out toward the light is sometimes defective.

<div align="center">PARASITES AND LESEES</div>

Often one finds other species occupying the nests or preying upon the wasps at home.   Among these are:

Parasites
  Cuckoo-bees, *Trichrysis tridens*[8] Lep. and *T. parvula*[8] Fab.
  Dipteron, *Toxophora americana* Guerin.
  Dipteron, *Spogostylum fur* O. S.
  Dipteron, *Argyromoeba obsoletum* Loew.
  Hymenopteron, *Melittobia*.

[8] Identified by Mr. S. A. Rohwer.

Museum pest, *Anthrenus scrophulariae* L.

Mutillid wasp, *Sphaerophthalma scaeva* Blake.

House-renters

Bees, *Osmia cordata* Robt. and *O. lignaria* Say.

Eumenid wasp, *Ancistrocerus (Stenancistrocerus)
fulvipes* Sauss.

Eumenid wasp, *Ancistrocerus camestris* Sauss.

Wasp, *Trypoxylon clavatum* Smith.

Wasp, *Trypoxylon cockerellae* Rohwer.

Wasp, *Pseudagenia mellipes* Say.

Wasp, *Pseudagenia adjuncta* Banks.

Meal-worm larva, *Tenebrio obscurus.*

Small click-beetle.

Lepidopterous pupa, *Apatela*, possibly *radcliffei.*

Mites and spiders.

PARASITES

Perhaps the most destructive of these is *Melittobia.*[9] The parasites enter the mud nests by making holes about .013-inch in diameter, enter the pupal cases in the same way and lay their eggs. The larvae eat the contents of the cell (usually in the prepupal stage), and escape as adults, leaving the cocoon empty. These adults bore holes through the neighboring walls and enter other cells and the life cycle is repeated. That these parasites bore into cells promiscuously is evidenced by the fact that their borings are also found in empty cells. Considering their large broods and the rapidity with which they develop, and their ability when ready to migrate, to bore into the mud cells, it is surprising that even one larva should escape them. They usually attack the organism in the prepupal stage, boring into the cell and then into the pupal case. They do not eat the pupal case, nor do they mutilate it, but leave it intact excepting a few small punctures, and containing a quantity of fine debris—probably their own shedding-skins.

The Dipteron which is directly parasitic upon both *S. caementarium* and *C. caeruleum* is *Argyromoeba obsoletum*, Loew.[10] These flies are by no means rare. The larva is found in the wasp's pupal cocoon; this shows that the parasite attacks the

---

[9] Identified by Dr. L. O. Howard.
[10] Identified by Mr. F. Knab.

PLATE V
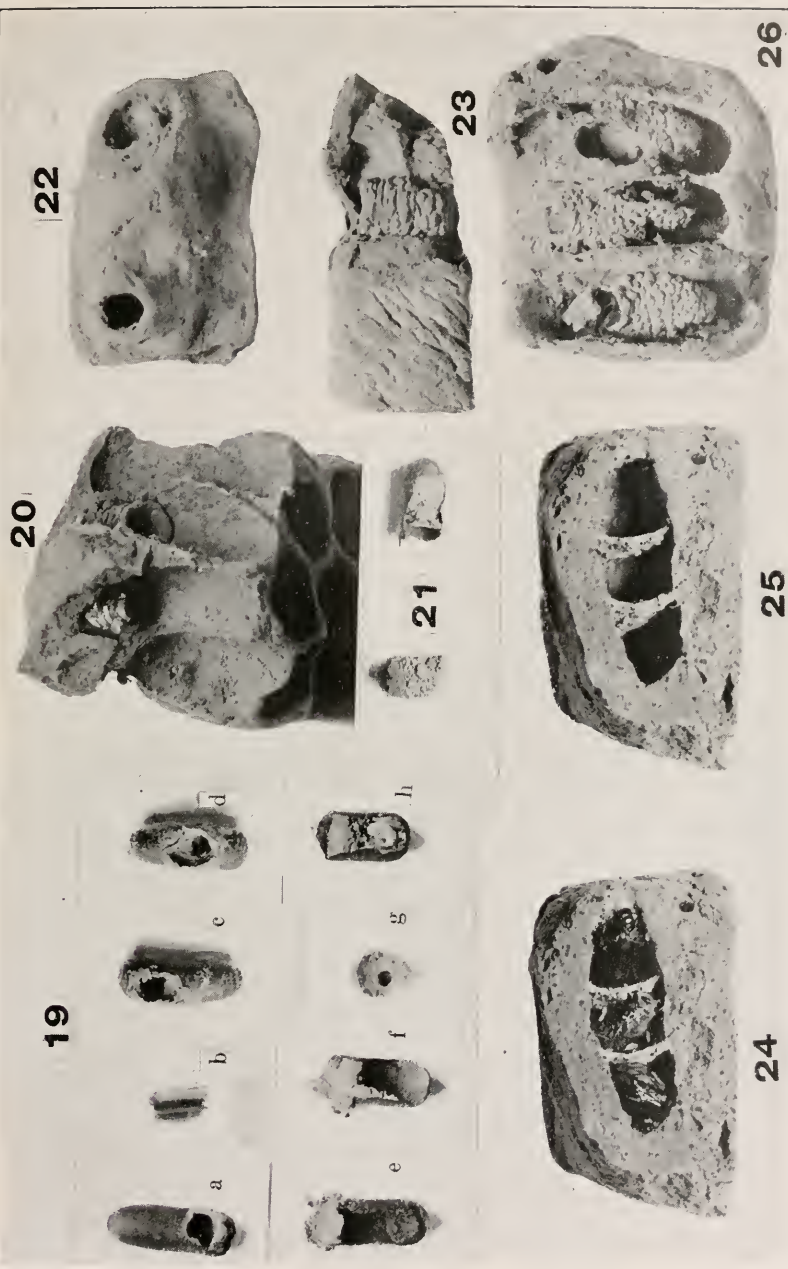
FIG. 19. A series of old pupal cases of *T. albitarsis*, used by *T. clavatum* for nidification: *a, c* and *d*, old cocoons with the exits plastered over and the interior lined with mud; *b*, cocoon of *T. clavatum* (one end open); *e, f*, sections of resealed cocoon; *g*, mud plug removed to show hole made by emerging *T. clavatum*; *h*, interior of nest, showing young larva. Natural size.

FIG. 20. Cells of mud-dauber opened to show the two small cells made by *P. adjuncta*. Natural size.
FIG. 21. New cells of *P. adjuncta* built in old pupal cells of *T. albitarsis*. Slightly reduced.
FIG. 22. Mud nest with two hilly protrusions which were cut down to show nest of *P. mellipes*. Natural size.
FIG. 23. Nest of *P. adjuncta* built in part of a nest of *T. albitarsis*. Natural size.
FIG. 24. Old nest of mud-dauber with side-wall removed to show partitions and plug and pupal cases of *T. clavatum*. Natural size.
FIG. 25. Same, with contents of cells removed.
FIG. 26. Cells of *P. adjuncta* in old mud-dauber's nest.

larva just before it reaches its prepupal stage. Even as late as June 1, one often finds upon opening the mud nests, these Diptera larvae which so closely resemble the wasp larvae as to be at first glance deceiving. When the time for emerging arrives this pupa works itself out through the mud wall until it protrudes half way; then the pupal case breaks and liberates the mature, winged insect, the old shedding skin still blocking up the hole made in the mud wall.

Sharp[11] says that the life history of these insects was unknown until Fabre ascertained that another belonging to this genus, *A. trifasciata*, was parasitic upon the mason-bee. This fly, according to Fabre, oviposits by dropping a minute egg on the mass of masonry by which the grubs of the mason-bee are protected. From this egg is hatched a minute larva, which is provided with a horny head and bristles serving as organs of locomotion; thus equipped it explores the surface of the masonry for a long time seeking an entrance. Having penetrated the wall, it undergoes a complete change of form, and without inflicting any perceptible wound upon the pupa it sucks day after day until it has completely emptied its contents. For some months it remains a quiescent larva in the cells of the mason-bee, but in the spring it undergoes another metamorphosis and appears as a pupa, provided with formidable weapons for breaking down the masonry by which it is imprisoned. It strikes against the opposing wall until a gallery of exit is formed; then the pupal skin bursts and the perfect fly emerges leaving the pupal case still fixed in the gallery.

These details describing the European species apply equally accurately to our *A. obsoletum.*

Other Diptera which emerge from the mud-daubers' nests although less frequently, are *Toxophora americana* Guerin[12] and *Spogostylum fur* O. S.[12]

In addition to these two species of Diptera one finds old pupal cases of flies of a smaller species, in the old remains of spiders, etc. in the cells, but I have never yet been able to obtain adults therefrom. There are sometimes from three to a dozen in a single cell.

Birds, while they are neither parasites nor inquilines, should

[11] *Cambridge Nat. Hist.*, Pt. II, p. 486.
[12] Identified by Mr. F. Knab.

be recorded as an enemy of *T. albitarsis*, which frequently causes heavy losses. It is a simple matter for a bird to peck through the mud walls of the pipe-organ nests and on one occasion a blue jay was actually seen breaking into the nest and to feast upon the larvae therein.

In addition to the above we have found one nest of *T. albitarsis* infested by an Ichneumon fly belonging to the tribe *Ophionini*.

In one collection of *Sceliphron* I found about a dozen cocoons which, when held to the light, revealed an inner cocoon just a little smaller than the mud-wasp's cocoon and of a lighter color. I had found previously that the blue wasp makes an outer webby cocoon over the papery one, but this seemed to be a reversion of that arrangement. At emerging time there issued from these *Sphaerophthalma scaeva* Blake,[13] a handsome black Mutillid parasite with orange abdominal markings. This species emerged from mud-daubers' nests collected in two different localities and years.

We find that the larvae of *Sphaerophthalma scaeva* Blake spin their cocoons within the cocoons of *Pelopoeus*. Since the nests containing both were gathered in December and remained in my living-room all winter, it was impossible for *Sphaerophthalma scava* to parasitize the cocoons of Pelopoeus after they became such, but in all probability the eggs of *S. scaeva* remained dormant until the Pelopoeus larva had finished feeding and spinning, and then it developed, forming its own white cocoon within the brown one of the Pelopoeus. Even this parasite we find parasitized by *Melittobia*.

Some old cells of *T. albitarsis* were infested by mites, probably *Pediculodes ventricosus* Newport, but since there was slight mortality in this lot of material I presumed that the mites had come after the emergence of the wasps to feed upon any old spiders which chanced to be there.

HOUSE-RENTERS

These occupancies other than parasites may be called little more than chance. But the empty cells of the three species of mud-daubers here considered serve a very important function in supplying permanent homes to at least four distinct species

[13] Identified by Mr. S. A. Rohwer.

of Hymenoptera. The bee[14] habitually uses the old cells for her young. She divides them into smaller cells by partitions of a waxy substance, making from one to five rooms out of each original cell. Fig. 14 is a section of two abandoned cells of the mud-dauber, revealing three pupal cases of *Osmia cordata* in each. In the spring one finds these pupal cases (fig. 15) of *O. cordata* in the cells, and occasionally a little pill of bee-bread also. The opening of the old cell is thickly plastered with the same brown, waxy substance (fig. 11.) The mother *Osmia* also uses the old cells of the pipe-organ nests, plastering the opening with a thick layer of wax, or even utilizes the hard cocoon-shells of that species in the same way. Fig. 12 shows these cells in use; *a* is a complete cell with the open end plastered up with wax; *b* is the waxy plug removed showing the hole at one side made by the emerging bee; *c* is part of the cell opened to show the pupal case containing the living organism; *d* is a cell complete, sectioned to show the partitions made of waxy substance, and the plug remains as it was placed over the opening made by the mother *Osmia*.

At what time of the year the *Osmia* fills the cells and oviposits we do not know. The bee is a honey-gatherer, I am sure, and not a parasite in any way. Our individuals kept in confinement fed readily upon sugar water. We conclude, from the occasional presence of the pellet of bee-bread in the cells, that the mother places this food in the partitioned room and lays her egg upon it. When we opened the cells on January 1, 1913, we found the adults in each cocoon completely grown. The bee would crawl about for a time and then when replaced in the nest would gladly creep back into its broken cell. Those which were not replaced were glad to get into any crevice. It seems that during cold weather they remain in their enclosures even though they are fully matured. If a bee is removed before its period of hibernation is completed, it may be replaced in its torn cocoon, or it often goes back into the shell or some other crevice of its own accord and resumes its sleep without ill effect. But when they emerge of their own accord (about the middle of April, if out-of-doors, or in March in the living-room), they have not the ability to rehibernate and soon die unless fed.

These bees have the power of emitting a very pleasant, sweetish

[14] Kindly identified by Mr. J. C. Crawford as *Osmia cordata* Robt.

odor when handled. This is not acquired from the environment, but seems to be inherent, for when one cuts open a cocoon containing a full-grown insect, the scent greets one. Whether this scent may be protective we do not know, but we have observed that the dead insects are very attractive to mice. On one occasion when I left nine *Polistes annularis* and *P. pallides* and seven *Osmia* pinned to a sheet of cork over night, I found the next morning that the *Osmia* were neatly nibbled from the pins and no crumb of wings or legs remained, while the *Polistes* were untouched. Many of these *O. cordata* pupal cases gave forth Hymenopterous parasites, May 18 to 20, which were identified by Mr. J. C. Crawford as *Monodontomerus montivagus* Ashm.

On September 16, 1915, in an abandoned log-cabin near Eureka, Mo., we took a number of mud nests which at once appeared interesting because the openings of exit had been resealed with mud. We thought they were the nests of *Trypoxylon clavatum* or possibly a species of Eumenidae, but upon opening the cells at home we found most of the wasps' cells partitioned with mud and containing from two to four little rooms each. In each compartment I found a pupal case identical in appearance with that of *Osmia cordata*, but *cordata* partitions the old cells with a waxy substance, while in all of these the partitions were of mud. I cut open several of the cocoons and found a living adult in each. Here again this species differs from *O. cordata*, since the latter appear as adults in the cocoon in early spring. These new bees were larger than *cordata* and the characteristic sweetish odor was lacking. Most of the cells were heavily parasitized by a Hymenopterous species and were in the pupal stage.

The specimens were sent to Mr. J. C. Crawford and identified by him as *Osmia lignaria* Say. Fig. 17 shows the nest of the mud-dauber, with *O. lignaria's* two mud partitions, and the mud plug in the old opening.

We find a note on this species by Packard (in his Guide to the Study of Insects, p. 139, 1889): "The ♀ of *Osmia lignaria* Say MS., according to Harris' MS. notes was found in the perfect state in cocoons within earthen cells under stones, April 15. The cell she constructs is one-half inch long, oval cylindrical, and contracted slightly into a sort of neck just before the open-

ing for the exit of the bee. From Mr. James Angus I have received the pellets of pollen, about the size of a pea in which it deposits its egg. The larvae were one-third grown in August."

This may indicate that the habits of the species have changed within a comparatively short period, and that now she has learned to repair old domiciles instead of building new ones.

Another insect which makes good use of the empty cells of old nests, as well as holes in fence-posts, etc., is the small *Trypoxylon clavatum* Smith.[15] This wasp uses the old cells in much the same way as does *Osmia*, but uses mud instead of wax for partition and sealing material. When this species takes possession of the old cells of *C. caeruleum* and *S. caementarium*, she uses them without alteration other than the partitions which she throws in, and the closure of mud. Fig. 25 shows these partitions and the mud plug with contents of the cells removed, while fig. 24 shows in situ the pupal cases amid the remnants of spiders' legs. But when she uses the old empty cocoons of *T. albitarsis*, she smoothly lines the old pupal case with fine mud and plasters the opening of the cocoon (which is usually flush with the opening in the mud walls), in the same way. Fig. 19 shows a series of old pupal cases of *T. albitarsis* as used by *T. clavatum*. Figs. *a. c* and *d* show the deserted cocoons of *T. albitarsis* with the exits plastered over or the interior lined with mud. These plugs of mud have in turn been pierced by the emerging *T. clavatum*. Fig. *b* (and also fig. 16) are the cocoons of *T. clavatum*, natural size. The material in this is the same as that of the *T. albitarsis* cocoons, but it is thinner. Since it is itself enclosed in the heavy cocoon of *T. albitarsis* it need not be heavier or stronger. Figs. *e* and *f* show sections of the resealed cocoons; fig. *g* is the mud plug removed from a cell to show the neat hole made by the escaping *T. clavatum*, and fig. *h* shows the interior of a nest of *T. clavatum* where the larva is snug and thriving in the old pupal shell of *T. albitarsis*.

One often finds that the mother *T. clavatum*, before storing the spiders for her young in an old cell has had a thorough house-cleaning, but instead of brushing the rubbish, spiders legs, Anthrenus shedding skins, etc., out through the doorway she has swept them into the corner, as far back as possible, and walled them up with a partition of mud. This is poor

[15] Kindly identified by Mr. S. A. Rohwer.

economy however, since that room could have been used nicely for another babe.   This condition was seen so often that it cannot be attributed to the whim of an occasional individual. In one case we found a living *S. caementarium* prepupa pushed away back and entombed.   The mother *caementarium* had failed to seal her cell after laying the egg, and the little *clavatum* treated it as she usually treats rubbish.

In a collection of about a dozen mud-dauber's nests taken in the spring of 1909, one nest gave forth six individuals of *Trypoxylon cockerellae* Rohwer, identified by Mr. Rohwer.

Another member of this group of house-renters is *Pseudagenia adjuncta* Banks.   (Identified by Mr. S. A. Rohwer.)   This wasp makes complete new cells inside the old cells of mud-daubers' nests (see figs. 20, 23 and 26), and also makes complete cells in the old empty cocoons of *T. albitarsis* (fig. 21).These insects emerged from material gathered at several places near St. Louis, and the adults emerged in late April and early May.   I have not observed the insect in the larval stage, but their pupal covering is very thin and papery and of a cream white color.

Likewise a sister species, *Pseudagenia mellipes* Say,[16] shares the benefits of the mud nests.   They do not make pretty little cells inside the old mud-daubers' cells, as does *P. adjuncta*, but they emerge from the outside walls of the nest, and I suspect that their nidification occurs in this way.   A mother finds the nest of a mud-dauber and with her mandibles digs a small cavity in the outer wall; this she fills with provisions and the egg.   Then with the mandibles she removes more earth from the nest and builds up and around her mass until it is completely hidden.   If the *Sceliphron* is at work at the time, so that *P. mellipes* can get the wet mud, the work is greatly facilitated. Fig. 22 illustrates the mud-daubers' nests with a portion of the top removed to show the cells from which *P. mellipes* emerged. It may be possible that *P. mellipes* does not dig out her supply of mud from the nest, for in that event she would be obliged to moisten it in some way.   But if she brings it from afar I cannot account for the mandible marks which usually are in evidence near by.   This species makes a pupal case of soft, white material which is identical with that made by *P. adjuncta*.   It appears that these little builders may often be aided in their work by

[16] Also identified by Mr. S. A. Rohwer.

the hostess *Sceliphron* or *Chalybion* who, when reinforcing her nest with layer after layer of mud on the outside, covers the little foreign cell as well and quite obliterates any traces of its presence.

Hartman (Bull. Univ., Texas, No. 65, p. 48-49, 1905) calls *mellipes* a blue insect and describes its habits of nest building. Since Dr. Hartman's *mellipes* differed in color and in habits from the *mellipes* which came from the mud nests of *Pelopoeus*, I again submitted the specimens to Mr. S. A. Rohwer for verification, and he writes: "I have looked over these specimens again and am sure that my determination of them is correct. In most cases Ashmead made the determinations for Mr. Hartman and in many cases Ashmead's determinations cannot be relied upon. We had in the collection of the Museum after it had been arranged by Ashmead three species under the name *mellipes*."

Among other insects which occupy the old mud cells are two wasps belonging to the Eumenidae. From the Kansas material of 1912 several specimens of *Ancistrocerus (Stenacistrocerus) fulvipes* Sauss,[17] emerged, and in a lot of material from Meramec Highlands in 1911 many *A. camestris* Sauss.[17] appeared. These wasps use the old cells without modification, filling them with caterpillars for their young and then resealing them with mud.

Spiders are often found occupying the old cells, buried deep in a mass of soft web. Often too the larva of the dark meal-worm *Tenebrio obscuris*, is there feeding on the rubbish that remains after the wasp has emerged. Cockroach egg-cases are sometimes found in the cells, and often the pupa of the hairy caterpillar (*Apatela*, possibly *radcliffei*)[18] is found all nestled down in the mass of its own hairs, with the opening of the cell well sealed with the same material.

THE CONTENTS OF THE NESTS
THE KANSAS WINTER BROOD OF 1912

In May, 1912, in an effort to obtain a supply of material for variation studies I shipped to St. Louis from Lake View, Kansas, about 650 of the mud nests of *Sceliphron caementarium* and *Chalybion caeruleum*. All of the nests were gathered in

[17] Identified by Mr. S. A. Rohwer.
[18] Identified by Dr. H. G. Dyar.

one barn near a stream, and care was taken to select only those which apparently contained pupae. The good nests may be distinguished from the old nests by the openings of egress which the latter contain. This point of distinction may not always be relied upon since occasionally these holes have been replastered with mud or wax by tenants of the old nests, such as *Osmia* bees or small *Trypoxylon* or even Eumenid wasps.

Unfortunately for the variation studies, the most of the cells were either parasitized by *Melittobia* or they had been eliminated in the larval stages by various agencies, so that only a meagre handful of normal adults came from all this collection. Variation studies were defeated, but there arose at the same time the equally important and inviting problem of the rate and causes of this appalling elimination.

So with this large number of nests on hand I took up the task of opening each cell and tabulating its contents. Since the resulting tables are too unwieldy to be practical for publication, it seems best to give the total results of each class of contents of the nests, adding thereto the details of some of the most interesting mother-wasp behavior as revealed by a study of the contents of her cells.

The 643 nests which constituted this lot had a total of 4,397 cells. The number of cells in each nest varied from 1 to 36, as presented in the table below.

Cells to each nest	Frequency	Cells to each nest	Frequency
1	35	15	12
2	73	16	8
3	61	17	7
4	75	18	4
5	72	19	3
6	61	20	6
7	49	21	1
8	37	22	2
9	34	23	2
10	23	24	1
11	26	25	2
12	17	28	1
13	18	30	1
14	11	36	1

The Peckhams[19] found, before the season was over, the number of cells to a nest to be 5 or 6 and the most they ever found was 21.

Out of 4,397 cells I obtained only 172 good adults in June.

[19] Loc. cit., p. 178.

Parasites and lesees

One third of the cells, or to be exact 1,524 contained the parasites *Melittobia* or evidences of their having been there. This parasite was very destructive and was instrumental in wiping out entire families in many instances. Of the 643 nests only 210 were entirely exempt from their attacks, and the smaller nests of 1 to 5 cells were the ones most favored in this exemption. Of the 210 which were quite free from these parasites, 143 or 68 per cent. of them were nests of 1 to 5 cells, while in the entire collection a scant 50 per cent. of the nests were of that size.

In this material we found that the common museum pest, *Anthrenus scrophulariae*, ate not only the dried food as is its custom, but larva and spiders as well. In some cases we found them in the open cells wherefrom the adults had emerged, feeding upon the remains of the pupal case and fragments of spiders' legs, but these were not counted; only those were considered which were found alive in the sealed cells or had matured and left their shedding skins amid the dissected spiders. In that case only were they considered true parasites, destroying living matter. Yet we cannot prove that even here they had destroyed living matter since they may have entered cells which contained no egg or in which the larva was already dead.

Of the 4,397 cells, 171 or 4 per cent. were in this condition, *i. e.*, the cell properly sealed and the contents destroyed by this pest.

Fifty cells gave forth Dipterous parasites, and 5 cells produced cuckoo bees; 54 cells contained the small house-renting *Trypoxylon clavatum*, and 2 cells had been filled with caterpillars and resealed, evidently by an Eumenid wasp; one cell contained an adult chick-beetle which was probably only using the cell for shelter and 3 cells harbored larvae of the dark mealworm, *Tenebico obscuris*, and 1 cell contained a Lipidopterous pupa which later gave forth an adult.

Since the young wasps in the Melittobia infested cells had completely spun their cocoons, it is quite likely that a large per cent of them would have emerged as good adults, had not the parasites killed them. In so far as building and provisioning were concerned the mother wasp was not at fault in these, while

in the case of the remaining cells still to be accounted for she probably was responsible to some extent.

Number of cells provisioned and sealed without the egg

Of the remainder of the cells we find 537, or 12 per cent. of the total, in which the mothers had completed the cell, adequately provisioned it and finally sealed it without laying the egg. This defect of instinct or intelligence is appalling when one thinks of the effort expended in building the nests and the great amount of spider hunting necessary to provision them. We tabulated the number of spiders that came out of 515 of these cells, as follows:

No. of spiders in each cell	Frequency	No. of spiders in each cell	Frequency
1	22	19	4
2	24	20	5
3	32	21	6
4	40	23	2
5	59	24	2
6	56	25	4
7	48	26	5
8	52	27	5
9	23	28	1
10	30	29	2
11	14	30	3
12	9	31	2
13	8	32	1
14	14	33	2
15	8	35	1
16	6	38	1
17	11	42	1
18	11	46	1
		Total 4,637	Average 9

Thus the effort spent in capturing and storing 4,637 spiders (an average of 9 to a cell) was utterly futile because the mother wasp failed to deposit an egg with them. We find the number of such cells in each nest varying from 1 to 17 and occurring with the following frequency.

Eggless cells in each nest	Frequency	Total cells
1	153	153
2	59	118
3	28	84
4	15	60
5	.11	55
6	6	36
7	2	14
17	1	17
	275	537

Assuming that each mother is responsible for one nest complete, we find from this tabulation that 275 mothers built and provisioned these 537 cells without laying their eggs therein, and the number of times each mother proved "forgetful" in this respect varied from 1 to 7 times, with the one exceptional case of the largest nest in the whole collection, wherein she failed to oviposit in 17 of them, about one half of the cells which she made. It may be that this exceptional mother was favored with extraordinary longevity and that even after her quota of ova was exhausted her domestic instincts prompted her to go on faithfully building and providing, even though the species would derive no benefit from her labor. The table shows that the greatest number of mothers erred in one or two of their cells, but this is the natural sequel to the fact that a great majority of the nests contain only a few cells. We sought for some correlation between this parental tendency and the number of cells in the nest, but we found none; the large and the small nests were equally likely to suffer from this form of neglect. The phenomenon seems to be largely a matter of individual temperament. Frequently a handsome nest of many cells was faultless in this respect, while sometimes a single cell, the only domestic attempt of the mother, was a dismal failure because she had failed in this vital point of depositing an egg in the otherwise perfect nest. Only in rare cases was the mother forgetful of her egg throughout her work (excepting in single-celled nests); in almost all of the nests we got evidence of fertile eggs in some of the cells. It was for a time thought that probably an infertile egg had been deposited and that this in its shrivelled condition might have been overlooked, so a careful search was always made for any evidence of such an egg, but none was ever found. Since more recently we have watched Mother Sceliphron fill and seal her cells without the egg, we feel reasonably certain in attributing this condition to her forgetfulness or her sterility, and not to infertility. We have not ascertained to what extent the wasp is forgetful of laying the egg, or to what extent this lack of egg-deposition is due to sterility or infertility. If she be sterile or unfertilized, it is even more strange that she should go on making and stocking her cell than that the unfertilized mantis should continue to make her egg-case, for in the mantis the material for the egg-

case comes from her own body, hence the process is physiological, while in the wasp, nidification plus provisioning is psychological in its origin.

Cells that were completed and sealed without provisions or egg

One hundred seventy-six cells, or 4 per cent. of the total number, were properly made but sealed empty. These were made by 132 mothers, who erred in this frequency:

No. unfilled cells in nest	Frequency, or No. mothers	Total No. cells
1	100	100
2	24	48
3	6	18
4	1	4
5	0	0
6	1	6
	132	176

Thus we see that it is an error which is committed occasionally by many wasps (in this population 1 mother out of every 5); but to a large extent by very few. The two cases of 4 and 6 empty cells to a nest were both in large nests, and of the many one-celled nests in the collection only 2 were empty. In other words, a mother frequently leaves one or two cells of her nest empty, but rarely leaves her whole nest, be it large or small, in that condition. In the nest of 36 cells, the largest in the collection, as we cited before, the mother had sealed 17 of the well-filled cells without the egg, but she had failed to provision only one cell. Some other mothers built large nests without even a single failure in this point.

Number of cells unsealed

We occasionally find cells which have been completed but not sealed; they are sometimes quite empty and sometimes partly filled with spiders. The sight of a deserted cell partly filled with provisions for the young at once suggests another tragedy of the insect world,—a mother wasp who has met her death while out foraging for her brood. But since the mother can meet such a death only once to forever prevent her return to her nest, and since we find some mothers having two to four such cells, we must attribute at least part of these cases to some other causes, such as forgetfulness, etc. There were 126 of

these unsealed cells, or about 3 per cent. of the total number. Of these, 7 were partly filled with spiders. They occurred in the following rate:

No. open cells in each nest	Frequency, or No. nests	Total cells
1	77	77
2	11	22
3	5	15
4	3	12
	96	126

The table above shows that 96 mothers failed to seal their cells, and while most of them (the 77 which failed in one case only) might be attributed to some accident that prevented the mother from returning, yet the 19 other cases prove that part of these failures must be attributed to her carelessness. On two occasions in my experience, adults emerged from these unsealed cells of the summer brood. The closure therefore does not affect the development of the larva, but it probably keeps out parasites.

Insufficient food in the cell

Another occasional fault to be attributed to the forgetfulness or carelessness of the mother wasp is that of laying the egg and closing the cell with a supply of food that is quite insufficient to bring her young to maturity. We find in some cases only enough food to carry the larva through half its period of growth, or even less. When the cells were opened up and dead larvae found, it was noted whether any food remained uneaten in the cell. If the larva was dead and part of the food was untouched, its death was attributed to unknown causes. If however a half-grown or stunted larva was found dead in the cell with no food, its death was attributed to starvation, due to the mother's failure to supply it with sufficient food.

Only 46 cells, or 1 per cent. of all, were found in this condition, and 35 mothers were responsible for this mischief; 29 of these mothers had one such cell each in their nests, and these nests were distributed among the large as well as the small nests (2 to 26 cells). Four cases of two such cells in a nest were among small nests. The mother that erred in this way three times had a 7-celled nest, and last of all one wasp with a 25-celled nest was woefully deficient six times.

One sees that experience counts for little, that there is no relation 'twixt large nests and learning to fill them properly.

Spiders that remained uneaten in the cell

In contrast to the condition mentioned above, there were some cells wherein the insect was past the feeding stage and in the prepupal, pupal or adult condition, and some spiders still remained uneaten. When this occurred, they were counted to see to what extent the mother may give a superfluity of food.

There were 135 such cells, in contrast to the 176 cells which the mothers had sealed stark empty, and 46 in which she had sealed up the egg with insufficient food. So it seems that the mother wasp is more likely to err by giving her child too little food than by offering too much. The following figures show the number of spiders that remained in each cell after the larva had spun its cocoon.

No. spiders	Frequency	No. spiders	Frequency
1	14	8	9
2	31	9	1
3	30	10	4
4	10	11	0
5	16	12	2
6	12	13	0
7	3	14	2
		15	1

The number of spiders that remained untouched varied from 1 to 15, the greatest frequency occurring between 1 and 6 spiders.

Mortality in the larval stage

Here we consider the mortality of the organism in the larval stage of growth, due to causes other than starvation. We know this because in every case some uneaten food remained in the cell. The 245 cells, near 6 per cent. of the whole mass, were distributed as follows:

No. such cells in a nest	Frequency or No. nests	Total No. cells
1	95	95
2	29	58
3	9	27
4	4	16
5	2	10
6	3	18
7	3	21
	145	245

Mortality in the prepupal stage

Those eggs which are deposited in late August and September winter over as prepupae in the nest. In a comparatively short time the larvae consume their food and grow to full size, and long before cold weather sets in they have spun their cocoons about themselves and there they remain inactive, not transforming into pupae until spring (about May). In this condition they pass through the coldest part of the winter, and a part of the mortality among prepupae may be attributed to the cold.

When the cells are opened and dead prepupae are found, they are of two kinds, (*a*) those which are dead, but are yet white in color, which shows that they have died more recently than (*b*) those which are of a decayed-looking, brown color, showing their death to have been more remote, and hence having occurred earlier in the season, when they had not experienced much cold. In this collection we found 415 belonging to class *a* and 629 to class *b*. This shows that the mortality was greater in the earlier and milder period than during the colder season. Of course other external factors may have been responsible for the life or death of the insects, such as the thickness of the mud walls, etc.

The mortality at this stage including both early and late deaths was 1,044, or about one fourth of the cells. There may have been some inherent weakness in whole families, but this will be discussed under mortality in individual families.

Mortality in the pupal stage

After the insects have survived the winter in the prepupal stage they transform into pupae. Here in the more advanced stage of the insect's life the mortality was comparatively small, 110 cells, or 2 per cent. of the total. But even this number is large when one considers that the insect is past most of its frailties and difficulties, feeding, spinning and transforming; why should these have died for no apparent cause at this vigorous stage? This subject too will be considered again in the probable inherent weakness of certain families.

Mortality in the adult stage before emergence

Here we have a rather perplexing form of mortality. The insects had transformed properly into adults, had wings, legs,

antennae and mouth-parts, and yet were dead in their cells, some of them still in their cocoons; others were out of the cocoon but had died before biting their way out of the cell or even while doing so. In this stage we find the mortality to be 130, or 3 per cent of the total.

Elimination within individual families

We have found that a certain per cent. of the cells that are built cannot possibly bring forth adults. In some cases the defect is the fault of the mother in not having properly filled the cell, or having forgotten to lay the egg, etc. In other cases no adults can be expected to emerge, but through no fault of the mother, as for instance, where the young are destroyed by parasites. However, there is in each nest or colony a portion of the cells which contain all the rudiments for producing a new generation, but the organism may or may not have the inherent vitality to press on to the completion of its development. For want of a better name we shall be obliged to refer to these throughout the succeeding paragraphs as the potentially productive cells or the potentially emergable young wasps.

There were in this collection 1,701 such cells, or 39 per cent. of all built by these mothers. Even among these which were apparently unhampered by any obstacles to their growth and were supplied with all things required for their development to adulthood, we find heavy elimination in different stages. This loss of life is due largely, I presume, to inherent weakness, or if not inherent weakness, to what might be called the inability of some individuals to resist extreme conditions which only the most vigorous individuals can survive. It is a startling discovery that in this population, barely one out of ten of even these apparently perfectly equipped young ever lived to see the light of day.

When we examine certain nests we find the potentially good organisms eliminated in some colonies in many different stages of their development; in other nests it is clear that these unmolested and promising young have all dropped off at the same stage of their development, although not at the same time of the calendar, from which we may infer that their death cannot be attributed to some environmental catastrophe, but to some cause within themselves.

I assume that each nest is built and filled by only one mother, and in this assumption I feel fairly confident. So when we find all of the young of one mother (as in some nests we do), either emerging as adults or dying in the stage just preceding emergence, then I say this mother has endowed her offspring with better constitution to do battle with adversities during its postembryonic development than the mother whose entire progeny has died in early larvahood.[20]

The greatest elimination occurred in the prepupal stage. Of course we must bear in mind that in the winter brood this stage covers a long period when the organism rests in this condition during the winter, not transforming into a pupa until early spring; hence we must expect a proportionately greater mortality. In some cases we find whole families dying in this stage of their development; in other colonies the individuals live through this critical period only to drop off later, for reasons unexplained, and still others all survive to adulthood. In some cases they never reach even full growth in the larval stage. But the point that we would emphasize here is that the young not only die, but a certain considerable proportion of them die with precision and system. When we find all of the population of a nest arriving at an advanced stage, or in another all dying at an early stage of their development, are we not right in suspecting that the good tendency or the bad tendency "runs in the family" or may be heritable?

In going into a study of elimination in this group, we should bear in mind that the mud-daubing wasps offer us material which is peculiarly simplified for such a study. Many species during their development from egg to adult would have to face the chance of elimination in open competition with their fellow-beings and enemies, and can only reach adulthood by surviving climatic conditions in the open and also by exercising enough energy and art to procure their own food during tender youth as well as avoiding being food for others. But with these wasps the case is very different. Not an iota of exertion or responsibility is required of them until they arrive at adulthood. In this part of the population, where the young are constantly

[20] Variable environment can scarcely have been a factor here, since all of the nests here considered were taken from the rafters of the same barn, in equally sheltered positions.

sheltered from the weather and enemies, and their food is at hand for them when they arrive, and with the two fierce struggles removed (hunting for food and being hunted), one would expect little or no loss of life, and it certainly would appear that, aside from inherent tendencies, all had exactly equal chances of survival.

Hence we must admit that Natural Selection is vigorously at work here, eliminating weaklings while the vigorous survive, even in this secluded life where the individuals do not in any way come into the open struggle for existence. It is precisely this elimination in the potentially viable young in single families that we shall now take up.

It is difficult when so many elements are involved to get any tangible proof that inherent characteristics of families have anything to do with the mortality or viability of these young. We may approach it however by calculating what the death-rate would be in each of the five stages or combinations of stages[21] if the elimination followed only chance. The entire formula for all of the possible combinations of the five stages is so long that we shall only take from it what we want to compare with the actual occurrences in the preceding tables. It is obviously necessary that all of the nests must have at least five good cells to justly compare them with the distribution of five chances, so we use in the following comparison only the nests of that size or greater. Of these, we had 120.

Now if no factor but mere chance controlled the distribution of the fatalities, then there would be only one chance in 3,125 of all five of the young in a nest meeting death in any one stage, while in fact we find this actually occurring at a much higher rate, e. g., all died in the prepupal stage in 22 of the 120 large nests, or at the rate of 572± in 3,125. Other comparisons are as follows:

<hr/>

[21] We must make due allowance for the fact that in this calculation we have assumed that the chances of death are equal in the five stages, while in fact some stages are obviously of longer duration or more trying than others.

	Proportion in 3,125		Fact, in 120	
	Chance	Proportion of actual occurrence	Chance	Fact
All larvae............................	1	26	.04	1
All prepupae.........................	1	572	.04	22
All pupae............................	1	52	.04	2
All dead adults......................	1	0	.04	0
All emerged adults...................	1	78	.04	3
Dead adults + emerged...............	30	104	1.15	4
Dead adults + pupae.................	30	52	1.15	2
Larvae + prepupae...................	30	494	1.15	19
Prepupae + pupae....................	30	234	1.15	9
One or more of each.................	120	52	4.61	2
One or more in 4 of the 5.............	1200	494	46.15	19

Of course, by the time we have selected only the nests of five good cells or more, the numbers are so small that the probable errors are absurdly high, yet to my mind the evidence gives sufficient and conclusive proof of the point we are seeking, viz., the existence of family tendencies of survivability, entirely apart from environment. In the above we see all or nearly all of the family dying in the same stage or in two consecutive stages at a far higher rate than chance would produce, while in the last two groups of miscellaneous distribution of mortality, where the chances run vastly higher, the actual occurrence drops proportionately lower.

So in this heavy elimination which goes on we may justly lay a considerable part of the responsibility upon the parents. In turn they themselves may not have been properly endowed, and we can only regard with the kindliest respect those mothers whose offspring we see surviving in large numbers. There are a few family records which we cannot pass by without marvelling at their perfection, while at present we can only vaguely say that the best of mothers endowed their offspring with the characteristics that make for survival, and the poor mothers put their young here minus these survivabilities, and they went to the wall in spite of the luxurious ease of their young lives.

We regret being unable to go further into the details of this fascinating study of inherent tendencies in individual families, but these numbers scarcely warrant further analysis. The problem is pregnant with biological suggestions for anyone who can obtain the material in unlimited quantities, and it lends itself admirably to mathematical analysis for anyone who might care to work it up by such methods.

Summary of the Kansas winter brood

The 4,397 cocoons from our 643 nests fall into the following classes:

	No.	Per cent
Cells giving good adults.................................	172	4
Cells sealed and filled with spiders, but no egg...........	537	12
Cells sealed entirely empty.............................	176	4
Cells unsealed with few spiders and no egg..............	7	..
Cells unsealed and empty...............................	119	3
Cells having dead larva and insufficient food.............	46	1
Cells having dead larvae and sufficient food..............	245	6
Cells having dead prepupae.............................	1044	24
Cells having dead pupae................................	110	2
Cells having dead adults................................	130	3
Cells infested by *Melittobia*...........................	1524	34
Cells infested by *Anthrenus*............................	171	4
Cells containing cuckoo bees, Diptera, *Trypoxylon*, etc....	116	3
	4397	100

Thus the elimination in this lot is so high that we are almost forced to believe that this is in some way an abnormal population. It is clear that the species could not endure under this rate of elimination indefinitely — in fact, at this rate the species would be exterminated in four years. We know that the abundance of any species varies from year to year, according to its environment. We may have taken this sample after the population had just passed through especial adversity, such as a severe winter, a raid of parasites, etc.

There is a possibility also that a fault exists which we could not avoid in the collection of the material, and that a few old nests of a former year or brood were mixed with these. While collecting them we were careful to keep only those nests which had no openings of egress or other evidence of their being old; hence it is clear that unbroken old nests wherein the young had died in an early stage or had been riddled by parasites, would be indistinguishable from those of the present brood. The number of old nests cannot be large, however, because most of the nests gave positive evidence of newness in at least a part of their cells.

THE ST. LOUIS WINTER BROOD OF 1913

In the early spring of 1913, 31 nests containing 171 cells of these two species of mud-daubers were taken at Meramec Highlands, near St. Louis, Mo.

The number of cells varied from 1 to 17 to the nest. The adults emerged the following June. The contents of these 171 cells were as follows:

	No.	Per cent
Cells producing good adults............................	47	27
Cells filled and sealed without egg.....................	18	10
Cells sealed empty......................................	16	10
Cells unsealed, containing few spiders..................	0	..
Cells unsealed and empty...............................	8	5
Cells containing dead larvae and insufficient food.........	3	2
Cells containing dead larvae and sufficient food...........	1	..
Cells containing dead prepupae.........................	29	17
Cells containing dead pupae............................	3	2
Cells containing dead adults............................	4	2
Cells parasitized by *Melittobia*..........................	37	22
Cells parasitized by *Anthrenus*..........................	1	..
Cells parasitized by Diptera............................	4	2
	171	99+

We shall here compare this lot only briefly with the preceding winter brood from a different locality, and go into fuller comparison with the summer brood to follow.

There is a conspicuous difference in the proportion of adults emerging. Here 27 per cent. of the cells built produced adults, yet even this is not enough to maintain the population. In this lot the nests contained on an average only 5.5 cells; if they had averaged 9 cells to each mother, as the Kansas material did, then the population would just maintain itself under the rate of elimination shown here. The principal differences in the mortality in the groups is found in the larval and prepupal stages and the parasitized cells. The lower percentage of loss here just balances the gain in the increase in the productiveness of the population.

THE ST. LOUIS SUMMER BROOD

The second brood, or first summer brood, emerged from nests built in June and July of the same summer. The 110 nests which furnish the data of this group were gathered during July at Meramec Highlands, St. Louis, Mo. Owing to the earliness of the season, the greatest number of cells in a nest was 8, and the total number of cells examined in this lot was 438. Their contents were as follows:

	No.	Per cent
Cells producing good adults............................	225	51
Cells sealed with spiders but no egg.....................	27	6
Cells sealed empty......................................	28	6
Cells unsealed, with few spiders........................	1	..
Cells unsealed and empty................................	16	4
Cells containing dead larvae and insufficient food.........	3	1
Cells containing dead larvae and sufficient food...........	9	2
Cells containing dead prepupae..........................	42	10
Cells containing dead pupae.............................	13	3
Cells containing dead adults.............................	8	2
Cells parasitized by *Melittobia*...........................	32	7
Cells parasitized by *Anthrenus*...........................	32	7
Cells containing Diptera or *Trypoxylon clavatum*..........	2	..
	438	99+

It is at once apparent that this summer brood was far more prosperous than the winter broods just considered. We are not at all surprised at this when we consider that their whole development was accomplished during a brief period of favorable conditions. They did not have to endure the rigors of winter and the increased chances of casualty incident to the prolonged period of dormancy.

Let us take up briefly a comparison of the causes of failure in the two broods. In the first entry in the tables, *viz.*, the per cent. of the cells which brought forth good living adults we are startled by 51 per cent. of the summer cells being fruitful against only 4 per cent. and 27 per cent. of the winter crops of cells. In an attempt to account for this we shall compare the other classes, to locate the discrepancy. The per cent. of cells properly made and provisioned, but sealed without an egg, is noticeably larger in the winter broods. Since we found in a previous chapter (see p. 47) that the large nests were no more likely than the small ones to be affected thus, we cannot attribute this difference to the smaller summer nests. It might be, however—this is mere conjecture—that a part at least of the winter nests are constructed by the wasps late in the fall, in their feeble old age, and hence a larger proportion of these eggless cells might occur than in the nests built by the vigorous young mothers early in the season. In other words, this kind of failure might be attributed to some real physical inability of the parent, and not to mere carelessness or faulty instinct.

The next five groups are surprisingly similar, down to the number of larvae which died of starvation, which is 1 or 2 per cent. in all broods. Hence we have every reason to believe

that the mothers' habits or instincts relative to nest-building are fairly constant at all times.

In the group of those which died as larvae amid plenty of food, the death-rate runs higher among the winter brood than in the summer brood. At present I see nothing to account for this unless it be that the cold of winter caught a few which had not yet pupated. However, the per cent. is so small in both cases that the difference might be little more than mere chance.

Those which died as prepupae show even a more marked difference, 24 and 17 per cent. against 10 per cent. Now this is the stage in the insects' development which is greatly prolonged in the winter brood to cover the period of dormancy. Also it is the stage wherein the insects pass through the winter cold and may succumb to it. Both of these factors cause the probability of fatality to increase. But when we turn to the pupal and adult stages, which are very similar in duration and conditions in the two broods, we again find the per cents of mortality practically identical.

The greatest difference of all occurs in the proportion of young wasps killed by parasites (or riddled by them after their death from other causes. *Melittobia* had infested 34 per cent. of the Kansas winter brood, and 22 per cent. of the Meramec Highlands lot, while it had reached only 7 per cent of the summer lot. This is probably due to the prolonged period of exposure to chance of attack during the prepupal stage. *Anthrenus* was somewhat more destructive in the summer brood.

Hence, we see that practically the whole difference in the mortality in the two broods occurs in these three groups which we have pointed out, where the mothers late in the fall failed to deposit eggs in the cells, where the young died in the prolonged prepupal stage, and where they were the victims of parasites

But this does not end the problems of regeneration of these species. Some large factor is as yet undiscovered. Let us first look at the winter crop of nests. If we may assume that each nest stands for one mother, then the 643 females gave to the next spring's population only 172 new wasps. Now supposing one half of these were males, then the task of keeping up the stock is left to 86 females. If they in turn build nests and

produce a summer brood in the same proportions as the summer brood which we have just analyzed, then these 86 females will in turn produce 172 new young wasps, males and females. Hence the summer brood, by far the more thrifty of the two, can barely reproduce its population without any increase, and that only if we allow nothing at all for the death of the adults as they work in the fields, or for the utter destruction of the nests by man, etc. So if this rate of elimination were typical, (even without, as just mentioned, any elimination in free adult life), the species in this locality could continue for only four years, by which time it would be exterminated. Or if we take the Meramec Highlands winter population as typical, this extermination would go on as surely, although more slowly. But we know that these species have continued abundant in these regions for a great number of years. So how is the population maintained? Is there still another brood or two each year, besides those two here analyzed?[22] If so, they must be very prolific to replenish the fast diminishing stock. Some explanation must still be advanced to account for the presence and continuance of this large population here. Of course it may be that for some reason our samples are not typical of what regularly occurs in the population. Every care was taken to avoid any injury or abnormal exposure of the material at any time. Since I know of no work similar to this, we can only look to future investigations for comparative data to determine whether these were in all ways typical samples. Of course the two populations came from different localities, but they are so near and so similar in climatic conditions that I can scarcely believe that the differences of locality would cause such different results.

THE CONTENTS OF THE PIPE-ORGANS, THE NESTS OF
TRYPOXYLON ALBITARSIS

The pipe-organ nests are not so abundant in the vicinity of St. Louis as are the clustered mud cells. This chapter deals with these nests gathered in the early springs of 1912, 1913 and 1914. The data for the three years represent 1,282 cells. Since many of the nests were broken in transporting them home, we shall study each season's lot separately in considering the contents, but for the data of the number of cells in each nest,

---

[22] Ent. News. Vol. XXVI, p. 469-471.

we shall select the complete ones from the entire series.   These
43 nests were of the following sizes:

No. of cells to nest	Frequency	No. of cells to nest	Frequency
42	1	13	1
27	1	12	4
26	1	11	3
25	2	10	2
22	1	9	2
19	1	8	1
18	3	7	2
17	1	6	2
16	3	5	3
15	3	4	2
14	2	3	2

This series shows no pronounced mode. The nests were
gathered in the winter, hence we have reason to believe that
they were as nearly complete as were available. It may be,
however, that the population of mother wasps which constructed
these nests included old wasps which may have worked all
summer on the nest, as well as newly hatched ones which had
only a short time in which to build a few cells before being over-
taken by winter.

The contents of all these cells were recorded. In addition,
the broken nests were likewise examined and tabulated; these
made 709 more cells. The table below is a summary of the
data of these three annual collections, comprising 1,282 cells.

Year	Total No. of cells	No. of cells giving good adults	No. of cells sealed with food no egg	No. of cells sealed empty	No. of cells unsealed with food	No. of cells unsealed and empty	No. of cells having dead larvae with insufficient food	No. of cells having dead larvae with sufficient food	No. of cells with dead prepupae	No. of cells with dead pupae	No. of cells with dead adults	Parasitized by Melittobia	Parasitized by Anthrenus	Cells having other parasites	Per cent of cells that gave good adults
1912	552	447	51	15	..	..	2	18	1	1	6	..	2	4, O 5, D	81%
1913	203	112	15	11	1	2	2	1	12	10	1	17	12	7, D	55%
1914	527	413	60	1	..	..	..	1	24	1	6	9	..	7, O 5, D	79%
Total	1282	972	126	27	1	2	4	20	37	12	13	26	14	28	76%

How cheering it is to find that 972 of these, or 76 per cent. gave forth good adults in the spring after wintering in the cells. In 126 cases (10 per cent.) did the mothers err in filling the cell or fail to oviposit; 27 cells (2 per cent.) were sealed empty, but in some of these cases the sealing partition was so placed that the room was so small that a growing larva could not possibly have had room to develop anyway. We have never yet noticed *Sceliphron* committing this blunder of constructing her cells too small to permit the full development of her young. There was only one cell that was unsealed containing a few spiders; this case may well have been due to the sudden death of the mother. In only 4 cases can death in the larval stage be attributed to insufficient food, while 20 others died in the larval stage despite the fact that much food remained untouched in their respective cells.

The deaths in the prepupal, pupal and adult stages were 37, 12 and 13 respectively, lower per cents than occurred in the other species.

These insects were preyed upon by some of the parasites of *Chalybion* and *Sceliphron* but not to so great an extent; 26 cells were parasitized by *Melittobia* and 14 showed that the *Anthrenus* beetle had played havoc; 28 cells were divided between a Dipterous parasite and an Ichneumon belonging to the tribe Ophionini, indicated in the table by "D" and "O."

Thus elimination in all the stages of development is far less in *T. albitarsis* than in the other species.

So here we have three species so similar in morphology that we cannot discern any differences which would give one or the other the least advantage in the struggle for existence. Likewise their life history, their habits of living and their habits of nesting are so similar that it would appear to us that they have equal chances of surviving. And yet there exists this remarkable difference in the survivability of these species, and even more strange it is that the species which has the fewest numbers in this vicinity is the one which thrives far better than the others. Had the variation studies, for which the material was first intended, been carried to a conclusion, we *might* thereby have located some tendencies which would account for the comparative vigor or weakness in these species, but I think it more than likely that in pursuing variation problems

purely, we would have been sidetracked on some feature of the insect's anatomy which is entirely irrelevant to its ability to work out its own salvation. But if now the variation studies could be taken up in the light of the preceding paragraphs, they might lead us to profitable problems of the existence or nonexistence of correlation between variation and elimination, or in other words, to add one more word to the hypothesis of selective elimination.

THE IMPORTANCE OF PRIMACY IN THE LEARNING OF A PIG

GARRY C. MYERS

Brooklyn Training School for Teachers

During the summer of 1911 the writer performed some experiments on an eight-week old pig. While there are many obvious imperfections in the experiments the records emphasize an important aspect in the learning process, namely, the tendency of the first of a series of habits to possess a relatively high persistency.

The apparatus was very simple. When not fed the pig was shut in a pen X from which a door Y led into a lane L 23 feet in length. Near the end of the lane was an opening O which led into the general pen P whose measurements were 10 x 12 feet. Five feet from either side of P was a board K 7 inches high, parallel to the lane. This board was so high that the pig could not naturally see over it. In either of the corners of P farthest from O and equally distant from it was placed a food receptacle which could be transferred from one corner (A) to the other corner (B).
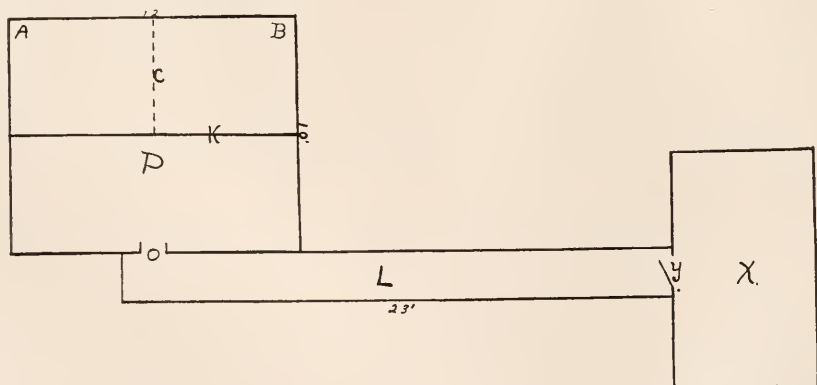
In the first instance the pig was released at Y and found his way into A where he soon found the food, morning noon, and

evening of the first day.   On the second and third feedings he
ran directly to A without hesitancy.   Each time, as soon as his
meal had ended, he was shut up in X.

The food always, was put into the receptacle before the pig
was released so that he could not see it until he had crossed K.

Second Day

Fed every 2 hours.   Food was put regularly into B.

First feeding.   When released the pig ran directly to A as
on the first day, not finding food he rambled about much dis-
turbed for several minutes.   Finally he ran a little farther to
the right than before and found the food at B.

Second feeding.   The same procedure as in the first, but in
about half the time.

Third feeding.   He ran as before, directly into A; then
immediately to B.

Fourth feeding.   Same as third feeding, but in less time.
Each time when he had consumed the food at B he would return
to A looking for food there.   He was never fed to satiety.

Fifth feeding.   Before he was released, a partition C, 8 inches
high was placed mid-way between the two feeding places.   He
entered the A side directly then, with almost no hesitancy,
jumped over the partition toward B.   There he was so dis-
turbed he did not get the food at B but jumped out over K.
After a number of quick false movements he jumped back over
K to B and ate the food.   There was no more running to A
after the food was eaten.

Sixth feeding.   Jumped directly into the A side, came out
over K and with no false moves turned to the right and jumped
over K to B.

Seventh feeding.   Same as sixth.

Third Day (Still fed at B)

First feeding.   He made a bee-line from O to A, back over
K, to the right, and to B over K.

Second feeding.   He made a bee-line for A but only raised
his head and looked over K, paused a few moments, turned
and jumped over K near partition, into B side.

Third, fourth, and fifth feedings.   Made a bee-line from O
to B.

Fourth Day

He was fed only three times, morning, noon and evening, when he always made a bee-line from O to B.

Fifth Day (Feeding place changed to A)

First feeding. He made a bee-line for B, searched for food with restless movements, jumped out over K, then scarcely moving to left at all, jumped over K to A.

Second feeding. He jumped into B, then with practically no pause, over partition to A.

Third feeding. Started for B side, but looked over, paused, then into A. In going to B side, however, his pathway diverged a little toward the partition, a decided modification of old pathway from O to B side.

Fourth feeding. Same as third but divergence greater, i. e., nearer partition.

Fifth feeding. He ran directly toward A side but very close to partition, paused without looking over, and jumped directly into A side.

Sixth and Seventh feedings. Made a bee-line to A.

Sixth Day (Feeding place changed to B)

First feeding. He made a bee-line to A but jumped over partition quickly to B, as if planned, with no appreciable pause. Now another board of 6 inches was added to partition C, making it 14 inches high.

Second feeding. He made a bee-line to A but this time he came out of A over K, then to right into B side.

Third and fourth feedings. Same as second.

Fifth feeding. In bee-line to A side but near partition looked over, then turned and jumped into B.

Sixth feeding. He ran directly into B side, but near partition. No pause.

Seventh Day (Morning. Feeding place changed to A)

First feeding. He ran in a bee-line into B out over K, and into A.

Second feeding. He ran directly to B side near partition looked over and very quickly jumped into A.

Third feeding. Bee-line to A.

Seventh Day (Afternoon.   Feeding place changed to B)

First feeding.   He ran directly to A looked over cautiously, then jumped into B.

Second feeding.   He ran to B side, near partition, looked over and jumped into B side.

Third feeding.   Directly over B side near partition.

Fourth and fifth feeding.   Same as third.

Sixth and Seventh feedings.   Bee-line from O to B.

Eighth Day (Morning.   Feeding place changed to A)

First feeding.   In bee-line toward B, looked over K, and put fore feet over K, then drew back and jumped into A.

Second, third, fourth, and fifth feedings.   Bee-line from O to A.

Eighth Day (Afternoon.   Feeding place changed to B)

First feeding.   Bee-line for A, quickly out and into B.

Second feeding.   Directly to A side, looked over, then into B.

Third feeding.   Same as second.

Fourth feeding.   Directly to B side near partition and into B.

Fifth feeding.   Bee-line from O into B.

The following figures show the number of times the pig was fed A and B respectively and the number of right and wrong trips to each.

	No. times fed in A	Wrong trips to A	No. times fed in B	Wrong trips to B
First Day.....................	3	0	0	0
Second Day...................	0	7	7	0
Third Day....................	0	2	5	0
Fourth Day...................	0	0	3	0
Fifth Day....................	7	0	0	4
Sixth Day....................	0	5	6	0
Seventh Day (Morning).........	3	0	0	2
Seventh Day (Afternoon).......	0	1	7	0
Eighth Day (Morning)..........	5	0	0	1
Eighth Day (Afternoon)........	0	3	5	0
	18	18	33	7

While in all, the pig was fed 18 times in A and 33 times in B, he wrongly entered B (i. e. when the food was placed in A), 7 times and wrongly entered A 18 times or, 33.3 per cent. and 54.5 per cent of the responses, respectively, were wrong.

It took only the first feeding to establish a direct pathway from O to A, but after two repetitions of this trip it took ten

trials before the subject learned to go directly from O to B. After going directly to B three successive times it took only five trials to learn to go directly from O to A again. To make the next transition of the pathway (from OA to OB) it took six trials. Hence, while primacy tends to persist throughout it decreases somewhat with time.

The modification in the learning is worthy of note. The excited, random movements so obvious in the earlier new situations which successively appeared with the alternation of feeding places, decreased as the experiment progressed. On the other hand the responses to the later situations were characterized by hesitancy and by attempts to use the eyes to help determine, before jumping over the board K, which was the right way to go. To illustrate, on the twelfth feeding which was the second feeding of the third day, after having gone from A to B eight successive times, he paused at K at a point on a straight pathway to A from O, raised his head high enough to look over K, then turned and jumped over K near the partition into the B side. Likewise at the third and fourth feeding of the fifth day, after making two wrong trips to B, he paused at K, looked over and turned and jumped into A. His pathway, moreover, instead of being in a straight line from O to B diverged a little toward the partition, and on the succeeding trip diverged still more, so that the next time he jumped directly into the A side but near the partition. At the fifth feeding of this same day, instead of looking over K, he ran to it in line with A, paused, and jumped into the A side. These gradually shifting pathways seem to indicate the resultant of two antagonistic impulses. It must be remembered here that although the subject often took the wrong pathway from O, eventually he always found the food; but in finding the food after first entering the wrong side the subject never went back to O for a new start, but sought the food by the shortest way he could find from where he was. No doubt the transitions from one pathway to another, from O, could have been completed with fewer errors if the corrections could have been made from O. Even then, theoretically, there would have been some tendency to make the wrong trip again and to return to O rather than to go to the food directly. In any event, the mere recency of the appeal of the stimulus where it once was, does not so much account for the tendency to con-

tinue to take the wrong pathway as the persistency of the impulse to go from O by the pathway that last was successful from O to the food. It is interesting to note that the pathway taken at the first feeding of each morning was always the same as the pathway taken last on the previous day.

An example from the writer's experience of an attempt to break a certain habit of forgetting may help explain the principle involved. On two successive evenings he forgot to extinguish the gas light in the cellar after he had made the fire. On the third evening as he closed the cellar door behind him, on entering the kitchen he remembered that he had left the light burning and he at once returned to extinguish it. For about a score of evenings he went through exactly the same process of forgetting and correcting. Just as soon as the thought of the light suggested itself when the fires had been made, the proper reaction to the light was elicited. Again, it is not so much the attraction of a stimulus that determines a certain reaction as it is the precedence and strength of that reaction to that stimulus.

The results of this experiment are significant in showing the tremendous force and persistency of the first of a series of habits. Of course humans are not pigs but fundamentally the methods of learning for pigs and people are about the same. Therefore, these records suggest the gravity of the "first impression," and emphasize the importance of correct reactions at the outset in any kind of learning.

It is to be regretted that the time for each reaction was not recorded and that some device was not provided whereby the exact part of K over which the pig jumped in his search or the food could be determined, and that the experiment was not continued for a much longer time. While these results are not at all conclusive they probably suffice to warrant further study along the same lines on small children as well as on animals.

THE MARRIAGE-FLIGHT OF A BULL-DOG ANT
(*MYRMECIA SANGUINEA* F. SMITH)

WILLIAM MORTON WHEELER

During a recent visit to Australia I had an opportunity to study in the field the habits of a number of species of the large ants popularly known as "bull-dog ants," belonging to the very primitive genus *Myrmecia*. This genus comprises some sixty described species, subspecies and varieties, all confined to Australia and the island of New Caledonia. They bear about the same relation to the more specialized and more modern ants that the Marsupials of Australia bear to the placental mammals of other continents. Many of the species are among the largest of ants, several of them are beautifully colored and sculptured, and all of them sting or both sting and bite severely. In his latest work on the Ponerinae in the "Genera Insectorum" Emery divides the genus *Myrmecia* into three subgenera, *Myrmecia* sens. str., *Pristomyrmecia* and *Promyrmecia*. I have found that the species of these three groups differ greatly in nesting and other habits. A detailed account of my observations will be published later in connection with taxonomic descriptions of the various forms. Here my remarks will be mainly confined to one of the largest and most aggressive species, *Myrmecia sanguinea* F. Smith, an ant which must be widely distributed in Australia, since it has been recorded from Queensland, New South Wales, South and Western Australia and Tasmania. I found it very abundant at Salisbury Court, near Uralla in northern New South Wales, where, through the courtesy of the government entomologist, Mr. W. W. Froggatt, I was able to spend a few days at a laboratory recently established for the study of the blow-flies that have acquired the unfortunate habit of injuring living sheep.

In the open forest surrounding the laboratory there are many large nests of *sanguinea*, mounds of earth of a more or less conical shape, varying from three to five feet in diameter at the base and one to two feet in height. The surfaces of these

mounds are covered with a thin layer of bits of charred wood, dead leaves, twigs and pebbles collected by the ants. The entrance to the nest is a rather small hole, scarcely more than half or three quarters of an inch in diameter and usually situated on one of the slopes near but not at the summit.

Each nest contains about 200 to 500 workers. These are subopaque, rich brownish red in color, with the gaster shining black, and vary considerably in size, from 12 to 28 mm. The females measure 26 to 28 mm., the males 18 to 20 mm. The smallest workers, not exceeding 12 to 15 mm. in length, function as door-keepers and are usually found stationed just within the nest-entrance, with their long, scissor-like mandibles directed outward. When the nest is disturbed these small workers are the first to sally forth, followed by others of the same or medium size, and it is only somewhat later that the huge and formidable individuals, measuring 25 to 28 mm. advance to the attack with wide open jaws and threatening sting. This behavior is the reverse of that observed in other ants (e. g. in species of *Camponotus*, *Colobopsis*, *Atta*, *Pheidole*, etc.), the major workers or soldiers of which act as door-keepers and are among the first to rush to the defence of the colony. Unlike the puny, small-eyed ants of our northern latitudes, the bull-dogs can clearly discern objects at a distance of several feet with their great, prominent, abundantly facetted eyes. They lose no time in running about in all directions hunting for the intruder, but with ferocious unanimity make directly for him. The extraordinary tenacity with which they hold on with their mandibles to any moving object that comes in their path is, of course, responsible for their popular name, but no one has been able to suggest a polite epithet that will do justice to the virulence of their sting.

At the time of my visit to Salisbury Court, during the last week of November, there were no winged males or females in the nests, though there were plenty of larvae and a small number of worker pupae. This is rather surprising because the sexual forms of most of the ants of New South Wales are to be found in the nests during late October and early November. Mr. Froggatt expressed the opinion that the males and females of the various species of *Myrmecia* do not mature till January. This opinion has been confirmed in a letter recently received, in which he describes a remarkable marriage flight of *sanguinea*

in a locality very near the one in which I studied the nests. Fully to appreciate his description, the reader must bear in mind what I have said about the size of the females of this ant. They, of course, have powerful stings, like the workers, though the males are stingless and have feeble mandibles. Mr. Froggatt's account runs as follows:

"On January 30th, after some very hot, stormy weather, while I was at Chevy Chase, near Armidale, N. S. W., I crossed the paddock and climbed to the top of Mt. Roul, an isolated, flat-topped, basaltic hill, which rises about 300 feet above the surrounding open, cleared country. The summit, about half an acre in extent, is covered with low "black-thorn" bushes (*Busaria spinifera*). I saw no signs of bull-dog ant nests till I reached the summit. Then I was enveloped in a regular cloud of the great winged ants. They were out in thousands and thousands, resting on the rocks and grass. The air was full of them, but they were chiefly flying in great numbers about the bushes where the males were copulating with the females. As soon as a male (and there were apparently hundreds of males to every female) captured a female on a bush, other males surrounded the couple till there was a struggling mass of ants forming a ball as big as one's fist. Then something seemed to give way, the ball would fall to the ground and the ants would scatter. As many as half a dozen of these balls would keep forming on every little bush and this went on throughout the morning. I was a bit frightened at first but the ants took no notice of me, as the males were all so eager in their endeavors to seize the females."

Except for the great size of the participants, this nuptial flight presents an exact picture of occasional flights of some of our common Myrmicine ants, especially of *Myrmica scabrinodis* Nyl. That such enormous swarms of *Myrmecia* as the one described must be of rare occurrence, is evident from the statement of such a keen observer as Mr. Froggatt that he has "never before seen more than a dozen winged bull-dog ants of any species together." I find, however, a brief description by Tepper[1] of what must have been a very similar scene. He describes a nuptial flight of one of the large species of *Myrmecia*

[1] Observations about the Habits of Some South Australian Ants. *Trans. & Proc. Roy. Soc. S. Austr.*, **5**, 1882, pp. 24-26, 106-107.

(probably *sanguinea* or *pyriformis*), early in April in South Australia, as "rather a formidable affair, owing to many hundreds of the large creatures (the female above an inch in length while alive) flitting about one's head, all armed with a sting about a quarter of an inch in length, while the shrubs near the nest were covered with scores of pairs and single ones."

The observations of Tepper and Froggatt prove conclusively that the species of the Ponerine genus *Myrmecia* celebrate a regular marriage flight like all the ants of the other taxonomic subfamilies, except the species with wingless males or females, and that these flights occur during January in northern New South Wales or a few months later in the more southern and colder portions of Australia. This season corresponds, of course, to our autumn months, which are likewise the nuptial season of some of our species of *Lasius* (*L. claviger* Roger, *brevicornis* Emery, etc.) We may also infer from the accounts of the two Australian observers that each female *Myrmecia*, after fecundation, loses her wings in the same manner as other ants, except certain parasitic species, enters the ground and establishes a small colony without the assistance of workers of her own species. I am able to show that this is actually the case. On September 19, 1914, I found under a stone in one of the deep sandstone canyons near Katoomba, in the Blue Mts. of New South Wales, a fine deälated female of *Myrmecia tricolor* Mayr occupying a little cavity in the soil and engaged in caring for about a dozen small larvae. This little incipient colony was very similar to those just established by our common carpenter ants (*Camponotus pennsylvanicus* DeGeer and *noveboracensis* Fitch) under the bark of old logs. That the most primitive of existing ants should found their colonies in precisely the same manner as the most highly specialized species, is not without interest.

JEAN-HENRI FABRE

William Morton Wheeler

Through the death of Jean-Henri Fabre on October 11th, 1915, the world has lost its greatest entomologist, a man who combined in an extraordinary degree the gifts of a virile and penetrating observer and those of a literary artist of high distinction. During the greater portion of a life of poverty, extending over a period of 92 years, he ceaselessly devoted himself to an intensive study of insect behavior and to the recording of his observations in such fascinating language that Victor Hugo styled him the " Homer of the insects."

Like the life of his countryman Latreille, who preceded him as the " prince of entomologists," Fabre's life was uneventful. His biography has been written by a sympathetic admirer, C. V. Legros, and rendered into English by another admirer, Bernard Miall, but from many passages scattered through Fabre's great work, the " Souvenirs Entomologiques " it is possible to glean an even more illuminating and intimate knowledge of his powerful individuality and of his methods of working and thinking. He was born of humble peasant parents on December 22nd, 1823, in the hamlet of Saint Léon, in the part of the Provence known as the Haute-Rouergue. Through diligent application to the classics, physics, chemistry and mathematics in the rather mediaeval schools of his day he prepared himself to become a teacher. At 19 he entered on this profession in the College of Carpentras and in 1850 accepted a position as professor in the lycée of Ajaccio, Corsica, at a salary of £72. Here he met the naturalist Moquin-Tandon, who seems to have had an important influence in determining his career as a biological investigator. Even as a boy, however, Fabre had been greatly interested in insects, so that Moquin-Tandon probably only helped to reveal to him his innate aptitude for observation and experimentation. He realized that he had a genius for observing small animals, and from that time forth,

like Socrates, he implicitly obeyed the voice of his daemon almost to the hour of his death. Falling ill with malaria at Ajaccio he was compelled to return to France, and in 1853 was appointed assistant professor of physics at the lycée of Avignon. This post he held for nearly 20 years (till 1871), without advancement, and with a salary not exceeding £64! During this period he made some of his most important observations. The written accounts of his work, contributed to the "Annales des Sciences Naturelles" include a study of the habits of the solitary wasp *Cerceris* and of the cause of the long conservation of the beetles on which it feeds (1855), notes on the life-history of *Cerceris*, *Bembex* and *Sitaris* (1856), followed by his classic memoir on the hypermetamorphosis and habits of *Sitaris* (1858) and studies on the rôle of adipose tissue in the urinary secretion of insects (1862).

In 1871 he left the lycée of Avignon to devote the remainder of his life to the study of instinct in insects. He moved to Sérignan, a hamlet near Orange, not far from Avignon. Here he lived henceforth and worked as a hermit and here he died, in a little cottage on a plot of ground called the " harmas," a beautiful description of which is given in the opening chapter of the second series of " Souvenirs." [1] During the early years of his residence at Sérignan he was compelled to devote much time to writing text-books on natural history subjects for the purpose of keeping the wolf from the door. It will probably be found that these little books were the forerunners of the modern " nature books." He also continued to contribute scientific articles to the " Annales des Sciences." Two of these, on the habits and parthenogenesis of some bees of the genus *Halictus* (1880) and one on the repartition of the sexes in the Hymenoptera (1884) are of unusual interest. But the great work accomplished at Sérignan is embodied in the ten volumes of the " Souvenirs." Anything like an adequate review of this monumental work would require much time and labor. Only the entomologist who has endeavored to work out complicated insect life-histories will fully appreciate Fabre's powers as an observer and will not be greatly surprised to learn that during the course of years he wore a groove in the stone floor of his

[1] Translated by A. T. de Mattos in the "Life of the Fly," Dodd, Mead & Co. 1913.

laboratory by walking around his table. The complete eluci-
dation of some of the life-histories, like that of the sacred scara-
baeus, required observations extending over a period of nearly
forty years.

The newspapers and magazines have made us familiar with
the romance of the closing years of Fabre's life. Mistral, the
Provençal poet, Maeterlinck and Rostand are said to have dis-
covered Fabre and to have called the attention of the world
to his destitute condition. According to a well-known French
magazine, "In 1910 he was revealed to the people; a group
of litterateurs and savants conceived the idea of offering this
modest, almost unknown man a plaque to perpetuate the memory
of his work. Two years later his ninetieth birthday was cele-
brated by a ceremony at which the Institut was represented,
and somewhat later the President of the Republic paid him a
visit." "Why," asks Le Gros at the close of his account of
the celebration of 1910, "at this jubilee of the greatest of ento-
mologists, was not a single appointed representative of ento-
mology present?" And he goes on to say: "The fact is that
the majority of those who 'amid the living seek only for corpses',
according to the expression of Bacon, unwilling to see in
Fabre anything more than an imaginative writer, and being
themselves incapable of understanding the beautiful and of dis-
tinguishing it in the true, reproached him, perhaps with more
jealousy than conviction, with having introduced literature into
the domains of science." This is an unfair statement of the
case. Fabre has long been known to naturalists and especially
to entomologists and many of them, from Darwin to the Peck-
hams and Forel have referred to his work in terms of the greatest
admiration. It is only the litterati and general public who have
just discovered Fabre, and it is not difficult to account for this
belated appreciation. Insects are so peculiarly organized and
offer to the casual observer so few points of contact with the
general trend of human interests that even the magic style of
a Fabre failed to elicit a widespread desire to know about their
activities. But when a great writer like Maeterlinck announced
that, "Henri Fabre is one of the greatest and purest glories in
the present possession of the civilized world, one of the most
erudite naturalists and the most marvellous poet in a modern
and truly legitimate sense of the word," and added that Fabre

was one of the profoundest admirations of his life, people who had never devoted five minutes of their lives to studying an insect, began to sit up and take notice.

Whenever there is complaint of the neglect of a genius by the world, it is well to scrutinize the behavior of the genius. If we do this in Fabre's case we shall have little difficulty in accounting for the neglect from which he suffered, both on the part of the general public and the scientific fraternity. Fabre and his publisher are undoubtedly responsible for much of the popular neglect. The title of the great work, " Souvenirs Entomologiques," is inept, to say the least; the ten volumes were unattractively printed and inadequately illustrated and the arrangement of the articles in the series might have been much better. All rights of translation, even of extracts, were, moreover, rigidly withheld till very recently. When Fabre became more generally known these faults were corrected by the publication of selected essays in more pleasing volumes and under more appropriate titles, such as " La Vie des Insectes " and " Moeurs des Insectes," an arrangement which has been followed in the English translations now displayed in all our bookstores.

The reserved and unsympathetic attitude of entomologists towards Fabre was very largely due to the fact that he was a crotchety and opinionated recluse, who seems never to have made the slightest attempt to enter into friendly personal or epistolary relations with other entomologists, who never mentioned and probably never read the work of his contemporaries, who lost no opportunity of holding up to ridicule some of the most important entomological studies, such as insect taxonomy, and who repeated investigations that had been made by others, without intimating and evidently without knowing that such investigations had long been known to the entomological world. He failed to realize that entomologists are more human than the objects of their studies and that " wer Liebe ernten will, muss Liebe säen." It is not surprising, therefore that there was no afflux of entomologists to Sérignan to celebrate his jubilee. While their presence might have been commendable, we can hardly blame them, under the circumstances, for staying at home.

Another reason for the attitude of entomologists towards

Fabre is to be found in his peculiar views concerning instinct, views that were prevalent enough in the early part of the nineteenth century but are singularly foreign to the psychology and theoretical biology of the present day. He not only declined to accept the doctrine of evolution but vigorously attacked it in more than one of his essays, although many of his criticisms so far overshoot the mark that one reads them with amazement. It must be remembered, of course, that Fabre was nearly 36 years old when the "Origin of Species" appeared. He was not, therefore, like the naturalists of the present generation, suckled, so to speak, at the breasts of evolutionary doctrine, and his life-long lack of contact with biological speculation kept him from viewing the phenomena of instinct from a genetic standpoint. But even in his chosen field, the study of instinct, he confined himself to a comparatively circumscribed group of phenomena. He worked only on a series of insects selected from his immediate environment and for certain peculiar reasons took little interest in the social species, (ants, social bees and wasps) which are, nevertheless, abundant in southern France. His studies on these forms are limited to an essay on the amazon ant (*Polyergus ·rufescens*) and a few essays on wasps (*Vespa vulgaris*). He seems to have borne a grudge against the ants because they so often entered his breeding cages and killed the insects with which he was experimenting. There were also other and more weighty reasons for this neglect of the very insects which naturally suggest a genetic interpretation of instinct. Fabre believed that instinct manifests itself in its purest form in the solitary species. He was, moreover, greatly impressed by its fixity and mechanical aspect, and his rigid training in physics, chemistry and mathematics and his keen analytical ability probably biased him in favor of views which have grown more and more repugnant to modern biologists. He had a strong tendency to schematize his observations and to ignore the variability of instinct. This tendency has been pointed out by several observers and is most clearly marked in his classic work on the solitary wasps.

Although Fabre suffered in the estimation of many biologists on account of the theoretical views which he elaborated and very stubbornly upheld through the course of a long life in voluntary isolation from the great current of biological thought,

we are bound to confess that in some very important matters his vision was clearer than that of his contemporaries. He alone realized the great significance of the study of animal behavior at a time when other biologists were absorbed in purely morphological work. No better proof of this statement can be given than the concluding paragraphs of the first essay in the second series of the " Souvenirs " published in 1882. I quote from de Mattos' translation (pp. 26 and 27): " Laboratories are being founded, at great expense, on our Atlantic and Mediterranean coasts, where people cut up small sea-animals, of but meagre interest to us; they spend a fortune on powerful microscopes, delicate dissecting instruments, engines of capture, boats, fishing crews, aquariums, to find out how the yolk of an Annelid's egg is constructed, a question whereof I have never yet been able to grasp the full importance; and they scorn the little land-animal, which lives in constant touch with us, which provides universal psychology with documents of inestimable value, which too often threatens the public wealth by destroying our crops. When shall we have an entomological laboratory for the study not of the dead insect, steeped in alcohol, but of the living insect; a laboratory having for its object the instinct, the habits, the manner of living, the work, the struggles, the propagation of that little world, with which agriculture and philosophy have most seriously to reckon ?

" To know thoroughly the history of the destroyer of our vines might perhaps be more important than to know how this or that nerve-fibre of a Cirriped ends; to establish by experiment the line of demarcation between intellect and instinct; to prove, by comparing facts in the zoological progression, whether human reason be an irreducible faculty or not; all this ought surely to take precedence of the number of joints in a Crustacean's antenna. These enormous questions would need an army of workers, and we have not one. The fashion is all for the Mollusc and the Zoophytes. The depths of the sea are explored with many drag-nets; the soil which we tread is consistently disregarded. While waiting for the fashion to change, I open my harmas laboratory of living entomology; and this laboratory shall not cost the ratepayers a farthing."

Not only was Fabre the first to realize the full importance of a scientific study of animal behavior but he was the first

consistently to apply the experimental method to the investi-
gation of the animal mind. The " Souvenirs " abound in ac-
counts of experiments, performed for the purpose of elucidating
the nature of instinct, not the less illuminating and conclusive
because they were carried out with crude, home-made appa-
ratus. It is as instructive as it is humiliating to read his results
and to reflect on the mountains of complicated apparatus in
our modern laboratories and the ridiculous mice in the form
of results which only too frequently issue from the travail of
" research."

Another valuable service of Fabre consisted in his calling
attention to the fact that the applications of zoology to human
welfare must be based on an accurate knowledge of animal
behavior. This has been tacitly assumed by economic ento-
mologists, but neither they nor the modern behaviorists have
sufficiently emphasized the fact that we cannot hope to control
animal depredations or to compel animals to contribute to our
well-being and wealth without an exhaustive knowledge of such
apparently remote phenomena as the animal sensations, reac-
tions and instincts. Fabre is quite explicit in this matter.
Though he lived as a recluse from the scientific world, he re-
mained in intimate contact with the life of the Provençal peas-
ant and had no doubts concerning the important bearing of
his own work on such a fundamental industry as agriculture.

FINANCIAL STATEMENT FOR THE JOURNAL OF ANIMAL BEHAVIOR,
DECEMBER 2, 1914 TO DECEMBER 1, 1915 (VOLUME 5)

RECEIPTS

Balance from 1914.......................	$191.88	
Receipts from sales of complete volumes and odd numbers...........................	719.75	
Receipts from advertising.................	25.00	
Gifts and contributions toward the cost of illustrations and tabular material.........	292.00	
Interest...............................	19.41	
From Behavior Monographs for office expenses, etc............................	75.51	$1,323.55

EXPENDITURES

Cost of manufacturing and distributing volume 5................................	$1,111.41	
Office expenses, including postal and express items................................	208.00	1,319.41
Balance on hand.....................		$4.14

THE REACTIONS OF NECTURUS TO STIMULI RECEIVED THROUGH THE SKIN

MARY HONORA SAYLE

University of Wisconsin

CONTENTS

INTRODUCTION

The mud puppy, *Necturus maculosus* (Rafinesque), of the fresh waters of North America has long been of interest on account of its primitive structure and its systematic position near the base of the amphibian line, but its reactions have been little studied.

For over two centuries it has been known that fishes possess various highly specialized sense organs in the skin, and later work along this line has been done by Herrick ('03), Parker ('09, '10), Sheldon ('09), and Reese ('12). During recent years the reactions of amphibians have been studied by Torelle ('03), Parker ('03), Cole ('07), and others, but upon Necturus very little has yet appeared. Reese ('06), and Pearse ('10) have worked upon the reactions of Necturus to light and heat. Reese

found that though all parts of the body could be stimulated by white light, the head was the most sensitive region. He also worked with light passed through "red" and "blue" glass, and found that slow responses were thus induced. In his heat experiments he found Necturus to be sensitive to considerable changes in temperature. Pearse showed that Necturus is negatively phototropic and that it comes to rest in shaded areas. Both the skin and eyes act as photoreceptors, and the stimulation of either brings about negative reactions.

The present study endeavors to ascertain the sensitiveness of the general body surface of Necturus to touch, chemicals, heat, and light.

The experiments were performed on four individuals of average size, though only three of them were used for the light and heat experiments. Just before each experiment the individual to be used was transferred from the aquarium tank into a zinc tray, three by one and one-half feet. The transfer was made by grasping each animal just behind the front legs. The method of measuring movement employed in the experiments was a rather simple one. A coarse wire screen that covered the tray was divided off with twine into inch squares. It was possible in this way to observe and at the same time measure the movements of Necturus beneath the screen.

When not being used for the experiments the animals were kept in running water in an aquarium tank, six by three feet, in the vivarium of the Biology Building, University of Wisconsin. The tank was divided into four compartments, one for each animal. Bricks and strips of wood were used to make suitable dark nooks like the natural haunts of Necturus.

This work was accomplished under the direction of Professor A. S. Pearse, for whose helpful suggestions and encouragement it gives me great pleasure to express my appreciation.

REACTIONS TO TOUCH

The whole outer surface of Necturus is open to stimulation from a deforming pressure, that is, it is sensitive to touch. Animals were tested for touch sensitiveness with wood, glass, and a soft brush.

A blunt piece of wood the size of an ordinary pencil was touched gently to various regions of the body. When any

portion was stimulated, there was a forward movement of two or three inches. The nostrils, gills, and tail were the most sensitive regions. Stimulation with a glass rod induced similar reactions as were noted for wood. Stimulation with a soft brush, however, induced no locomotion. The tail and feet were drawn close to the body when stimulated; the gills closed, and when the nostrils were touched with the brush, there was at first a backward jerk, but further stimulation produced no reaction.

In stimulating the ventral side of the body, the mouth region and the tip of the tail were found to be most sensitive. When either of these regions was touched, locomotion followed, but the response was slow. The gills and feet upon stimulation were drawn close to the body. No other regions of the ventral side were sensitive.

Experiments were next performed to ascertain if the nerve endings fatigued by chemical stimuli would react to tactile stimuli. Necturus was stimulated over its entire body with ten per cent hydrochloric acid until it ceased to respond. A blunt point was then used to induce tactile response, but very little reaction followed. The same experiment was tried after sulphuric and nitric acid of the same strength. It was found that there was more response to tactile stimulation after Necturus was fatigued by hydrochloric than after sulphuric or nitric acids.

In performing the touch experiments several points worthy of note were observed:

1. Necturus is nowhere as sensitive to a blunt as to a sharp instrument.

2. When the mouth region was stimulated the head was jerked backward.

3. The regions of greatest sensitiveness are the nostril region, gills and tail.

4. When the gills were touched their movement ceased, but when the wood, glass or brush was removed their motion went on at an increased rate.

5. When the tail was stimulated it was curled up. It was most sensitive at the tip.

6. When the hind legs were stimulated they were drawn backward under the body, while the front legs started to walk.

7. The dorsal region between the legs was the least sensitive of all.

REACTIONS TO CHEMICALS

For testing the effect of chemicals on the skin, the surface of the body of Necturus was divided into seven regions, selected mainly for the different responses that result from their stimulation. They were the regions of the nostrils, head, gills, pectoral girdle, pelvic girdle, back, and tail. With each solution used all the regions were tested with each concentration, and the time given for reaction was always the same, fifteen seconds. If no response was made during the period, it was recorded as no action. The location of the regions are shown in figure 1.
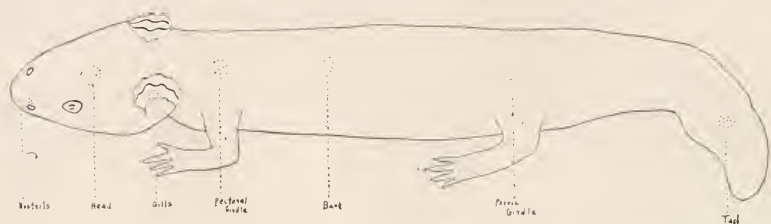
FIG. 1. Outline of *Necturus maculosus*, showing the regions stimulated in the experiments

The substances used in the work were hydrochloric, sulphuric, nitric and acetic acids; potassium hydroxide, ammonium hydrate, magnesium chloride, magnesium sulphate, alcohol and clove oil. In the experimental work all of these solutions were gradually diluted until the limit of reaction was reached. Sufficient time was given between tests at different degrees of concentration and with different substances to eliminate after effects.

The solutions were applied by means of a pipette and were ejected slowly with the tip of the pipette held about two millimeters from the skin. In all cases the animal was completely covered with water during the experiment.

(a) *The Reactions to Acids*

In tables I to XI are given the reactions of Necturus to the four acids used. Necturus responds to acid stimuli by locomotion or by a movement of the regions stimulated. If the acid is strong, locomotion takes place; if it is weak, local response

is induced.   Necturus is most sensitive to nitric acid at all
concentrations and hydrochloric gives the weakest response,
except acetic.   The reactions were found to become weaker and
fewer as the acid was diluted.   The gills were in nearly all
cases the most sensitive region, with the nostrils, head, and
tail following in order.   Stimulation of the nostril with a ten
per cent solution usually produced an expulsion of air from the
nostrils and mouth in addition to locomotion.   The limit of
reaction for hydrochloric, sulphuric and nitric acids was 0.015
and for acetic 0.01 per cent.

TABLE I*

REACTIONS TO 10% HYDROCHLORIC ACID

Individual No.	Nostrils	Head	Gills	Pectoral Girdle	Back	Pelvic Girdle	Tail
I	B 9	B F 14	X F 15	F 3	Squirm	Squirm	Switch tail F 9
II	B F 14	B F 15	X F 14	Squirm	Squirm	Squirm	Switch tail F 15
III	F 15	B 7	F 14	F 3	Squirm	Squirm	Switch tail
IV	B F 7	B 7 F 8	F 13	F 7	0	0	Switch tail F 17
Average	11.2	12.7	14	3.2	0	0	10.2

* *Explanation of the Tables.*—For convenience, several signs have been employed
in the tables.   They indicate as follows: F, forward; B, backward; X, animal
turned around; O, no reaction.   A letter not followed by a number indicates a
very slight movement, such as a jerk.   The numbers I, II, III and IV indicate
the four individuals under experiment.   The reactions are noted for seven regions
of the body, as indicated at the top of each table, making a total of twenty-eight
reactions of four individuals in each concentration.   The reactions are measured
as inches of locomotion, as described elsewhere, and the average is for total move-
ment, backward and forward, for each region stimulated.

.

TABLE II

REACTIONS TO 0.1% HYDROCHLORIC ACID

Individual No.	Nostrils	Head	Gills	Tail
I	B 1	B 2	F 14	0
II	B 4	B 2	F 14	F 6
III	B 3	B 2	F 12	0
IV	0	0	F 12	Switch tail
Average	2	1.5	13	1.5

TABLE III

REACTIONS TO 0.09% HYDROCHLORIC ACID

Individual No.	Nostrils	Head	Gills	Tail
I	F 2	Head moved	Head moved	0
II	B ¼	0	Head moved	0
III	F 3	Head moved	F 4	0
IV	F 4	F 3	F 3	Curled tail
Average	2.2	.75	1.7	0

TABLE IV

REACTIONS TO 10% SULPHURIC ACID

Individual No.	Nostrils	Head	Gills	Pectoral Girdle	Back	Pelvic Girdle	Tail
I	F 24	B 13	F 24	F 13	Switch body	Switch body	Switch tail F 10
II	B 2	B F 14	Moved in place	F 14	Switch body F 7	X	Tail curled
III	F 14	F 4	F 24	F 14	Switch body	F 14	F 14
IV	X F 15	B 15	F 14	F 10	F 10	F·7	F 12
Average	13.7	14	15.5	12.7	4.2	6.6	9

TABLE V

REACTIONS TO 0.1% SULPHURIC ACID

Individual No.	Nostrils	Head	Gills	Pectoral Girdle	Back	Pelvic Girdle	Tail
I	B 5	B 4 F 6	F 7	F 4	0	F 3	F 5
II	B 3	F 2	Head moved	B 2	0	Moved in place	0
III	B F 8	Moved in place	F 7	F 6	0	F 4	F 4
IV	B F 7	F 7	X	F 7	0	F 5	F 5
Average	5.7	4.7	5.2	4.7	0	3	3.5

TABLE VI

REACTIONS TO 0.09% SULPHURIC ACID

Individual No.	Nostrils	Head	Gills
I	B	F 3	F 3
II	B 1	0	0
III	B	F 2	F 2
IV	B 2	0	B 2
Average	.75	1.2	1.7

TABLE VII

REACTIONS TO 10% NITRIC ACID

Individual No.	Nostrils	Head	Gills	Pectoral Girdle	Back	Pelvic Girdle	Tail
I	B 4	F 10	F 22	F 16	F 14	F 14	Switch tail F 14
II	B 7	F 8	F 14	F 14	F 8	F 12	Tail curled
III	B 5	F 20	F 14	F 15	F 10	F 15	F 14
IV	B 5	F 15	F 22	F 10	F 8	F 10	F 14
Average	5.2	13.2	18	13.7	10	12.7	10.5

TABLE VIII

REACTIONS TO 0.1% NITRIC ACID

Individual No.	Nostrils	Head	Gills	Pectoral Girdle	Back	Pelvic Girdle	Tail
I	B 4 F 6	F 4	0	F 2	0*	0	F 3
II	B 4	F 4	F 7	F 2	F 1	F 5	F 6
III	B 3 F 10	F 6	F 10	F 5	F 3	F 3	F 4
IV	B 1 F 6	F 10	F 3	F 3	F 4	F 2	F 4
Average	8.5	6	5	3	2	2.5	4.2

TABLE IX

REACTIONS TO 0.09% NITRIC ACID

Individual No.	Nostrils	Head	Gills
I	B 2	Moved in place	F 5
II	B 2	Moved in place	F 6
III	B 3	0	F 4
IV	B 1	Moved in place	F 2
Average	2	0	4.2

TABLE X

REACTIONS TO 1% ACETIC ACID

Individual No.	Nostrils	Head	Gills	Pectoral Girdle	Back	Pelvic Girdle	Tail
I	B 3 F 5	B 1	F 6	0	0	0	0
II	B 3 F 6	F 3	F 6	F 3	0	F 1	Tail curled
III	B 2 F 12	B 2 F 6	B 6	B 6	0	F 3	0
IV	B F 14	F 10	F 22	F 10	0	F 4	Tail curled
Average	8.7	5.5	10	4.7	0	2	0

TABLE XI

REACTIONS TO 0.05% ACETIC ACID

Individual No.	Nostrils	Head	Gills
I	B 1	Moved head	F 2
II	B 2 F 3	F 1	Closed gills
III	B 1	F 2	F 1
IV	B 1	F 1	F 2
Average	2	1	1.2

(b) *The Reactions to Alkalies and Alkaline Earth Salts*

The reactions of Necturus to alkalies are given in tables XII-XV. Potassium hydroxide and ammonium hydrate did not produce as definite responses as did the acids. The different regions of the body varied in sensitiveness, but the gills were always the most sensitive region. The reactions of the gills to one per cent potassium hydroxide were greater than to ten per cent nitric acid, but the other regions of the body were less sensitive to potassium hydroxide or ammonium hydrate. The limit of reaction for both was a 0.01 per cent solution.

It is apparent from inspecting tables XVI-XIX that Necturus is more sensitive to magnesium sulphate than to magnesium chloride. The nostril region was the most sensitive to magnesium sulphate. At 0.05 per cent magnesium chloride the nostril region only was sensitive, while at the same per cent Necturus was sensitive to magnesium sulphate in the regions of the nostrils, head and gills. Necturus will not react to either chemical at 0.01 per cent.

TABLE XII

REACTIONS TO 1% POTASSIUM HYDROXIDE

Individual No.	Nostrils	Head	Gills	Pectoral Girdle	Back	Pelvic Girdle	Tail
I	Switch body F 14	B F 7	Switch body F 22	Switch body F 12	Switch body F 14	Switch body F 14	Switch tail
II	F 12	B F 7	Switch body F 22	F 7	F 9	F 9	Switch tail
III	B F 14	B F 12	Switch body F 22	Switch body F 12	F 9	F 12	F 12
IV	F 13	B F 8	Switch body F 14	Switch body F 10	F 8	F 7	Switch tail
Average	13.5	8.5	20	10.2	10	10.5	3

TABLE XIII

REACTIONS TO 0.05% POTASSIUM HYDROXIDE

Individual No.	Nostrils	Head	Gills
I	B 2 F 4	F 1	F 4
II	F 12	Moved in place	F 2
III	F 10	Head moved	Head moved
IV	F 6	F 5	F 7
Average	8.5	1.5	3.2

TABLE XIV

REACTIONS TO 1% AMMONIUM HYDRATE

Individual No.	Nostrils	Head	Gills	Pectoral Girdle	Back	Pelvic Girdle	Tail
I	X	B 6 F 4	F 20	F 4	F 6	F 7	F 5
II	F 9	B 2	F 6	F 5	F 2	F 10	F 10
III	F 12	B F 10	F 8	F 12	F 7	F 5	F 5
IV	F 10	X	F 12	F 12	F 7	F 8	F 10
Average	7.7	5.5	16.5	8.2	5.5	7.5	7.5

TABLE XV

REACTIONS TO 0.075% AMMONIUM HYDRATE

Individual No.	Nostrils	Head	Gills
I	B 2	X	F 2
II	B 2	F 2	F 1
III	0	0	0
IV	B 2 F 8	B 3	X
Average	3.5	1.2	.75

TABLE XVI

REACTIONS TO 2% MAGNESIUM CHLORIDE

Individual No.	Nostrils	Head	Gills	Pectoral Girdle	Back	Pelvic Girdle	Tail
I	F 14	F 10	F 22	F 8	F 8	F 6	F 7
II	F 9	F 14	F 10	F 10	F 5	F 5	0
III	B 2 F 6	F 12	F 18	F 8	F 3	F 7	F 10
IV	F 5	B 5	0	B 5	F 2	F 4	F 8
Average	9	10.2	12.5	7.7	4.5	5.5	6.2

TABLE XVII

REACTIONS TO 0.05% MAGNESIUM CHLORIDE

Individual No.	Nostrils
I	F 2
II	B 3
III	Moved head
IV	F 2
Average	1.7

MARY HONORA SAYLE

TABLE XVIII

REACTIONS TO 2% MAGNESIUM SULPHATE

Individual No.	Nostrils	Head	Gills	Pectoral Girdle	Back	Pelvic Girdle	Tail
I	F 22	F 7	F 6	F 5	X	F 4	F 3
II	B F 26	F 8	F 10	F 10	F 10	F 6	F 6
III	F 10	F 12	F 22	X	F 9	F 4	F 5
IV	B F 14	F 20	F 12	F 18	F 6	F 7	X
Average	18	11.7	12.5	8.2	6.2	5.2	3.5

TABLE XIX

REACTIONS TO 0.05% MAGNESIUM SULPHATE

Individual No.	Nostrils	Head	Gills
I	B 1 F 2	F 2	F 2
II	B 2 F 2	B 1 F 2	F 3
III	Moved head	Moved head	Moved head
IV	B 1	B 1 F 2	F 1
Average	2	2	1.5

(c) Reactions to Alcohol

A study was made of the reactions of Necturus to alcohol at fifty per cent and ten per cent. Tables XX and XXI show these reactions. There was no reaction with one per cent. When nostrils were stimulated with either of the effective solutions there was a greater response than with any other region

of the body.   The gills and head were less sensitive.   All regions responded when stimulated with a ten per cent solution and all regions except the pelvic and back were sensitive to ten per cent.   Necturus is less sensitive to alcohol than to any other chemical used, as indicated by the stronger solution necessary to induce reaction.

TABLE XX

REACTIONS TO 50% ALCOHOL

Individual No.	Nostrils	Head	Gills	Pectoral Girdle	Back	Pelvic Girdle	Tail
I	B 4 F 18	F 14	B 2 F 12	F 4	F 2	F 10	F 3
II	B 6	F 9	B 4 F 12	F 10	F 3	F 8	Tail curled
III	B 3 F 20	F 12	B 3 F 12	F 18	F 7	F 8	F 2
IV	B 1 F 10	F 12	F 12	F 10	F 5	F 7	F 7
Average	15.5	11.7	14.2	10.5	4.2	8.2	3

TABLE XXI

REACTIONS TO 10% ALCOHOL

Individual No.	Nostrils	Head	Gills	Pectoral Girdle	Tail
I	F 4	F 3	F 4	F 2	F 3
II	B F 10	F 8	F 7	F 5	F 4
III	0	0	0	0	0
IV	F 12	F 8	F 10	F 4	F 7
Average	6.5	4.7	5.2	2.7	3.5

(d) Reactions to Clove Oil and Turpentine

Drops of clove oil were ejected upon the skin of Necturus with no results, except a slight response in the region of the nostrils. When Necturus, however, raised its body out of the water and thus carried some of the oil upon its skin, every portion was sensitive.

Cotton was saturated with turpentine and applied to Necturus with no result, whether the animal was in or out of water.

(e) Summary of the Chemical Reactions

1. Necturus is more sensitive to nitric than to hydrochloric or sulphuric acid. It is least sensitive to acetic. Responsiveness, is therefore, roughly proportional to degree of electrolitic dissociation.

2. Necturus is more sensitive to potassium sulphate than to potassium chloride.

3. Necturus is less sensitive to alcohol than to the acids, alkalies, or alkaline earth salts, as indicated by the high per cent of alcohol necessary to induce reactions.

4. The skin of Necturus is sensitive to clove oil in the air but not when under water. Whether in or out of the water, Necturus does not react to turpentine.

THE REACTIONS TO HEAT

Several experiments were performed with three individuals to determine the thermic reactions of Necturus.

When taken from the tank where the water was 10° C. and put into water at 30° C. the three animals made the most violent struggles, beginning almost immediately and lasting until they were completely exhausted. The violence of these struggles was quite remarkable, though less pronounced in some cases than in others. A very short stay in the warm water was sufficient to completely exhaust all the individuals, so that they turned ventral side up; but when returned to water of moderate temperature they soon recovered.

Removal from water at 10° C. to 25° C. induced locomotion also. The gills were spread out and moved rapidly. The nostrils were often lifted above the water and air was expelled.

At 18° C. and 15° C. the animals remained quiet, but the

gills were moved rapidly. Reese ('06) in a similar experiment found two of the five Necturus under experiment gave locomotor responses at 18° C.

When put into water at 4° from 30°, the animals showed the same responses as noted by Reese ('06)—that is, marked activity, walking rapidly up and down the tank.

The reactions of certain regions of the body of Necturus to hot water was tested. A pipette that ejected 5 C.C. of water at a time was used and tests were made in water at 10° C. When the gills were stimulated with water at 70° C. the animal walked forward thirty inches, switching the body from side to side. The head, nostrils and tail were somewhat less sensitive. Their stimulation with water at 70° C. resulted in a forward movement of from eight to twelve inches. Water of the same temperature ejected on the back, caused only two or three inches of movement. The same regions of the body were tested in a like manner with 30° C., with no response.

Local heat stimulation was tested in another manner. A long rubber tube was run through the tank of water containing the animals. At one end of the tube was a funnel; the other end was open and hung outside of the tank. This arrangement allowed water to be poured in at the funnel, run through the tube and empty outside of the tank. To secure local response to heat, the tube was placed in contact with that region of Necturus to be stimulated. The tank water during this test was 0° C. and the water poured through the tube was 96° C. The tube was placed in contact with the body and the water was poured in at the funnel. When the nostrils, head and gills were stimulated the animal drew away from the tube immediately. This showed that direct response resulted from the heat radiating from the tube containing the heated water. Scarcely any response was induced from any other region of the body.

Another experiment was performed in which one end of a large pan, three by one and one-half feet, containing water was placed over a lighted gas burner and the other end on a cake of ice. The temperature of the heated end was 40° C., the cold end was 3° C., and the middle 10° C. Three animals were placed in the pan. They walked up and down several times, and finally rested in the cold end. When in the hot end they

splashed and struggled, but several times remained in the heated portion and tried to get out of the pan. In many cases they stayed in the hot end for some time and burned themselves over and over again, before finally reaching the middle or cold end of the pan.

From the experiments described above it is evident that Necturus is sensitive to considerable changes in temperature. It is apparent that Necturus could not live successfully in water above 18° C. and that life in water at 30° C. would probably be impossible.

THE REACTIONS TO LIGHT

The experiments performed to determine the sensitiveness of the skin of Necturus to light were carried on in a dark room, the temperature of which ranged from 75°-70° F. A 144 candle-meter Nernst lamp was used in all the experiments.

The first experiment tested the reactions of Necturus to light and shadow, the lamp being at the side one foot from the tank and a movable screen interposed in such a way that one-half of the tank was in shadow and the other half in light. Three animals were successively introduced. At 23.4 candle-meters, all three immediately went to the dark end of the tank. When the screen was changed to the opposite half of the tank the animals again moved into the shaded area. At 5.7 candle-meters each animal moved about for some time, equally in the light and dark areas of the tank. At 2.5 candle-meters the response was slow. After three minutes all three animals moved their heads and about one-half of their bodies into the shaded area. When the screen was changed to the opposite half of the tank the animals did not attempt to move again into the shaded area but remained in the light. With the intensity at 1 candle-meter the response was very slow. After five minutes all three moved their heads into the dark and remained in that position.

Definite reactions in determining the relative sensitiveness of the body region of Necturus were brought about by illuminating small areas of the skin. The apparatus was in the same position as for the experiments first described, except that the screen was arranged in such a manner that a band of light (144 candle-meters above the water at the center of the tank)

could be suddenly thrown on different regions of the body
through a hole in the screen, three-eighths of an inch in diam-
eter.   Three individuals were used for this experiment and all
of them behaved in essentially the same manner.

After an animal had remained quiet in the dark for five
minutes it was suddenly illuminated and a following behavior
noted.   The reactions observed agree with those of Pearse ('10,
p. 169) who performed similar experiments with Necturus. When
the light fell on the tail the animal moved forward, but when
it was allowed to fall on the head the movement was usually
backward.   The various regions of the body exhibit great varia-
tion in the time between stimulation and response.   The reac-
tion times of the regions subjected to the ray of light are shown
in table XXII.

TABLE XXII

The Reaction Times in Seconds of Various Regions of the Body
to Light, 144 C. M.

Individual No.	Head	Pectoral Girdle	Back	Pelvic Girdle	Tail
I	19	90	162	159	153
II	22	130	203	180	120
III	15	180	240	120	120
Average	18.6	133.3	201.6	153	131

As Pearse ('10, p. 170) found the head most sensitive in
normal Necturus while the tail was most sensitive in individuals
with eyes removed, the greater sensitiveness of the head is
due undoubtedly to stimulation received through the eye.

When the eye only was stimulated by a ray of light (144
C. M.) through a hole in the screen one-eighth of an inch in
diameter, each animal moved away from the light in about
thirty seconds, thus indicating the greater sensitiveness of the
eye over any other region of the body.

As Pearse ('10) says: " It is evident that Necturus is nega-
tively phototropic and that it comes to rest in shaded areas.
Both the eyes and skin are photoreceptors, and the stimulation
of either brings about negative reaction."

DISCUSSION

Let us try to picture Necturus in its daily life on the bottom of a lake or slow flowing stream. It frequents quiet waters from four to eight feet deep where a clean, sandy bottom is fairly well covered by vegetation. During the day it rests quietly beneath boards, logs or stones. One is rarely fortunate enough to get a glimpse of it; it is extremely shy and disappears at the slightest disturbance of the water, such as that caused by the approach of a boat. In walking, the diagonally opposite legs move in unison. When disturbed it swims swiftly, with a vigorous lateral motion of the broad and powerful tail, the feet being held closely against the body. Necturus never swims long distances, at most a few yards, then seeks concealment either in the mud or beneath some object. If it is undisturbed it usually rests with its head protruding from beneath a rock. The animal thus presents a curious appearance with its ruby gills moving gracefully to and fro. When one is disturbed the gills change from bright red to a dusky color and are at once drawn down tightly against the neck.

During the night Necturus moves from place to place. If it wanders into a warm area it becomes restless and walks away quickly into cooler water. It may approach dead vegetation that is giving off acids and alcohol. Such an environment drives Necturus away immediately. If it swims into an area containing an excess of salts or alkalies it quickly withdraws. Thus Necturus moves about, being directed hither or thither by the various changes in the chemical constitution or temperature of the water, till it comes into cool, pure water. Here it seeks crustaceans, insect larvae, small fish and earthworms, which constitute its food.

From the consideration of the facts of behavior one is naturally led to ask what the artificial conditions are which best suit the needs and instincts of Necturus. In aquaria it avoids the sunlight, and always seeks concealment. A tank well supplied with dark sheltered nooks is therefore best. Necturus can not live in warm water, and hence an aquarium should be supplied with running water and kept cool. Everything should be kept free from fungus, for a Necturus infected with Saprolegnia will not live long.

When Necturi are kept in aquaria they are frequently ob-

served to thrust their snouts above the water, open the mouth wide, and then return to the bottom where they soon expel the air, both through the gill-slits and from the mouth. It would thus seem that, while the branchiae are the chief means of respiration, the lungs play considerable part.

The great tenacity of life showed by mud-puppies is a matter of frequent comment. They are able to live for months without food and may be easily revived after being left for three or four hours out of water. After severe mutilation they recover and regenerate lost parts. Notwithstanding this great vitality they seem to fall easy victims to Saprolegnia, especially if there is a slight abrasion on the skin.

SUMMARY

1. The skin of Necturus is everywhere sensitive to tactile stimulation. The regions about the nostrils, gills and tail are most sensitive and the back the least sensitive.

2. Necturus is sensitive to chemical stimuli over the entire body surface, the reactions being characteristic for the different regions stimulated. The gills are usually the most sensitive region, with the nostrils and head following in order.

3. Necturus is more sensitive to nitric than to hydrochloric or sulphuric acid. It is least sensitive to acetic acid. It is more sensitive to potassium sulphate than to potassium chloride.

4. When any region of the body is fatigued for a given chemical, it rarely responds to tactile stimuli, although it usually reacts to other kinds of chemical stimuli.

5. Necturus is sensitive to considerable changes in temperature. All parts of the body are sensitive to hot water (70° C.), but the gills, head and nostrils are the most sensitive regions.

6. Necturus is negatively phototropic and comes to rest in shaded areas. Both the eyes and skin are photoreceptors and the stimulation of either brings about negative reactions. The head and tail are the most sensitive regions.

BIBLIOGRAPHY

COPELAND, M. The Olfactory Reactions of the Puffer or Swellfish, *Speroides*
1912.   *maculatus* (Block and Schneider). *Jour. Exper. Zool.*, **12**, 363-368.
1913. The Olfactory Reactions of the Spotted Newt, *Diemyotylus viridescens*
(Rafinesque). *Jour. Animal Behav.*, **3**, 260-273.
EYCLESHYMER, A. C. The Habits of *Necturus maculosus*. *Amer. Nat.*, **40**, 123-
1906.   136.

HERRICK, C. J.   On the Morphological and Physiological Classification of the
    1903.   Cutaneous Sense Organs of Fishes. *Amer. Nat.,* **37,** 313-318.
HURWITZ, S. H.   The Reactions of Earthworms to Acids. *Proc. Amer. Acad.*
    1910.   *Arts and Sci.,* **46,** 67-81.
MILLER, W. S.   The Lung, Vascular System, and Brain of *Necturus maculatus.*
    1900.   *Bull. Univ. Wis., Sci. Ser.,* **2,** 199-246.
PEARSE, A. S.   The Reactions of Amphibians to Light. *Proc. Amer. Acad. Arts*
    1910.   *and Sci.,* **45,** 162-206.
PARKER, G. H.   Influence of the Eyes, Ears, and other Allied Sense Organs on
    1910.   the Movements of the Dogfish, *Mustelus canis* (Mitchell). *Bull.*
               Bur. of Fisheries, **29,** 45-57.
    1909.   The Integumentary Nerves of Fishes as Photoreceptors and their Sig-
               nificance for the Origin of the Vertebrate Eyes. *Amer. Jour. Physiol.,*
               25, 77-80.
REESE, A. M.   Food and Chemical Reactions of the Spotted Newt, *Diemyctylus*
    1912.   *viridescens. Jour. Animal Behav.,* **2,** 190-208.
    1906.   Observations on the Reactions of Cyptobranchus and Necturus to
               Light and Heat. *Biol. Bull.,* **11,** 93-99.
SHELDON, R. E.   The Reactions of the Dogfish to Chemical Stimuli. *Jour. Comp.*
    1909.   *Neur. and Psych.,* **19,** 273-311.

EXPERIMENTS ON THE BEHAVIOR OF CHICKS HATCHED FROM ALCOHOLIZED EGGS

JOHN MADISON FLETCHER, EDWINA ABBOTT COWAN AND
ADA HART ARLITT

*From the Callender Laboratory of Psychology and Education of H. Sophie
Newcomb Memorial College of Tulane University*

During 1912, in the Biological Laboratory of H. Sophie New-
comb College of Tulane University, experiments were carried
on relative to the effect of subjecting chicken eggs to alcohol-
ization before hatching. It was discovered possible to hatch
from eggs so treated chicks which were apparently of normal
physical structure. When a technique had been evolved which
attained this end the experiment was taken up and carried on
by the Department of Psychology in an attempt to discover
whether there was any characteristic modification of behavior
which could be attributed to the effect of the alcohol on chicks
hatched from alcoholized eggs.

The experiments extended from October, 1913, to June, 1914,
and from March, 1915, to May, 1915. In the course of the
work five sets of eggs were hatched. The first, fourth and fifth
hatchings were from mixed stock; the second was in part pure
bred Buff Orpington and part pure bred White Leghorn and
the third was of Rhode Island Red stock. The eggs numbered
seventy in each hatching except the third, when only sixty eggs
were used. Of each of the first four sets of eggs twenty-five
were not tampered with. The remainder of the eggs, just before
being placed in the electric incubator, were treated in the fol-
lowing manner: A hole was made in the air chamber of the egg
with a dissecting needle. Into the air chamber was injected,
by means of a hypodermic needle, five drops of 95% ethyl
alcohol. In some cases the air chamber was found to be too
small to hold five drops so some eggs had less than five drops.
None had more. After the alcohol was in, the hole was sealed
with hot sealing wax. Of the last hatching of eggs ten were

left untampered with, ten were merely pierced with the dis-
secting needle and sealed, twenty-five were injected with five
drops of distilled water in place of the alcohol, and twenty-five
were injected with alcohol as usual.   The incubator was always
divided into compartments which prevented the chicks from the
different groups of eggs from mixing as they hatched.   As the
chicks were taken from the incubator they were marked with
pigeon markers having numbers on them and from that time
on were kept together and treated in exactly the same way
except in the case of a few which were isolated as a check on
the imitation factor.   For purposes of convenience the chicks
which were hatched from normal eggs will be designated " nor-
mal;" those hatched from alcoholized eggs will be designated
" alcohol;" those hatched from eggs with distilled water in
them will be designated " water;" and those hatched from eggs
with holes in them will be designated " holes."

In observing the behavior of the chicks their reactions were
divided into two groups, inherited and acquired.   The inherited
reactions studied were, reactions to light, pecking and drinking
reactions, and reactions to height.   The acquired reactions were
those involved in choice between two visual stimuli presented
by means of the Yerkes apparatus, as modified by Breed,[1] and
those involved in learning to run mazes.   Promptness and direc-
tion of response to light, speed and accuracy of the pecking
and drinking reactions, and the height from which a chick
would jump were used as criteria of the types of behavior of
the first group.   The number of trials necessary before making
ten correct choices and the time spent in the mazes were criteria
of the second group of reactions.

The instinctive reactions of alcohol chicks differed little, if
at all, from those of normal chicks except in the case of reac-
tions to height.   After the fifteenth day the alcohol chicks
jumped from greater heights than did the normal.   Alcohol
chicks were, as a group, slower in reacting within the mazes
and had to be given more trials before they made ten correct
choices in the Yerkes apparatus.   The water chicks and the
hole chicks were tested only for pecking reactions and mazes.
Their behavior resembled much more nearly that of the alcohol

[1] Breed, F. S.   The Development of Certain Instincts and Habits in Chicks.
Behav. Monog., vol. 1, no. 1, 1911.

chicks than that of the normal chicks. The different reactions will be taken up in detail in the following pages.

We are happy to have this opportunity to express our lasting gratitude to President B. V. B. Dixon for hearty co-operation in the experiment and to Dr. Irving Hardesty and Dr. Gustav Mann, of the Medical College of Tulane University, to whose suggestions for technique we owe much. Our greatest debt is to Miss Ellinor H. Behre, of the Department of Biology, whose biological resourcefulness and unmeasured helpfulness in the carrying on of the work made it possible. To Professor J. A. Lyon, of the Department of Physics, we are indebted for the apparatus used in the experiments with reactions to light. To Professors Angell and Carr of Chicago University we are also indebted for valuable suggestions.

EXPERIMENTS WITH INHERITED REACTIONS

Reactions to Light

The apparatus used to test the first reactions to light of the first set of chicks consisted of a hooded light placed behind a cardboard screen in such a way that a single horizontal strip of light 5 mm. in width was visible between the screen and the table, affording a single, highly localized stimulus. The experimental table stood in a dark room used for photographic purposes. No light was permitted to enter the incubator from the nineteenth to the twenty-fourth day of the hatch.

On the twenty-fourth day the incubator was taken to the dark room. Fourteen chicks, seven normal and seven alcohol, (the extent of the hatch) were removed from the incubator one at a time, numbered and marked with cloth markers and placed one at a time on the experimental table eighteen inches from the stimulus. Of the seven normal chicks only one reacted definitely. This chick walked towards the light, stopped, went on towards the light, stopped, then went straight to the light streak and tried to nestle in a corner of the screen. Four of the seven normal chicks walked away from the screen. Of the seven alcohol chicks, five went to sleep after making a few random movements, one stood still screaming and one ran about the table, finally running off and up the experimenter's arm. Light was thrown on the heads of the first two chicks which were tested but elicited no response.

After this test this apparatus was discarded because so much

light from the stimulus was reflected on the walls of the room. The following apparatus was found eminently satisfactory and was used throughout the rest of the series of experiments with light. It consisted of a one-candle power incandescent light connected in series with a rheostat and so arranged that by varying the resistance of the circuit the light could be adjusted from zero to full intensity. The stimulus was found to give best results when adjusted to about one-half full intensity. The apparatus was on a table covered by a cloth of dull black material having a minimum refractive power. The experiments were conducted at night.

At the time of the second hatch all light was excluded from the incubator from the nineteenth to the twenty-fourth day. On the evening of the twenty-fourth day ten chicks, five normal and five alcohol, were removed from the incubator one at a time, numbered and marked with aluminum pigeon markers and placed on the table, eighteen inches from the stimulus. They were so placed that their heads were turned slightly away from the light. Three alcohol and two normal chicks reacted positively. Turning and facing the stimulus, they walked toward it. The other chicks walked diagonally or directly away from the light. Two normal and one alcohol chick walked off the table.

On the following night the same procedure was repeated with the ten chicks previously tested and eleven others, four normal and seven alcohol, which had been too weak to be handled on the first night. Of the ten previously tested, eight reacted positively. No. 36, which had reacted slowly and Nos. 4, 6 and 35, which had not reacted at all, walked directly to the light as soon as placed on the table. Of the four normal chicks not tested before one reacted positively to the stimulus, walking directly to the light and placing its bill against it; the other three walked away from the light. Of the alcohol chicks not tested before three immediately moved toward the light, one after an interval of three minutes, and the other three walked around the table, going sometimes towards, sometimes away from the light.

The twenty-one chicks were tested again on the third day. Normal chick No. 3 and alcohol No. 34, which had reacted positively on the first and second days, did not react on the third; normal No. 4 reacted on the second, but not the first and third days; alcohols No. 21 and No. 33 reacted on the

third, but not on the second day; normal chicks Nos. 2, 6 and 10, and alcohol chicks Nos. 36, 22, 27 and 35 reacted positively through the third day; normal chicks Nos. 11, 8, 7 and 1, and alcohol chicks Nos. 27, 26, 31, 28 and 24 did not react positively at any time.

The apparatus and procedure employed with the third hatching of chicks was the same as that used with the second hatching but these chicks were not removed from the incubator until the evening of the third day. At the end of the first day a partition was placed in the incubator in such a manner that the chickens hatching later would not mingle with those already hatched. Only those which had hatched the first day were tested. Of the six alcohol and eleven normal chicks tested, two alcohol chicks reacted positively, the other fifteen chicks did not react at all, wandering aimlessly about the table or standing still and screaming.

There is nothing in these results or in the behavior of the chicks, as they moved toward or away from the light stimulus, to indicate the presence of a phototropism either positive or negative. There seems to be a highly variable instinctive tendency to react positively to a single light stimulus of very weak intensity and small area. This tendency may appear for the first time on the first or second day and rarely on the third day. When it does appear before the third day it may not persist through that day. This reaction failed to show any characteristic difference between normal and alcohol chicks.

Pecking Reaction

The pecking reactions of the first set of chicks are not recorded here as the cloth markers which distinguished normal from alcohol chicks dropped off the evening of the fourth day. These chicks were not used for further experiments.

The following method was used with the second set of chicks. On the morning of the third day after hatching the chicks were placed, one at a time, on a table covered with a smooth, black cloth. On this cloth were scattered several bits of light colored grain. The time before the first peck and the accuracy of the pecking reaction was carefully noted. For the first test with each chick a record was kept during the first five minutes of its pecking activities. For succeeding tests the record was kept for three minutes. It was found convenient to use the Breed

method of recording reactions, i.e., to use "1" to denote peck-
ing at but missing grain; "2", pecking at and hitting grain;
"3", pecking, hitting, picking up and dropping grain; "4", peck-
ing at, striking, picking up and swallowing grain, or the com-
plete reaction.

On the occasion of the first test the alcohol chicks with the
exception of Nos. 22 and 29, pecked after longer intervals than
did the normal chicks. Alcohols Nos. 28 and 21 did not peck
at all. Alcohols Nos. 33, 39 and 34 went to sleep a number
of times before they pecked at the grain. All of the alcohol
chicks were quieter than the normal, made fewer random move-
ments and showed little or none of the tendency to explore,
so apparent in all of the normal chicks. They did, however,
peck with accuracy equal to that of the normal chicks and
their records show they improved with equal rapidity.

Alcohols Nos. 33 and 34 made only 24% and 20% of "4"
reactions respectively on the third day. On the eleventh day
No. 34 made 51.1% and No. 33 made 44.4% of "4" reactions.
One of the normal chicks, No. 10, made a better record than
any made by alcohol chicks, making 78.9% of "4" reactions on
the eleventh day; but the records of Nos. 8, 6 and 1 were not
so good as those made by some of the alcohol chicks. No. 7
had 35.2%, No. 6, 44.4% and No. 1, 47% of "4" reactions on
the eleventh day. The following table shows the comparative
rate of progress of normal and alcoholic chicks of the second
group.

TABLE 1

CHICKS 1, 2, 6 AND 10 WERE NORMAL CHICKS. CHICKS 21, 22, 29,
32, 34 AND 35 WERE ALCOHOL CHICKS

No. of Chick	Day 3 Reaction				Day 4 Reaction			
	1	2	3	4	1	2	3	4
1............					1	2	4	2
2............								
6............	0	8	5	2				
10............					0	3	3	2
Average.......	0	8	5	2	1/2	2 1/2	3 1/2	2
21............								
22............	1	2	5	3				
29............	4	9	7	5				
32............	8	7	6	4	2	3	5	5
34............	0	5	5	2				
35............	0	1	9	3				
Average.......	2 3/5	4 4/5	6 2/5	3 2/5	2	3	5	5

TABLE 1—*Continued*

No. of Chick	Day 5 Reaction 1	2	3	4	Day 8 Reaction 1	2	3	4
1............					1	1	13	1
2............	0	4	4	11	0	1	13	11
6............	0	5	5	4	0	1	1	1
10...........					0	3	4	12
Average.......	0	4 1/2	4 1/2	7 1/2	1/4	1 1/2	7 3/4	6 1/4
21...........	1	1	1	0	0	3	7	5
22...........	5	3	2	2	0	0	11	12
29...........	4	5	4	4	0	0	7	14
32...........	2	5	7	6	8	2	10	6
34...........	4	3	9	3	0	0	11	3
35...........					0	4	6	5
Average.......	3 1/5	3 2/5	4 3/5	3	1 1/3	1 1/2	8 2/3	7 1/2

No. of Chick	Day 10 Reaction 1	2	3	4	Day 11 Reaction 1	2	3	4
1............	0	1	11	8	0	1	8	8
2............	0	0	5	18	0	0	5	11
6............	0	3	4	12	0	4	6	8
10...........	0	0	6	21	0	0	4	15
Average.......	0	1	6 1/2	14 3/4	0	1 1/4	5 3/4	10 1/2
21...........	0	0	11	15	0	1	9	6
22...........	0	1	8	8	0	0	1	4
29...........	0	0	3	19	0	2	8	5
32...........	1	1	10	8	0	4	6	6
34...........	0	1	8	8	0	1	8	10
35...........	0	5	4	5	0	1	12	3
Average.......	1/6	1 1/3	7 1/3	10 1/2	0	1 1/2	7 1/2	5 2/3

TIME UNTIL FIRST

No. of Chick	Time Until First Peck	No. of Chick	Time Until First Peck
1	1' 20"	21	
2	1' 30"	22	15"
6	2' 10"	29	30"
10	30"	32	2' 29 1/2"
		34	5'
		35	9' 50"
Average	1' 22 1/2"	Average	3' 36.9"

The same apparatus and procedure was repeated with the third set of chicks with approximately the same results. The highest record in this group as in the second was made by a normal chick, the lowest by an alcohol, but the records of the other chicks differed little if at all. The following table (Table

2) presents the rate of improvement of the pecking reaction of normal and alcohol chicks.

TABLE 2

CHICKS 2, 3, 5, 6, 8, 15 AND 16 WERE NORMAL CHICKS. CHICKS 21, 22, 24, 29, 31, 33 AND 34 WERE ALCOHOL CHICKS

No. of Chick	Day 3 Reaction				Day 4 Reaction			
	1	2	3	4	1	2	3	4
2............	12	3	6	5				
3............	10	0	5	6	3	5	7	6
5............	0	2	8	13				
6............					0	9	7	5
8............								
15............								
16............	5	9	6	5				
Average.......	6 3/4	3 1/2	6 1/4	7 1/4	1 1/2	7	7	5 1/2
21............	7	6	9	1				
22............								
24............					0	7	4	9
29............					9	6	2	2
31............	0	13	6	3				
33............								
34............					0	5	2	16
Average.......	3 1/2	9 1/2	7 1/2	2	3	6	2 2/3	9

No. of Chick	Day 5 Reaction				Day 6 Reaction			
	1	2	3	4	1	2	3	4
2............	0	3	1	2	0	0	2	18
3............	0	5	5	14	0	3	3	16
5............	0	3	3	14	0	3	8	22
6............					0	6	6	19
8............	3	7	4	7	0	6	8	22
15............	3	0	0	0	0	3	8	25
16............	12	5	2	5	0	5	5	15
Average.......	3	3 5/6	2 1/2	7	0	4 1/3	6 2/3	22 5/6
21............	0	9	4	17				
22............	0	4	5	12				
24............					0	19	3	19
29............	7	9	4	2	0	13	4	3
31............	0	4	4	13				
33............	1	11	3	13	0	0	5	16
34............	0	5	2	16	0	0	5	15
Average.......	1 1/3	7	3 2/3	12 1/6	0	8	4 1/4	13 1/4

TABLE 2—*Continued*

No. of Chick	Day 8 Reaction 1	2	3	4	Day 10 Reaction 1	2	3	4
2............	0	4	4	14	0	1	5	13
3............	0	6	7	7	1	2	8	11
5............	0	1	5	14	0	1	7	12
6............	0	5	9	6	0	3	7	15
8............	0	4	5	16	0	1	6	14
15............	0	2	7	11	0	7	3	12
16............	0	3	4	15	0	1	7	15
Average.......	0	3 4/7	5 6/7	11 6/7	1/7	2 2/7	6 1/7	13 1/7
21............	0	3	6	14	0	2	5	15
22............					0	3	4	17
24............	0	14	4	14	0	14	3	14
29............	0	6	6	9	0	0	2	5
31............	1	2	4	18	0	7	4	14
33............	0	5	4	16	0	4	3	16
34............	0	6	6	17	1	4	7	9
Average.......	1/6	6	5	14 2/3	1/7	4 6/7	4	12 6/7

No. of Chick	Day 11 Reaction 1	2	3	4	Time Until First Peck
2............	0	3	3	14	17′ 4″
3............	0	7	1	20	2′ 10″
5............	0	4	4	14	4″
6............	0	2	5	18	38′ 4″
8............	0	4	2	19	51.6″
15............	0	5	3	20	1′ 28″
16............	0	7	4	14	
Average.......	0	4 4/7	3 1/7	17	9′ 56.9″
21............	0	1	4	20	3′ 34″
22............	0	3	3	19	4″
24............	0	13	5	13	15″
29............	0	3	3	14	4′
31............	0	5	4	16	2′ 20″
33............	0	3	2	19	4′
34............	0	2	3	19	8″
Average.......	0	4 2/7	3 3/7	17 1/7	1′ 52″

The fifth hatching of chicks, which consisted of seven normal, four hole, seven water and five alcohol chicks, were also tested for pecking reactions. The method differed slightly from that of the preceding tests in that a record was kept of the first

twenty reactions in each test rather than of the total reactions for a certain length of time. No record was made of the time which elapsed before the first pecking reaction in the first test. In all other respects the method for this group was like that for the preceding groups.

The following table shows the rate of improvement in pecking accuracy of each chick tested:

TABLE 3

CHICKS 1, 2, 3, 4, 6, 10 AND 14 WERE NORMAL CHICKS. CHICKS 20, 21, 23 AND 25 WERE HOLE CHICKS. CHICKS 41, 43, 46, 47, 48, 51 AND 54 WERE WATER CHICKS. CHICKS 71, 72, 74, 80 AND 81 WERE ALCOHOL CHICKS

No. of Chick	Day 2 Reaction				Day 3 Reaction			
	1	2	3	4	1	2	3	4
1.............	0	14	1	5				
2.............	6	6	0	8				
3.............	0	10	3	7				
4.............	2	6	1	11	0	4	2	14
6.............	1	9	4	6				
10............	0	4	1	15				
14............					0	8	1	11
Average.......	1 1/2	8 1/6	1 2/3	8 2/3	0	6	1 1/2	12 1/2
20............					0	13	1	6
21............	4	4	2	10				
23............	0	7	6	7				
25............	1	8	1	10	0	8	6	6
Average.......	1 2/3	6 1/3	3	9	0	10 1/2	3 1/2	6
41............	0	6	3	11				
43............	0	12	4	4				
46............	9	3	4	4				
47............					0	7	8	5
48............					0	8	1	11
51............	1	4	5	10				
54............	7	5	5	3				
Average.......	3 2/5	6	4 1/5	6 2/5	0	7 1/2	4 1/2	8
71............	3	10	4	3				
72............	1	6	0	13				
74............								
80............					0	9	3	8
81............	7	5	2	6	1	2	1	16
Average.......	3 2/3	7	2	7 1/3	1/2	5 1/2	2	12

TABLE 3—*Continued*

No. of Chick	Day 5 Reaction				Day 6 Reaction			
	1	2	3	4	1	2	3	4
3............					0	1	10	9
6............					2	1	10	7
10...........					0	3	15	2
Average.......					2/3	1 2/3	11 2/3	6
21...........					0	1	11	8
23...........					0	1	17	2
Average.......					0	1	14	5
43...........					0	5	7	8
46...........					0	0	19	1
Average.......					0	2 1/2	13	4 1/2
71...........					0	4	9	7
72...........	0	5	8	7	0	0	5	15
74...........					0	2	10	8
Average.......	0	5	8	7	0	2	8	10

No. of Chick	Day 7 Reaction				Day 10 Reaction			
	1	2	3	4	1	2	3	4
2............	0	0	3	17				
3............					0	4	7	9
4............	0	0	7	13				
6............					0	1	8	11
10...........					0	1	13	6
14...........	0	2	5	13				
Average.......	0	2/3	5	14 1/3	0	2	9 1/3	8 2/3
20...........	0	0	1	19				
21...........					0	3	4	13
25...........					0	0	4	16
Average.......	0	0	1	19	0	1 1/2	4	14 1/2
41...........	0	1	10	9				
43...........					0	4	13	3
46...........					0	0	6	14
47...........	0	1	13	6				
48...........	1	4	9	5				
51...........					1	3	6	10
Average.......	2/3	2	10 2/3	6 2/3	1/3	2 1/3	8 1/3	9
71...........					0	2	7	11
72...........					0	0	3	17
74...........					0	4	7	9
81...........	0	0	7	13				
Average.......	0	0	7	13	0	2	5 2/3	12 1/3

TABLE 3—*Continued*

No. of Chick	Day 13 Reaction 1	2	3	4
2............	0	0	1	19
4............	0	1	5	14
14............	0	3	7	10
Average.......	0	1 1/3	4 1/3	14 1/3
20............	0	2	3	15
Average.......	0	2	3	15
41............	0	1	9	10
47............	0	4	7	9
48............	0	9	8	3
Average.......	0	4 2/3	8	7 1/3
80............	0	0	13	7
81............	0	1	7	12
Average.......	0	1/2	10	9 1/2

No. of Chick	Day 14 Reaction 1	2	3	4	Day 16 Reaction 1	2	3	4
3............	0	0	4	16				
6............	0	1	3	16				
10............	0	0	6	14				
Average.......	0	1/3	4 1/3	15 1/3				
21............	0	0	1	19				
23............	0	1	13	6				
25............	0	0	2	18				
Average.......	0	1/3	5 1/3	14 1/3				
43............	0	0	3	17				
46............	0	1	3	16				
48............					0	4	7	9
51............	0	2	4	14				
Average.......	0	1	3 1/3	15 2/3	0	4	7	9
71............	0	1	8	11				
72............	0	0	1	19				
74............	0	0	1	19				
Average.......	0	1/3	3 1/3	16 1/3				

TABLE 3—*Continued*

No. of Chick	Day 17 Reaction				Day 19 Reaction			
	1	2	3	4	1	2	3	4
2............	0	1	9	10				
3............					0	2	15	3
4............	0	1	9	10				
6............					0	2	10	8
10............					0	2	9	9
14............	0	1	2	17				
Average.......	0	1	6 2/3	12 1/3	0	2	11 1/3	6 2/3
20............	0	2	7	11				
21............					0	1	8	11
23............					0	2	7	11
25............					0	2	6	12
Average.......	0	2	7	11	0	1 2/3	7	11 1/3
41............	0	0	7	13				
43............					0	3	13	4
46............					0	2	9	9
47............	0	5	6	9				
51............					0	2	8	10
Average.......	0	2 1/2	6 1/2	11	0	2 1/3	10	7 2/3
72............					0	0	3	17
74............					0	1	7	12
80............	0	3	14	3				
81............	0	0	11	9				
Average.......	0	1 1/2	12 1/2	6	0	1/2	5	14 1/2

No. of Chick	Day 20 Reaction				Day 21 Reaction			
	1	2	3	4	1	2	3	4
2............	0	1	4	15				
3............					0	3	10	7
4............	0	1	3	16				
6............					0	1	9	10
10............					0	2	6	16
14............	0	1	4	15				
Average.......	0	1	3 2/3	15 1/3	0	2	8 1/3	11
20............	0	2	4	14				
21............					0	0	5	15
23............					0	2	8	10
25............					0	2	5	13
Average.......	0	2	4	14	0	1 1/3	6	12 2/3

TABLE 3—*Continued*

No. of Chick	Day 20 Reaction				Day 21 Reaction			
	1	2	3		1	2	3	4
41............	0	1	2	17				
43............					0	1	13	6
46............					0	3	6	11
47............	0	6	6	8				
48............	0	4	6	10				
51............					1	2	5	12
Average.......	0	3 2/3	4 2/3	11 2/3	1/3	2	8	9 2/3
71............					0	1	4	15
72............					0	0	2	18
74............					0	3	2	15
80............	0	6	3	11				
81............	0	1	4	15				
Average.......	0	3 1/2	3 1/2	13	0	1 1/3	2 2/3	16

No. of Chick	Day 24 Reaction				Day 27 Reaction			
	1	2	3	4	1	2	3	4
2............	0	3	5	12				
4............	0	2	7	11				
6............					0	1	6	13
10............					0	2	8	10
14............	0	1	8	11				
Average.......	0	2	6 2/3	11 1/3	0	1 1/2	7	11 1/2
20............	0	0	1	19				
21............					0	4	6	10
23............					0	0	13	7
25............					0	4	3	13
Average.......	0	0	1	19	0	2 2/3	7 1/3	10
41............	0	2	2	16				
43............					0	1	9	10
46............					0	2	8	10
47............	2	4	6	8				
48............	2	3	9	6				
51............					0	1	6	13
Average.......	1 1/3	3	5 2/3	10	0	1 1/3	7 2/3	11
71............					0	1	14	5
72............					0	5	3	12
74............					0	1	7	12
80............	0	5	9	6				
81............	0	5	5	10				
Average.......	0	5	7	8	0	2 1/3	8	9 2/3

The Effect of Imitation on the Pecking Reaction

Some authors, notably Lloyd Morgan,[2] and Holmes[3], are of the opinion that imitation plays a large part in the perfecting of the pecking reaction. Holmes states that imitation is an important factor in the education of young birds. The following passage may be quoted from Lloyd Morgan: "A hen teaches her little ones to pick up grain and other food by pecking on the ground and dropping suitable materials before them, while they seemingly imitate her action in seizing the grain."

Thorndike,[4] is of the opinion that the pecking instinct is practically perfect at birth. Watson,[5] believes that the improvement in the speed and accuracy of the pecking reaction is due solely to practice. In support of his view he quotes the results of Breed's[6] experiments with five-day old chicks which had been prevented from previous pecking. These chicks pecked with the accuracy of twenty-four-hour old chicks and required two days' practise before their accuracy was up to standard.

In order to determine what rôle, if any, imitation played in the perfecting of the pecking reactions of our normal and alcohol chicks, three normal and three alcohol three-day old chicks of the second set were placed in separate pens. These pens were so constructed that each chick was kept completely isolated from and out of sight of the rest. The chicks were kept in these pens for eleven days and tested on the same days and by the same method as the group from which they were taken. Alcohols Nos. 21 and 28 were among the six chosen as they had not pecked at all when under observation on the third day.

Two chicks, alcohol No. 28 and normal No. 7, died when seven days old. The pecking reactions of the four remaining chicks improved as rapidly as those of the group from which they were taken. Alcohol No. 21 made a higher record than was made by any other alcohol chick in spite of the fact that it did not peck at all while under observation on the third day and did not see any other chick peck at that time or any time

---

[2] Morgan, Lloyd. Animal Behavior., p. 189.
[3] Holmes, S. J. The Evolution of Animal Intelligence, p. 254.
[4] Thorndike, E. L. Animal Intelligence, 1911, p. 160.
[5] Watson, J. B. Behavior: An Introduction to Comparative Psychology, p. 141.
[6] Breed, F. S. Maturation and Use of an Instinct. *Jour. of Animal Behav.*, 1913, **3**, 274.

FLETCHER, COWAN AND ARLITT

thereafter until replaced with the other chicks on the eleventh day.

The following table gives the record of the pecking reactions of these chicks during their period of isolation:

TABLE 4

CHICKS 4 AND 8 WERE NORMAL CHICKS. CHICKS 20 AND 21 WERE ALCOHOL CHICKS

No. of Chick	Day 3 Reaction 1	2	3	4	Day 5 Reaction 1	2	3	4
4...........	4	2	1	1	0	7	4	7
8...........	3	2	2	2				
Average.......	3 1/2	2	1 1/2	1 1/2	0	7	4	7
20...........					0	5	6	7
21...........					2	3	9	13
Average.......					1	4	7 1/2	10

No. of Chick	Day 8 Reaction 1	2	3	4	Day 10 Reaction 1	2	3	4
4...........	0	4	6	10	0	5	9	2
8...........	0	2	12	11	0	5	7	7
Average.......	0	3	9	10 1/2	0	5	8	4 1/2
20...........	0	1	8	13	0	0	5	12
21...........	0	0	3	19	0	1	15	1
Average.......	0	1/2	5 1/2	16	0	1/2	10	6 1/2

No. of Chick	Day 11 Reaction 1	2	3	4
4...........	0	0	8	9
8...........	0	4	7	6
Average.......	0	2	7 1/2	7 1/2
20...........	0	0	7	10
21...........	0	0	8	10
Average.......	0	0	7 1/2	10

Drinking Reaction

A watch glass containing a few drops of water was used as a stimulus for the drinking reaction. This glass stood on a square of smooth, white paper, ten by ten inches. The chicks were placed one at a time on the paper, six inches from the glass, and a record made of the time before they drank and of their manner of doing it.

The drinking reactions of twenty chicks of the first set were observed, seven on the third and thirteen on the fourth day. Only one of the seven three-day old chicks drank and that one apparently found the way by accident, first walking into the glass and then drinking. Five of the thirteen four-day old chicks, three alcohol and two normal, walked to the glass and drank, one drinking at once, the others after a short interval. Three, one normal and two alcohol, afterwards performed the drinking reaction on the smooth, white paper and the edge of the glass. One chick pecked at the water, then swallowed and immediately performed the drinking reaction. The others were placed close to the glass after a long interval during which they had run about the table and the water was ruffled as in the Breed[7] experiment. The chicks then drank.

The same apparatus and method was used with the second set of chicks. The twenty-two chicks of this set found the water by accident, walking into the watch glass, or pecking at it and then drinking. One alcohol chick, No. 32, walked into the glass and immediately made the drinking reaction on the white paper on which the glass stood, walked out of the glass on to the paper, then walked back into the glass and went through the movements of the drinking reaction, scratching in the water at intervals. The touch of the water on the chick's feet had evidently served to start the drinking reflex. There was no difference in the behavior of alcohol and normal chicks of either set.

Reaction to Heights

Thorndike[8], experimenting with reaction to heights with chicks ninety-four hours old, found the chicks hesitated for a longer and longer interval before jumping, as the height of

[7] Breed, F. S. The Development of Certain Instincts and Habits in Chicks. *Behav. Monog.*, vol. I, no. 1, 1911.
[8] Thorndike, E. L. Animal Intelligence, 1911, p. 159.

the boxes on which they were placed increased, finally refusing to jump from boxes thirty-nine inches in height.

We undertook to determine the height at which our chicks would refuse to jump and whether this height differed for normal and alcohol chicks. The subjects were six seven-day old chicks, three normal and three alcohol, and seven fifteen-day old chicks, two normal and five alcohol.

The chicks were placed on stands above the box in which the other chicks were kept. The distance from the top of the stand to the floor of the box increased gradually from 10.7 cm. to 171.5 cm. The alcohol chicks were not placed on stands of greater height than 171.5 cm., as it was feared that they might be injured in jumping to the box. The chicks were allowed to rest and feed for thirty seconds after each return to the box.

There was little difference in the reactions of normal and alcohol six-day old chicks (see Table 5), but in the case of the fifteen-day old chicks the difference in behavior of the normal and alcohol chicks was marked. The normal chicks hesitated for longer and longer intervals as the height of the stands increased, waiting for over five minutes before jumping from a stand 106 cms. above the box. Though repeatedly pushed they would not jump from stands above this height. The alcohol chicks jumped with little or no hesitation. No. 32 would not jump from a stand 134 cm. in height, but Nos. 21, 28 and 22 jumped with almost no hesitation from stands 171.5 cm. above the box.

The following tables present in detail the results of the experiments with heights:

TABLE 5

CHICKS 1, 2 AND 10 WERE NORMAL CHICKS. CHICKS 27, 35 AND 34 WERE ALCO-
HOL CHICKS. THE FACT THAT THE CHICK JUMPED IS INDICATED BY +. THE
FACT THAT THE CHICK REFUSED TO JUMP IS INDICATED BY —.

Chicks Six Days Old

No. of Chick	10.7	22.3	59.6	74	84.6	95	119.6	130	134	143
1............	+	+	+	+	+	+	+	+	—	—
2............	+	+	+	+	+	+	+	—		
10...........	+	+	+	+	+	—				
27...........	+	+	+	+	+	+	+	+	—	
35...........	+	+	+	+	+	+	+	+	—	
34...........	+	+	+	+	—					

TABLE 6

CHICKS 4 AND 8 WERE NORMAL CHICKS. CHICKS 21, 22, 28, 29 AND 32 WERE
ALCOHOL CHICKS. THE FACT THAT THE CHICK JUMPED IS INDICATED BY +.
THE FACT THAT THE CHICK REFUSED TO JUMP IS INDICATED BY —.

Chicks Fifteen Days Old

Height

No. of Chick	10.7	22.3	74	89.8	95.5	106	134	158.3	171.5
4..................	+	+	+	+	+	—			
8..................	+	+	+	+	+	—			
21.................	+	+	+	+	+	+	+	+	+
22.................	+	+	+	+	+	+	+	+	+
28.................	+	+	+	+	+	+	+	+	+
29.................	+	+	+	+	+	+	+	+	+
32.................	+	+	+	+	+	+	—		

ACQUIRED REACTIONS

Experiments on Behavior in Mazes

During the course of the experiments with mazes three mazes of varying complexity were used which will be designated as Maze 1, Maze 2 and Maze 3. Maze 3 was used only with the fifth hatching of chicks, which contained hole and water chicks as well as normal and alcohol ones. The time which the animal spent in the maze was the criterion of learning.

So far as the general behavior of the chicks in the mazes was concerned there seemed to be one main difference which was, however, quantitative rather than qualitative. The alcohol chicks were on the whole less prone to react to the maze situation with general activity. An ordinary normal chick, when placed in a maze, will run about and attempt to get out. It will normally continue this running until it does get out and subsequent trials are made shorter by a gradual reduction of this running about. In other words, the process of learning the maze is like that of any other animal so placed. The alcohol chicks, as well as chicks raised from eggs which had been tampered with in other ways, that is, the three different kinds of abnormal chicks, did not seem to be inspired by this desire to get out of the maze. The situation did not seem to call forth the reaction of running about as it did with the normal chicks. The chick when placed in the maze might go promptly to sleep and sleep for some five minutes. It might then wake up and suddenly dart forward. If it brought up in a blind alley it might either go to sleep for another period, trying to the experimenter's nerves, or it might turn and go into the

correct path and so out. This sort of procedure naturally made the time record of the abnormal chick much longer than that of the normal chick. But there are many modifying points which must be considered when discussing this difference in the learning process involved in learning mazes. In the first place this time difference was not one which persisted throughout the learning process. The results will show that it is confined mainly to the first third of the number of trials used. After this point the time records of the abnormal chicks do not vary from those of the normal. On this account we are very doubtful whether this can be called a genuine difference in the learning process of normal and abnormal chicks. Another consideration is the fact that this lack of reaction while prevalent among the abnormals was not invariable among them and was occasionally found among the normals. A glance at the tables will show that there were chicks among the alcohols, among the water and among the hole chicks whose records were as good or better than the average of the normal chicks. And there were individuals among the normals who showed the same lack of interest during the first trials in the maze that the abnormal chicks showed. And the final consideration is that the fact that a chick, either normal or abnormal, exhibited this sluggish type of behavior in a maze on one day did not necessarily mean that it would exhibit this same type of behavior in a different maze on another day. Again a glance at the individual records will confirm this.

The experiments with the mazes seemed to indicate, then, that tampering with an egg in the ways we used would cause the chicken subsequently developing from it to be subject to fits of sluggishness and inactivity which might temporarily impede its progress in acquiring a new co-ordination. They did not in any way demonstrate the inability of such a chick to acquire new co-ordinations, nor did they even demonstrate that this sluggishness is an inevitable result of the tampering, or a constant characteristic of the chick in which it appears or a characteristic which does not sometimes appear in normal chicks. The ordinary chicken raiser who remarks that a certain chicken " looks droopy and may be sick " is well acquainted with the type of behavior or lack of behavior we have been trying to describe.

The following pages present the maze results in detail:

Maze No. 1

Maze No. 1 (which perhaps should not properly be called a maze) was a straight path between two boards 55 cms. in length. It stood on a table below which was the box in which all the chicks were kept during the tests. One end of the path was closed. The open end was even with the edge of the table just above the box. During the tests of chicks 2, 6, 7, 9 and 34 the box was 79 cms. below the table edge. The wire netting cover of the box was made to lean against the table in such a way as to form an inclined plane from the table edge to the box. The chicks showed such reluctance to leave the table under these circumstances that the box was raised to within six inches of the table and the inclined plane done away with.

The chick to be tested was placed at the back of the maze and the time it took to find its way back to the box recorded. Each chick was given ten trials in succession. An interval of one minute was allowed to elapse between the end of one trial and the beginning of another. The chick was sometimes placed in the maze by one experimenter and sometimes by another to correct any initial direction error which might occur.

The following table gives the results for Maze 1:

TABLE 7

CHICKS 1, 2, 3, 4, 5, 6, 7, 8 AND 9 WERE NORMAL CHICKS. CHICKS 27, 29, 32, 33, 34 AND 35 WERE ALCOHOL CHICKS

	Trial				
No. of Chick	1	2	3	4	5
1......................	7′ 15 ″	21 ″	2′ 27 ″	5 ″	4.8″
2......................	6′ 45 ″	26.2″	2′ 7 ″	38 ″	18 ″
3......................	1′ 9.4″	20.6″	8.4″	10 ″	10 ″
4......................	1′ 28.8″	30.8″	18.4″	7.2″	9 ″
5......................	12 ″	8′ 8.8″	6.8″	5.2″	3.6″
6......................	15.6″	15.6″	52.6″	5.2″	5 ″
7......................	1′ 15.6″	11.6″	5.2″	3.2″	21.2″
8......................	23.8″	38.8″	36 ″	24 ″	14 ″
9......................	3′ 51.6″	14 ″	27.8″	10.2″	11.2″
Average.................	2′ 30+″	1′ 14+″	44+″	12+″	10+″
27......................	27 ″	9 ″	8″	9 ″	11.2″
29......................	30.6″	8.4″	4.2″	4.4″	3.6″
32......................	32.2″	6 ″	7 ″	3 ″	4.2″
33......................	8′ 35.4″	8 ″	1′ 20 ″	2′	16.4″
34......................	12.4″	8 ″	7 ″	10.4″	7.4″
35......................	11′ 23 ″	8′ 5 ″	2′ 1 ″	55 ″	46 ″
Average.................	3′ 36+″	1′ 27+″	37+″	33+″	14+″

TABLE 7—*Continued*

No. of Chick	Trial				
	6	7	8	9	10
1.........................	10.5″	6.5″	11.5″	3.8″	4 ″
2.........................	9.8″	21 ″	28 ″	18.8″	45.2″
3.........................	9 ″	12 ″	10.8″	6 ″	12.4″
4.........................	11 ″	13.6″	13.2″	12.4″	9.4″
5.........................	2.6″	2.8″	2 ″	2.8″	3.4″
6.........................	3 ″	7 ″	5 ″	4.8″	4.4″
7.........................	15 ″	18 ″	26.6″	8.6″	23.2″
8.........................	9 ″	4 ″	4.2″	4.2″	11.6″
9.........................	9.6″	9.4″	24 ″	9 ″	13.6″
Average.............	8+″	10+″	13+″	7+″	14+″
27.........................	4 ″	2.8″	4 ″	5 ″	3.2″
29.........................	3 ″	4.6″	4.2″	2.8″	3 ″
32.........................	9 ″	8 ″	16 ″	8 ″	9 ″
33.........................	8 ″	15.6″	17 ″	8.2″	23. ″
34.........................	6.8″	5 ″	6 ″	10.8″	10.6″
35.........................	29 ″	15.2″	24 ″	27 ″	16 ″
Average.................	9+″	8+″	11+″	10+″	10+″

Maze No. 2

Maze 2 was a simple choice maze, consisting of one straight alley with two slightly shorter alleys running at right angles to it. The right hand alley ended blindly. The left hand alley was open, permitting the chick to jump to the box in which its companions were kept. The maze stood on a table, the edge of which was six inches above the box.

The subjects of the first experiment with this maze were six normal and six alcohol chicks of the second set. The procedure was the same as that used with Maze 1.

The difference in the behavior of normal and alcohol chicks was more pronounced in these tests with Maze 2 than in any of the other tests. It was thought at the time that this was due to the increased difficulty of the maze problem which emphasized differences in learning capacity. But later results with Maze 2 and with the still more complicated Maze 3 did not bear this hypothesis out. In these tests with Maze 2 the normal chicks with one exception, found the right path and thereafter chose it. One chick chose the wrong alley on the second trial and went half way to the end, then turned and chose the right path. The normal chicks which went to the box slowly did so because they stopped and pecked at the bright nail heads with which the strips where the alleys joined were studded.

All of the alcohol chicks made two or more wrong choices after the first trial. Several tried to peck their way through the side and two tried repeatedly to fly out at the back though they had several times found the path to the box. There is not one instance of this kind of behavior in the case of the normal chicks of this set. Two of the alcohol chicks went to sleep and had to be prodded repeatedly.

No. 27, whose record in Maze 1 was as good as that made by the normal chicks, found the right path, chose it three times in succession, made one wrong choice in each of the three following trials, went straight to the box in the seventh, eighth and ninth trials, then hesitated a long time before making a choice on the tenth trial.

Alcohol No. 35 failed to find its way out of the maze. The first trial it was slowly pushed to the entrance at the end of twenty-five minutes. After an interval of thirty seconds, during which it was allowed to feed with the other chicks, it was replaced in the maze. At the end of twenty-five minutes, during which it had repeatedly gone to sleep, it was replaced with the other chicks.

The following table gives the results in detail:

TABLE 8

CHICKS 1, 2, 3, 4, 6 AND 8 WERE NORMAL CHICKS. CHICKS 21, 22, 28, 29, 32 AND 35 WERE ALCOHOL CHICKS

No. of Chick	Trial				
	1	2	3	4	5
1......................	4′ 41.2″	40.2″	11.2″	2 ″	1.8″
2......................	4′ 20 ″	42 ″	13.6″	13 ″	2.2″
3......................	32.2″	18.6″	3 ″	4 ″	3.9″
4......................	6 ″	5 ″	4 ″	2.2″	2 ″
6......................	9′ 1 ″	1′ 35 ″	3′ 52 ″	1′ 13 ″	2′ 10 ″
8......................	3′ 22 ″	33 ″	10 ″	4 ″	3.6″
Average...............	3′ 40+″	38+″	45+″	16+″	23+″
21......................	1′ 59 ″	16 ″	20 ″	4 ″	5 ″
22......................	2′ 30 ″	32.8″	50.6″	15 ″	24 ″
28......................	39.9″	8.6″	16.4″	16 ″	6 ″
29......................	20′ 23 ″	6′ 42 ″	30 ″	17 ″	20.2″
32......................	19′	5 ″	15 ″	4.4″	3.6″
35......................	Failed				
Average...............	5′ 34+″	1′ 32+″	26+″	11+″	11+″

TABLE 8—*Continued*

No. of Chick	Trial				
	6	7	8	9	10
1......................	2 "	3 "	1 "	.9"	1 "
2......................	2.8"	1.4"	2.4"	1 "	2 "
3......................	3 "	4"	5 "	18.6"	2 "
4......................	2 "	2.4"	5 "	4 "	
6......................	2' 2.5"	4 "	6.8"	2.8"	3.4"
8......................	5.8"	4.4"	2 "	5 "	5 "
Average................	23+"	3+"	3+"	5+"	2+"
21......................	6 "	4 "	10.4"	5 "	2 "
22......................	18 "	4 "	4.8"	9.4"	4.4"
28......................	15 "	9 "	11.8"	5 "	5.8"
29......................	5 "	18 "	5 "	13 "	4.6"
32......................	3 "	2.8"	3 "	6.4"	2 "
35......................			Failed		
Average................	9+"	7+"	7+"	7+"	3+"

The second experiment with this maze was made on the chicks of the fifth hatching, consisting of six normal, four hole, six water and five alcohol chicks. The procedure was like that used with Maze 1.

The following table gives results in detail:

TABLE 9

CHICKS 2, 3, 4, 6, 10 AND 14 WERE NORMAL CHICKS. CHICKS 20, 21, 23 AND 25 WERE HOLE CHICKS. CHICKS 41, 43, 46, 47, 48 AND 51 WERE WATER CHICKS. CHICKS 71, 72, 74, 80 AND 81 WERE ALCOHOL CHICKS.

No. of Chick	Trial				
	1	2	3	4	5
2......................	2 "	3 "	3.5"	5 "	5.5"
3......................	9 "	6.5"	7 "	15 "	8 "
4......................	58 "	10.5"	4 "	14 "	3 "
6......................	4' 1.5"	13 "	4' 47 "	19 "	31 "
10......................	4 "	2 "	2.5"	3.5"	4.5"
14......................	30 "	39 "	4.5"	6 "	8.5"
Average................	57+"	12+"	51+"	10+"	10+"
20......................	1' 48 "	10 "	15 "	4.5"	3.5"
21......................	35 "	21 "	12.5"	14.5"	11 "
23......................	15 "	31 "	15 "	10 "	5 "
25......................	5'	11.5"	26.5"	4 "	4.5"
Average................	3' 24+"	18+"	17+"	8+"	6+"

TABLE 9—*Continued*

	Trial				
No. of Chick	1	2	3	4	5
41.....................	1′ 3 ″	14 ″	12 ″	5 ″	3.5 ″
43.....................	8′ 5 ″	10′ 42 ″	18 ″	4 ″	4 ″
46.....................	1′ 35 ″	47 ″	25 ″	23 ″	21 ″
47.....................·	55 ″	17 ″	22 ″	12 ″	10 ″
48.....................	7.5″	22 ″	5 ″	4 ″	2.5″
51.....................	17.5″	1′ 2 ″	7 ″	35 ″	13 ″
Average................	2′+	2′ 12+″	16+″	13+″	9+″
71.....................	10 ″	4 ″	9 ″	12 ″	10 ″
72.....................ᵥ	12 ″	8 ″	5 ″	6 ″	47 ″
74.....................	1.5″	11 ″	16 ″	9 ″	9.5″
80.....................	6 ″	9′ 2 ″	8 ″	5 ″	3.5″
81.....................	43 ″	22 ″	8.5″	10 ″	7 ″
Average................	12+″	1′ 57+″	9+″	8+″	15+″

	Trial					No. of wrong turns
No. of Chick	6	7	8	9	10	
2............	7.5″	13 ″	6.5″	5 ″	13 ″	0
3............	22 ″	5.5″	8 ″	11.5″	13.5″	0
4............	7 ″	3.5″	3 ″	3 ″	3 ″	1
6............	8.5″	7 ″	18 ″	7 ″	18 ″	1
10............	6.5″	4 ″	5 ″	3 ″	7.5″	0
14............	3.5″	3 ″	3 ″	6 ″	6 ″	2
Average........	9+″	6+″	7+″	5+″	10+″	
20............	6 ″	4 ″	6.5″	3 ″	3 ″	0
21............	33.5″	11 ″	24.5″	44 ″	24 ″	0
23............	22 ″	11 ″	?	45 ″	7 ″	?
25............	1′ 27 ″	7 ″	17 ″	9.5″	4 ″	0
Average........	47+″	8+″	?	27+″	9+″	
41............	10.5″	3 ″	4 ″	8 ″	9 ″	0
43............	12 ″	3 ″	4 ″	5 ″	4 ″	1
46............	11 ″	6.5″	15 ″	19 ″	17 ″	?
47............	17 ″	13 ″	20 ″	4 ″	9 ″	1
48............	2.5″	2.5″	2.5″	3 ″	2.5″	1
51............	7.5″	1′ 13 ″	25 ″	7 ″	8 ″	2
Average........	10+″	15+″	11+″	7+″	8+″	
71............	15 ″	20 ″	6 ″	13 ″	21 ″	3
72............	1′ 17 ″	10 ″	4′	1′ 40 ″	7′ 6 ″	0
74............	8 ″	17 ″	12.5″	19 ″	8.5″	2
80............	4.5″	3 ″	3 ″	3 ″	5 ″	1
81............	3 ″	5 ″	4 ″	5 ″	15 ″	0
Average........	21+″	11+″	53+″	28+″	1′ 15+″	

Maze No. 3

Maze 3 consisted of a series of short, straight alleys arranged in the following pattern:
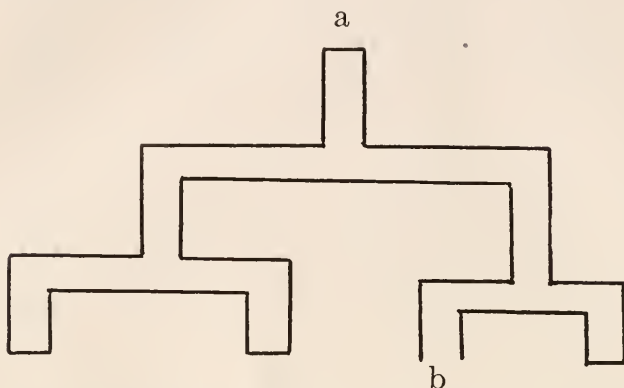
a was the point at which the chick was placed in the maze.
b was the open exit where the chick emerged at the edge of the table holding the maze and ran down a short incline into the chick pen ten inches below the table edge.

The chicks used with this maze were those of the fifth hatching. Each chick was given thirty successive trials without interval. The problem appeared to be as difficult as it could be and still be solved by the normal chicks. But even here the hole, water and alcohol chicks were at a disadvantage only during the earlier trials. Their records for the last ten trials are as good as those of the normal chicks.

Certain of the chicks of this hatching made little or no improvement in the course of the tests with Maze 2. These were chicks 10, 21, 51, 71 and 72. Chick 21 died before the tests with Maze 3 were begun. Of the others the only one which did not make a record which showed the normal rate of improvement in Maze 3 was chick 10, a normal chick. Chick 43 was the only other chick whose behavior was unusual in both mazes. This chick was amazingly sluggish during the early trials in Maze 2. Its record for that maze is entirely normal, however, in its improvement as the trials progressed. This sluggishness was not apparent in Maze 3 but the time record increases instead of decreasing gradually as the trials progress.

Chick 43 was a water chick. Alcohols 71 and 72, who made very bad records in Maze 2, both made excellent records in Maze 3. Water 51, although slow in Maze 3, showed a distinctly normal rate of improvement. If consistent inability to decrease the time in running a maze is any indication of inability to acquire a new co-ordination then our results would indicate that the only chick we had which showed such inability was one hatched from an egg any unusual characteristic of which we were neither responsible for nor cognizant of.

The following table gives the results for Maze 3.

TABLE 10

CHICKS 2, 4, 10 AND 14 WERE NORMAL CHICKS. CHICKS 20, 23 AND 25 WERE HOLE CHICKS. CHICKS 41, 43, 46, 47, 48 AND 51 WERE WATER CHICKS. CHICKS 71, 72, 74, 80, AND 81 WERE ALCOHOL CHICKS.

	Trial					
No. of Chick	1	2	3	4	5	6
2.............	2′ 15 ″	38 ″	30 ″	38 ″	25 ″	31 ″
4.............	42 ″	1′ 2 ″	12 ″	50 ″	44.5″	27 ″
10............	10 ″	11 ″	28 ″	17 ″	10.5″	10 ″
14............∴.	1′ 1.5″	41 ″	4 ″	16 ″	27 ″	21 ″
Average.......	1′ 2+″	38 ″	18+″	30+″	26+″	22+″
20............	13′	32.5″	52 ″	14′ 16 ″	31 ″	13 ″
23............	33 ″	55 ″	18 ″	45 ″	1′ 55 ″	1′ 4 ″
25............	1′ 7 ″	1′ 34 ″	8.5″	28.5″	1′ 36 ″	1′ 7 ″
Average.......	4′ 53+″	1′+	26+″	5′ 9+″	1′ 20+″	48+″
41............	34 ″	27 ″	2′ 44 ″	6′ 46 ″	43.5″	2′ 24 ″
43............	33 ″	8 ″	25 ″	29 ″	16 ″	16 ″
46............	1′ 19 ″	41.5″	2′ 1.5″	44 ″	1′ 37.5″	47 ″
47............	3′ 20 ″	43 ″	17 ″	38 ″	25 ″	42 ″
48............	28 ″	25 ″	2′ 30.5″	50 ″	33.5″	7 ″
51............	1′ 9 ″	2′ 50 ″	29 ″	6′ 11 ″	20 ″	9 ″
Average.......	1′ 13+″	52+″	1′ 24+″	2′ 37+″	39+″	44+″
71............	33.5″	10.5″	25 ″	5 ″	27 ″	11.5″
72............	5′ 30 ″	8′ 7 ″	5′ 16 ″	5′ 57 ″	3′ 12.5″	3′ 28 ″
74............	17 ″	53.5″	43 ″	51 ″	25.5″	3′ 34 ″
80............	48 ″	8.5″	5 ″	12 ″	9 ″	4.5″
81............	22 ″	14 ″	51 ″	18 ″	1′ 28 ″	41 ″
Average.......	1′ 30+″	1′ 54+″	1′ 28+″	1′ 28+″	1′ 8+″	1′ 35+″

TABLE 10—*Continued*

No. of Chick	Trial					
	7	8	9	10	11	12
2............	1′ 21 ″	43 ″	1′ 11 ″	13 ″	30 ″	18 ″
4............	20 ″	1′ 52 ″	37 ″	58.5″	1′ 2.5″	27 ″
10............	11 ″	4 ″	9 ″	3 ″	4 ″	12 ″
14............	23 ″	40 ″	13.5″	8.5″	9 ″	20 ″
Average.......	33+″	49+″	32+″	20+″	26+″	19+″
20............	42 ″	46 ″	7 ″	9 ″	7.5″	12 ″
23............	59 ″	49 ″	1′ 45.5″	40.5″	25 ″	1′ 12 ″
25............	18.5″	36 ″	30 ″	6 ″	5 ″	13 ″
Average.......	39+″	43+″	47+″	18+″	12+″	32+″
41............	1′ 1 ″	15 ″	7 ″	6 ″	7 ″	7 ″
43............	13.5″	9.5″	14.5″	24.5″	34 ″	20.5″
46............	20 ″	59 ″	1′ 6 ″	12 ″	19 ″	25 ″
47............	36 ″	25 ″	1′ 29 ″	23.5″	33 ″	20 ″
48............	34 ″	10 ″	15 ″	12.5″	11 ″	20 ″
51............	11.5″	22 ″	18 ″	18 ″	21 ″	3′ 2 ″
Average.......	29+″	23+″	34+″	16+″	20+″	45+″
71............	21 ″	11 ″	8 ″	58 ″	16 ″	4 ″
72............	1′ 1 ″	35 ″	55 ″	30 ″	1′ 1 ″	58.5″
74............	2′ 5″	16.5″	12 ″	16 ″	18.5 ″	19 ″
80............	5 ″	6 ″	7.5″	4 ″	43 ″	8 ″
81............	3′ 32 ″	1′ 13 ″	1′	7′ 53 ″	17 ″	1′ 19 ″
Average.......	84+″	28+″	28+″	1′ 56+″	31+″	33+″

No. of Chick	Trial					
	13	14	15	16	17	18
2............	40 ″	39 ″	39 ″	50 ″	43 ″	1′ 23 ″
4............	7 ″	3′ 8 ″	25 ″	30 ″	22 ″	1′ 36.5″
10............	4 ″	18 ″	5 ″	24 ″	28 ″	10 ″
14............	29 ″	6 ″	7′ 52 ″	15 ″	14 ″	2′ 31 ″
Average.......	20+″	1′ 2+″	2′ 15 ″	29+″	26+″	1′ 25+″
20............	1′ 27 ″	11.5″	38.5″	2′ 54 ″	10′ 56.5″	39 ″
23............	30 ″	3′ 4 ″	22.5″	35 ″	19 ″	27 ″
25............	22 ″	23 ″	25 ″	20 ″	21.5″	5.5″
Average.......	46+″	1′ 12+″	28+″	1′ 16+″	3′ 52+″	23+″

TABLE 10—*Continued*

Trial

No. of Chick	13	14	15	16	17	18
41............	6.5″	7 ″	8 ″	7 ″	8 ″	7 ″
43............	16 ″	29 ″	24 ″	15 ″	12.5″	13 ″
46............	13 ″	15 ″	16 ″	15 ″	21 ″	19 ″
47............	30 ″	55 ″	13.5″	38 ″	1′ 23.5″	39.5″
48............	14 ″	4 ″	21 ″	5 ″	27 ″	11.5″
51............	1′ 26 ″	17 ″	1′ 51 ″	25 ″	16.5″	46.5″
Average.......	25+″	21+″	32+″	17+″	28+″	22+″
71............	5 ″	19 ″	4 ″	4″	16 ″	4 ″
72............	55 ″	39.5″	47 ″	38 ″	53.5″	22 ″
74............	15 ″	19 ″	51 ″	29 ″	42 ″	14 ″
80............	3 ″	3 ″	6 ″	6 ″	4 ″	3.5″
81............	32 ″	30 ″	2′ 6 ″	1′ 36 ″	19 ″	16 ″
Average.......	22+″	22+″	46+″	34+″	26+″	11+″

Trial

No. of Chick	19	20	21	22	23	24
2............	45 ″	21 ″	16.5″	58.5″	15 ″	15 ″
4............	1′ 4.5″	21.5″	21.5″	6 ″	9 ″	9 ″
10...........	40 ″	12 ″	16 ″	19 ″	6.5″	7.5″
14...........	30 ″	9 ″	5 ″	22 ″	6 ″	5 ″
Average.......	37+″	15+″	14+″	26+″	9+″	9+″
20...........	6 ″	15 ″	9 ″	9 ″	7.5″	9 ″
23...........	48 ″	1′	42 ″	24 ″	29 ″	29 ″
25...........	19.5″	5 ″	5 ″	4 ″	4 ″	40 ″
Average.......	24+″	26+″	18+″	12+″	13+″	26+″
41...........	16 ″	1′ 11.5″	10 ″	8 ″	6 ″	5 ″
43...........	59 ″	1′ 33 ″	33 ″	25.5″	44 ″	1′ 5 ″
46...........	8 ″	13 ″	16 ″	58. ″	1′	14 ″
47...........	2′ 25 ″	18 ″	17 ″	15 ″	1′ 16 ″	1′ 36 ″
48...........	5 ″	6 ″	6 ″	4 ″	5 ″	19 ″
51...........	24 ″	3′ 23 ″	2′ 41 ″	12.5″	1′ 55 ″	14 ″
Average.......	42+″	1′ 7+″	40+″	20+″	51+″	35+″
71...........	5 ″	3 ″	3 ″	11 ″	3 ″	18 ″
72...........	43 ″	21 ″	46 ″	44 ″	45 ″	30 ″
74...........	15 ″	26 ″	11 ″	9 ″	1′ 23 ″	14 ″
80...........	13 ″	3.5″	7.5″	4 ″	4 ″	5 ″
81...........	14 ″	16 ″	14 ″	10.5″	6 ″	16.5″
Average.......	18+″	13+″	16+″	17+″	28+″	16+″

TABLE 10—*Continued*

No. of Chick	Trial 25	26	27	28	29	30	No. of errors
2.........	9 "	20 "	18 "	57.5"	49 "	36 "	21
4.........	24 "	39 "	1' 8 "	23 "	28 "	10 "	26
10.........	28 "	43 "	26 "	1' 24 "	53 "	7 "	14
14.........	11 "	5 "	27 "	15 "	9 "	12 "	19
Average.....	18+"	26+"	34+"	44+"	34+"	16+"	
20.........	7.5"	22 "	29 "	32 "	7 "	30.5"	13
23.........	43 "	51 "	18 "	31 "	4 "	35 "	20
25.........	5 "	36 "	24 "	6 "	6 "	21 "	20
Average.....	18+"	36+"	23+"	23+"	5+"	28+"	
41.........	5 "	7 "	6.5"	11 "	9.5"	6 "	8
43.........	21 "	50 "	30 "	32 "	53 "	41 "	23
46.........	12.5"	29 "	28 "	1' 3 "	23 "	9 "	21
47.........	8 "	19 "	19 "	29 "	23 "	11 "	12
48.........	5 "	6 "	4 "	4 "	10.5"	12.5"	16
51.........	1' 43.5"	1' 33 "	1' 13 "	2 "	36 "	2' 13 "	8
Average.....	25+"	34+"	26+"	23+"	25+"	35+"	
71.........	6 "	3 "	10.5"	2.5"	3 "	5.5"	14
72.........	1' 21 "	47 "	1' 38 "	55 "	45 "	1' 3.5"	29
74.........	10 "	19 "	26 "	11.5"	23 "	8 "	14
80.........	5 "	5 "	4.5"	1' 11 "	14 "	24 "	11
81.........	8 "	5 "	4 "	7 "	4 "	4 "	18
Average.....	22 "	15+"	28+"	29+"	17+"	21+"	

EXPERIMENTS WITH SENSORY DISCRIMINATION

The apparatus used for testing the ability of the chicks to make sensory discriminations was the Yerkes visual choice apparatus. Only the two middle alleys were used, the other two being shut off by wooden partitions. Stimulus screens with openings in them large enough to permit the chick to pass through were slipped into the grooves at each end of each alley. The screens were made of photographic mounting cardboard and two of them were light grey and two dark grey in color. The exit path in which the light grey screens were placed was always open and the chick choosing that path progressed directly out of the apparatus to the chicken pen and the society of the other chicks. The exit path characterized by the dark screens was always closed at the far end and the

wires crossing the floor of the path were electrically charged so that the chick choosing that path received a slight shock and did not get out of the apparatus until it had gone back and found the other exit. The light screens were placed alternately in the left and right hand alley.

The chick to be tested was placed in the release box at the back of the apparatus and the wire screen which led to the paths was not lifted until the chick crowded against or pecked at it. No chick was ever left struggling in the release box. The chick was always allowed to find its way in time into the correct alley and out of the apparatus but its record for the trial depended on its first choice of exit paths. Each chick was given ten preference trials with both exits open and the wires not charged. The one chick which showed a preference was not used in these experiments. Chicks of the third hatching were used with this apparatus.

Six normal and five alcohol chicks were each given three trials a day for twenty-five days. Immediately after this normal No. 5 and alcohol No. 24 and six days later normal No. 13 and alcohol No. 33 were given thirty additional trials in succession. The records for the last fifteen trials at the end of the first seventy-five trials are as follows: one normal chick made $73\frac{1}{3}\%$ correct choices; two made 60% correct choices; one made $46\frac{2}{3}\%$ correct choices; one made 40% correct choices; one alcohol chick (No. 24) made 80% correct choices; two made $46\frac{2}{3}\%$ correct choices; one made $33\frac{1}{3}\%$ correct choices, and one made $26\frac{2}{3}\%$ correct choices. The records for the last ten of the thirty additional trials given four of the chicks are as follows: normal No. 5 made 100% correct choices; normal No. 13 made 90% correct choices; alcohol No. 24 made 60% correct choices; and alcohol No. 33 made 40% correct choices.

Chicks of the fourth hatching were also used in this apparatus. These chicks were trained in pairs, each pair being composed of a normal and an alcohol chick. One normal chick was given a trial. Then an alcohol chick was given a trial. Then the normal chick was retested and the alcohol chick retested and so on. This procedure was continued until one of the chicks had made ten consecutive correct choices. Tests with that pair were then discontinued and tests with a new pair begun.

Normal No. 14 and alcohol No. 37 were each given 101 trials.

Normal No. 14's percentage of correct choices during the last
ten trials was 100; alcohol No. 37's was 30.   Normal No. 18
and alcohol No. 30 were each given 75 trials.   During the last
ten trials the normal chick's record was 100% correct choices
and the alcohol's record was 50% correct choices.   Normal No.
15 and alcohol No. 34 were each given 67 trials.   The normal
chick made a record of only 70% correct choices during the
last ten trials whereas the alcohol chick made a record of 100%.

The alcohol chicks plainly formed the association more slowly
than did the normal chicks and there were alcohol chicks which
seemed unable to form the association in the time at our dis-
posal for training them.   But as in the experiment with the
mazes there were individuals among the alcohols which did as
well as normal chicks and there were normal chicks which did
as badly as the alcohol chicks.

INHIBITION OF AN INSTINCTIVE REACTION

The apparatus used in this experiment was a large square
of dark grey paper over which was placed a pane of glass the
exact dimensions of the paper.   On the paper under the glass
were scattered bits of egg yolk.   Ten chicks of the fourth hatch-
ing, five normal and five alcohol, were used in this experiment.
The group of normal chicks was placed on the glass for five
minutes each day and the total number of pecks of all five
chicks was recorded.   The chicks were then replaced in the
box and the same procedure repeated with the group of alco-
hols.   These tests were repeated for twenty-five days.   There
was no appreciable difference in the behavior of the two groups.
The alcohol chicks learned to inhibit the reaction with approx-
imately the same rapidity as the normal chicks.

The following table gives the number of pecks each group
made on each of the trial days.

TABLE 11

	1	2	3	4	5	6	Day 7	8	9	10	11	12	13
No. of pecks made by normal chicks........	4	6	6	2	1	2	1	0	0	0	1	2	2
No. of pecks made by alcohol chicks........	4	6	6	1	3	0	1	0	4	0	0	0	1

TABLE 11—*Continued*

						Day						
14	15	16	17	18	19	20	21	22	23	24	25	26
No. of pecks made by normal chicks........ 0	1	2	1	2	4	2	5	1	1	0	0	1
No. of pecks made by alcohol chicks........ 1	0	3	3	2	5	3	4	0	3	0	1	0

INHIBITION OF AN ACQUIRED REACTION

It will be remembered that the chicks of the fifth hatching were used in Maze 2. This maze was a reversible maze so constructed that after it had been used with the exit at one side it could be turned over and present the same problem, except that the exit would be at the other side, requiring the chick to turn in the opposite direction from that in which it had formed a habit of turning. Each chick of the fifth hatching was given ten trials in this maze (for record see Table 9) and immediately thereafter the maze was reversed and the chick given ten more trials. The chicks which failed successfully to inhibit the previously acquired reaction were normal chick No. 2 and alcohol chicks Nos. 74 and 80. Chicks Nos. 10, 21, 51 and 72 made very poor records but these chicks, it will be remembered, had never acquired the proper reaction in the maze during the first ten trials. They were equally unsuccessful when the maze was reversed. These four chicks, it will be noted, represent the four different groups of chicks obtained in this hatching. In the matter of inhibiting an acquired reaction these results seem to give no pronounced advantage to any group of chicks.

The following table gives the results for Maze 2 reversed:

TABLE 12

CHICKS 2, 3, 4, 6, 10 AND 14 WERE NORMAL CHICKS. CHICKS 20, 21 AND 25 WERE HOLE CHICKS. CHICKS 41, 43, 47, 48 AND 51 WERE WATER CHICKS. CHICKS 71, 72, 74, 80 AND 81 WERE ALCOHOL CHICKS

No. of Chick	Trial				
	1	2	3	4	5
2.....................	8.5″	18 ″	8.5″	10 ″	7.5 ″
3.....................	1′ 34.5″	26.5″	10.5″	10 ″	19 ″
4.....................	2 ″	2 ″	4 ″	3 ″	3.5″
6.....................	6′ 42.5″	17 ″	3′ 28 ″	39 ″	26 ″
10.....................	16.5″	3 ″	13 ″	4 ″	14.5″
14.....................	4 ″	2 ″	3 ″	2.5″	2 ″
Average.................	1′ 28+″	11+″	41+″	11+″	12+″

TABLE 12—*Continued*

No. of Chick	Trial				
	1	2	3	4	5
20......................	1′ 3 ″	37 ″	13 ″	15 ″	13 ″
21......................	51.5″	37 ″	15.5″	33 ″	2′ 54 ″
25......................	12′ 57 ″	2′ 45 ″	1′ 54 ″	8 ″	21.5″
Average.................	4′ 57+″	1′ 19+″	47+″	18+″	1′ 9+″
41......................	27.5″	28 ″	9 ″	29 ″	8 ″
43......................	9 ″	8 ″	5 ″	12 ″	24 ″
47......................	1′ 3 ″	10 ″	34 ″	18 ″	16 ″
48......................	4′ 51 ″	10 ″	10 ″	4 ″	16 ″
51......................	25 ″	30 ″	13 ″	6.5″	8.5″
Average.................	1′ 23+″	17+″	14+″	13+″	14+″
71......................	20 ″	8 ″	3 ″	5 ″	6 ″
72......................	30 ″	21 ″	45 ″	17 ″	8′ 15 ″
74......................	12.5″	6 ″	5.5″	5 ″	11 ″
80......................	5 ″	13 ″	15.5″	7 ″	17 ″
81......................	7′ 12 ″	1′ 4.5″	14 ″	11 ″	5 ″
Average.................	1′ 38+″	22+″	16+″	9+″	1′ 46+″

No. of Chick	Trial					No. of wrong turns
	6	7	8	9	10	
2.............	19 ″	7 ″	19 ″	8 ″	31 ″	10
3.............	15 ″	6 ″	10 ″	12.5″	9.5″	0
4.............	3 ″	4 ″	2.5″	3.5″	3 ″	0
6.............	8 ″	6 ″	5 ″	1′ 3 ″	13.5 ″	3
10.............	4.5″	15.5″	15.5″	6.5″	25 ″	2
14.............	3.5″	2 ″	2.5″	5 ″	2 ″	0
Average........	8+″	6+″	9+″	16+″	14+″	
20.............	13 ″	28 ″	14.5″	17.5″	10 ″	2
21.............	35 ″	21.5″	3′ 10 ″	31 ″	46.5″	3
25.............	6.5″	45 ″	5.5″	5.5″	5 ″	3
Average........	18+″	31+″	1′ 10+″	18+″	20+″	
41.............	13 ″	23 ″	20 ″	7.5″	19.5″	4
43.............	14 ″	10 ″	32 ″	8 ″	9 ″	6
47.............	20 ″	8 ″	19 ″	4 ″	8 ″	2
48.............	12 ″	17 ″	9 ″	4 ″	12 ″	6
51.............	36 ″	16 ″	43 ″	1′ 40 ″	37.5″	2
Average........	19+″	14+″	24+″	24+″	17+″	
71.............	4 ″	5 ″	9 ″	3 ″	4 ″	1
72.............	6′ Became so inactive the experiment had to be dropped.					5
74.............	3.5″	8 ″	12 ″	8 ″	12.5″	0
80.............	13 ″	6 ″	17 ″	23 ″	4.5″	1
81.............	4.5″	4 ″	3.5″	20 ″	10 ″	1
Average........	1′ 15+″	5+″	10+″	13+″	7+″	

CONCLUSIONS

1. Chicks are neither positively or negatively phototropic. Some show what appears to be an instinctive positive response to light on the first but not on the second and third day; some on the second but not on the first and third day; a few not until the third day and some not at all.

2. Imitation plays no part in the perfecting of the pecking reaction of either normal or alcohol chicks.

3. It is possible by tampering with eggs before the hatching of chicks to modify the behavior of the chicks in the following ways; on the fifteenth day they do not show the caution in jumping from heights which chicks hatched from normal eggs show all the time and which the chicks hatched from abnormal eggs show earlier than the fifteenth day; they are less likely than normal chicks to react to a maze situation with general motor activity and consequently are slower in beginning to acquire the consequent motor co-ordination though they may eventually acquire it in the same number of trials required for a normal chick; they are slower in acquiring an association depending on sensory discrimination in the Yerkes visual choice apparatus; the instinctive reactions of pecking and drinking apparently remain unmodified; the processes of inhibition of both instinctive and acquired reactions seem to be alike in normal and abnormal chicks.

4. It is not possible to find any difference between the instinctive reactions of pecking or between the modifications of the acquiring of reactions in the maze in the case of chicks raised from eggs into which alcohol has been injected by our method, and chicks raised from eggs into which distilled water has been injected or eggs which have had the shell perforated and sealed. That is, alcohol, *per se*, seems to have no specific effect beyond an effect which can easily be explained by malnutrition during hatching and which may be as readily produced by other agents as by alcohol.

DEATH FEIGNING REACTIONS IN *TYCHIUS PICIROSTRIS*

E. MELVILLE DuPORTE

Biological Laboratories, Macdonald College (McGill University), Canada

The behavior of the lower organisms is of importance, not only for the intrinsic interest attached to the study of the subject but also for the light which it may throw on the more complicated reactions of the higher organisms. Any contributions, therefore, which will add to our knowledge of any phase of animal behavior or confirm results already obtained in this field, which has not been greatly exploited, will be of some interest to the student of comparative psychology; and for this reason the writer is publishing the following brief notes on observations incidentally made while studying the habits of *Tychius picirostris*, an European weevil observed this year for the first time in this country doing appreciable injury to clover.

The habit of feigning death is found in a large number of animals but is most marked in certain insects. This habit among insects is of interest not only to the student of behavior but also to the collector and to the applied entomologist. The entomological collector often takes advantage of this reaction in collecting beetles and other insects which fall to the ground in a death feint when a sudden jar is given to the plant on which they are feeding, and this practice of jarring has been used effectively in the control of certain insect pests such as the May beetles (*Lachnosterna* spp.) and the plum curculio (*Conotrachelus nenuphar* Herbst), especially prior to the advent of arsenical sprays.

Methods of Producing the Feint. The weevils congregate in large numbers on the leaves of the clover in the spring, and on the flower heads later in the season. If a plant attacked by these weevils is jarred, the majority of the insects will fall to the ground. Their action upon falling shows considerable individual variation; most of those which fall on their backs

will assume the death feigning attitude for a few seconds, and, on recovery, turn over and either scramble away immediately or remain quiescent for a brief period before moving away. A few of those which fall on their backs will not feign death but will turn over and move away at once.

Of those which fall to the ground right side up some will remain quiet for a short time with their legs in the normal resting position, others will run away immediately on reaching the ground but very few will assume the typical death feigning attitude.

In the laboratory the feint was obtained in one of three ways: by dropping the insect on the desk, by pinching it lightly with a forceps or by merely turning it on its back. The last method was usually successful in evoking the death feigning response and was generally employed. After remaining in the feint for a variable period the insect relaxes its legs and struggles to turn over. On turning over, or on being turned over the insect scrambles away, but while it is running it may be induced to feign a second time by again turning it on its back, and within certain indefinite limits to be indicated below this process may be repeatedly successful.

While struggling on its back the insect may be induced to feign death by tapping it on the sternum. If, however, it is in the normal position, with its back turned up it will not feign death on being tapped on the back; on the contrary a quiescent insect thus treated will become active.

The intensity of the shock seems to have no effect on the production or duration of the death feint, as an insect which has been merely turned over, or dropped from a height of six inches remains in the death feint as long as one dropped from a height of eight feet or more. It was also found that if the feint could not be elicited by overturning the insect or by dropping it from a height of six inches or thereabouts, it was impossible to produce it by dropping from greater heights up to eight feet, or even by lifting with forceps and forcibly dashing to the table.

It was found impossible to obtain the death feigning reaction with some individuals. As the insects experimented on had matured some time previous to the period of these investigations and had not been under constant observation from the

time of eclosion it is not possible to say whether these individuals always reacted negatively, or from what cause they had lost the power of response.

Death Feigning Attitudes. The attitude typically assumed by the insect during the death feint is not a simulation of the attitude of the dead insect. In death the femora are always extended more or less perpendicularly from the ventral surface of the body, and are never pressed against the sternum, even if the insect is killed when in the feigning attitude. The tibiae and tarsi are flexed in such a way that the latter are often more or less intertwined and always quite close to each other. In the death feigning attitude the legs are all pressed closely against the sternum and the tarsi are never very close to each other.
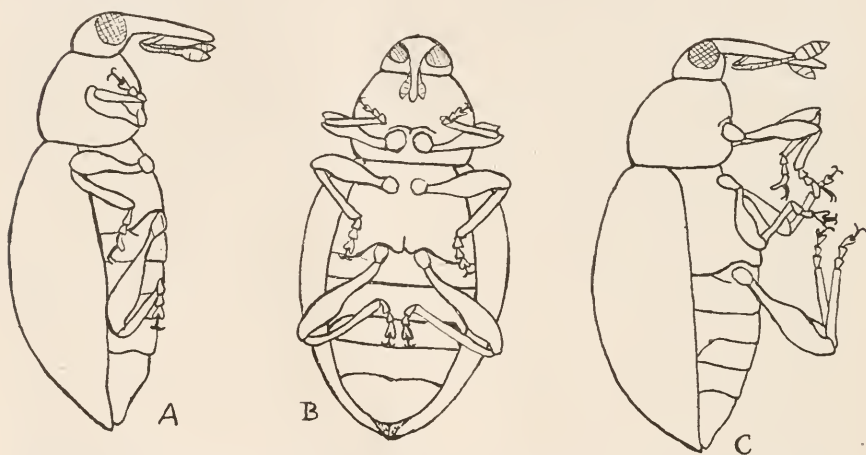
FIGURE 1.—Death-feint of *Tychius picirostris.* A and B, lateral and ventral views of the death-feigning attitude. C, lateral view of the insect after death. ×21

The fore femora extend straight out laterally, pressed against the prosternum, the tibiae are bent back against the ventral face of the femora and the tarsi are bent forward and outward. The middle femora also extend laterally and slightly forward, the tibiae bend caudo-mesad, their apex being situated in front and to one side of the meta-coxae. The tarsi run either straight or obliquely backwards. In the hind legs the femora are stretched obliquely backwards, the tibiae bent forward almost parallel to

the femora and the tarsi bent backwards. The rostrum is almost perpendicular to the body and the antennae are folded together behind the rostrum.

Often the insect becomes quiescent on being stimulated, without assuming the attitude described in the foregoing paragraph. In such cases it may remain perfectly still with the legs outstretched or partially and asymetrically flexed. This attitude I have termed the partial feint and it will thus be referred to when necessary to distinguish it from the typical feint. Sometimes the insect when stimulated assumes the typical death feigning attitude, but after a while it slowly relaxes its legs without becoming active. Usually but not invariably the partial feint is manifested after the insect has been repeatedly stimulated. It is therefore probable that the failure to flex the legs is due to muscular fatigue.

Variability of the Feigning Response. The feigning response to tactual or shock stimuli is not stereotyped as there exists a considerable range of variability in the duration of the feint, not only in the different individuals but in the same individual in successive feints. In some cases too, as stated above, I found it impossible to evoke the feigning response by any means. The reaction of mutilated specimens was also not constant owing no doubt to slight differences in the sensitiveness of the nervous system which would influence the intensity of the shock effects of mutilation. While any general statement made is based on the results of the reaction of the majority of individuals, the number failing to give the typical response was in some cases considerable, and for this reason special attention is called to the fact here.

As to the exact cause of this variability I am unable to give a positive explanation. Probably, however, it is not wholly due to the inherent individuality of the specimens but partly to the varying "experiences" of the individuals. If the insects had been kept under the same conditions from the time of their eclosion it is probable that the reactions would be more nearly uniform, or where a wide variability exists there would be an evident explanation.

Duration of the Death Feint. The duration of the feint at room temperature is usually very short, the insect recovering almost invariably before the expiration of a minute. The

longest feint obtained in these experiments lasted for seven minutes and twenty seconds. This case was unique, but occasionally feints lasting over a minute or even as long as two minutes were obtained. There seems to be no definite relation between the durations of successive feints. They are not gradational nor do they vary proportionately in any two individuals examined.

TABLE I

DURATION IN SECONDS OF TEN SUCCESSIVE FEINTS OF SEVEN INDIVIDUALS

	1	2	3	4	5	6	7	8	9	10	Average
B.......	15	11	22	15	15	10	5	0	3	10	10.6
C.......	5	10	15	14	6	11	9	18	10	7	10.5
D.......	12	7	440	36	31	10	277	2	4	32	85.1
E.......	10	8	20	7	15	48	15	0	3	20	14.6
F.......	*0	125	10	13	40	25	8	30	28	20	29.9
G.......	30	60	6	6	10	35	25	20	5	3	20.0
I.......	*0	*0	†3	0	†4	16	†80	18	15	15	15.1
Average...	10.3	31.6	73.7	13.0	17.3	22.1	59.9	12.6	9.7	15.3	26.5

* Failure to respond to stimulation.
† Partial feint.

Effects of Repeated Stimulation on the Death Feint. Experiments were conducted to determine whether the death feint could be induced indefinitely by repeated stimulation. It was found that the feint could not be elicited indefinitely, but the number of times that it could be elicited before the insect ceased to respond varied considerably with different individuals. In some cases the insect would feign death only a few times and then refuse to respond further, and in no case was I able to elicit more than forty successive feints. The results of other workers may be of interest in this connection. " Holmes found in the case of ten *Ranatras* successively put into death feints that these were continued without interruption from 9 a. m. to 5 p. m., when the last specimen refused to feign longer. The Severins found it possible in the case of *Belostoma* to induce feints successively for a total of five hours. The responses of the curculio (*Conotrachelus nenuphar* Herbst.) were very much less pronounced than was the case of these forms. Feints could not be elicited successively for a period of greater length

than two hours, fifty-three representing the largest number of feints successively produced in a single individual." [1]

The results obtained with *Tychius picirostris* did not differ markedly from those of Gee and Lathrop with the plum curculio, but the period during which the feint could be successively elicited was not so great, varying from a few minutes to somewhat over an hour.

Repeated stimulation results in a reduction of the average duration of the feints, although the duration of one of the later feints may be greater than that of some occurring earlier in the succession. The following table gives the average duration of the first ten feints of four individuals as compared with that of all succeeding feints. In computing the averages, cases in which the insects did not respond are omitted. If these were included the average duration of the later feints would be much lower.

TABLE II

AVERAGE DURATION (IN SECONDS) OF EARLIER AND LATER FEINTS

	D	F	G	I
First ten feints..................	85.1	29.5	20.0	27.4
Feints after tenth................	17.6	18.6	5.7	9.5

There is a certain irregularity to be noted in the later feints. With few exceptions, in cases where a long succession of feints was obtained, the first several attempts to produce the feint were successful. Later, however, the number of unsuccessful attempts increased until finally the point was reached at which the feint could no longer be elicited.

When the limit of successful response was reached the method of producing the shock stimulus was changed to discover whether this would have any effect in inducing the feint. It was found that in most cases either the insect did not respond, or it responded in the first few trials only. Only in one case did I succeed in obtaining a long succession of feints by changing the method of evoking the feint after the insect had failed to respond to the first means employed, and in this case seventy-six per cent were partial feints.

[1] Gee and Lathrop. Death Feigning in *Conotrachelus nenuphar* Herbst. *Annals Entomological Society of America*, 1912, **5**, 391-399.

Another question which suggested itself was whether the insect would recover its sensitiveness if allowed to rest. It was found that after one or two hours' rest the reaction was in general similar to that obtained by changing the method of producing the shock, except that there was a larger number of fairly long successions.

The history of the three following cases will serve to illustrate more definitely some of the points discussed in this section:

D1. Left for an hour after the fourteenth feint. On resuming the experiment, the first four trials were successful; of the six next, three were successful and after this there was a long series of failures with an occasional success. The method of inducing the feint was then changed and the insect dropped on its back instead of being merely turned over. In the first eight attempts there were five successes but after this, repeated endeavor could elicit no response.

E1. The feint was produced immediately by the first seven attempts. The fifteen following elicited the feint eight times, and after that the insect feigned death only twice in twenty trials. The method of producing the shock was changed and the insect feigned three times in the first ten trials.

I.   In the first forty-five trials there were thirty-three successes and after this a long succession of failures. The insect was left for an hour and the trials were then resumed. The first three attempts were successful, but after these twenty successive attempts elicited no response. A change in the method of stimulating the feint resulted in the production of several partial feints but few perfect responses.

During the feint the muscles of the legs are very tensely contracted and Gee and Lathrop suggest that muscular fatigue eventually occurs as a result of this contraction, thus explaining in part the failure to elicit indefinite response.

Effect of Mutilation on the Death Feint. Several specimens were placed in the death feint and while in this condition por-

tions of some or all of the legs were snipped off. In most cases the insect remained in the feint, either making no response or slightly twitching the legs. Sometimes, however, the insect ·became active on being dismembered. In some cases in which the insect was in a partial feint the shock of removing the tarsi induced a perfect feint.

Removing the antennae of the feigning insect almost invariably met with no response, the weevil remaining perfectly quiescent. Individuals with the antennae and legs mutilated could always be induced to feign again.

Snipping off the beak always resulted in renewed activity on the part of the subject except in one case, when the four tarsi, both antennae and the rostrum were successively removed without any manifestation of activity. It was found impossible to induce the feint until some time after the mutilation, when the shock effects of the operation had passed away.

Cutting away the tip of the abdomen always caused the insect to cease feigning. Insects thus mutilated, however, could usually be induced to feign again, though often with more difficulty than in the case of the normal individuals.

Insects divided between the thorax and abdomen or between the pro- and meso-, or meso- and meta-thorax always responded by coming out of the death feint. The hinder portion could not again be induced to feign death. In fact it did not live very long after being cut off. The anterior portion, however, gave the death feigning response but the threshhold of stimulation was raised by the mutilation for it was necessary to drop it to the table several times, or to tap it several times on the sternum before the death feint could be elicited. In this connection it may be advisable to state that only individuals which reacted readily previous to mutilation were used in these tests.

Decapitation invariably results in a feverish activity of the limbs. The legs are worked to and fro, and the tarsi rubbed against each other. At room temperature it was found impossible to obtain the feigning reaction with decapitated individuals. This is probably due to the shock effects of the very violent disturbance in the central nervous system caused by the mutilation, and not to any direct control of the supra-oesophageal ganglion over the death feigning reaction.

The results obtained with *Tychius picirostris* agree in general with those obtained by other workers.

Influence of Temperature on the Death Feint. Heat.—Insects feigning death were placed on their backs on a warm iron plate, the temperature of which was not high enough to be unbearable to the tips of one's fingers. Without a single exception the insects immediately became active and attempted to turn over and escape. It was impossible to produce the feint by dropping the insect on the hot surface. When the plate became cooled to a temperature slightly above that of the room, the feint, however, could be induced without difficulty. Insects dropped several times alternately on the warm plate and on the surface of the table feigned death in the latter case but would not on the heated surface.

Cold. Several individuals were placed in a refrigerator registering a temperature of 11° C. The feint could be very readily elicited and the duration was much greater than at room temperature. The duration of the initial feint varied from 55 seconds to 4 minutes and 35 seconds. The variability of the duration of successive feints was as marked as at room temperature, as may be seen from the following figures, which give the duration (in seconds) of the first five feints of one individual:

$$55, \quad 40, \quad 140, \quad 385, \quad 50$$

Other individuals were tested on a plate of thin glass placed on a block of ice. The feint lasted for periods ranging from nineteen minutes to upwards of an hour. At the end of an hour those which had not recovered spontaneously were removed to the table, where they immediately became active. On first being placed on the cold plate the insect becomes somewhat restive but does not actively struggle. After a short while the legs slowly and gradually relax, the degree of relaxation varying with the different individuals. In this condition the legs are never pressed against the body but their attitude resembles to some extent that of the limbs of the dead insect.

Cold alone, without mechanical shock, can produce a condition similar to that of the death feint. If an insect struggling on its back is placed on the cold glass plate it will after a while cease to struggle, become quiescent and assume a position similar to the feigning insects. This raises the question as to whether

at low temperatures some other factor than those concerned in the production of the death feint does not come into play.

As stated above it was found impossible at room temperature to induce the feint in decapitated insects. Near the freezing point, however, the feint was evoked without difficulty. Under the microscope a slight twitching of the legs could be observed in the decapitated insect during the feint. On being removed to the table the insect resumed the twitching movements.

The anterior portion of weevils severed across the thorax also feigned death readily, and the duration of the feint was longer than at room temperature.

It will thus be seen that cold lowers the threshhold of stimulation and reduces the shock effects of mutilation.

These results agree closely with those obtained by Gee and Lathrop on *Conotrachelus nenuphar* Herbst and by Holmes on *Ranatra*.

Effect of Chloroform and Ether on the Death Feint. Insects feigning death were introduced into the vapor of chloroform and of ether. Chloroform seemed to have little effect on the duration of the first feint, but of fourteen individuals tested five could not be induced to feign a second time. The others with one exception could only be induced to feign death twice and this one exception was anaesthetised during the fourth feint.

TABLE III

The Effect of Chloroform on the Duration (in Seconds) of Feint, and on the Number of Successive Feints of Fourteen Individuals

1	2	3	4	5	6	7	8	9	10	11	12	13	14
2,3	15	20	*15,4	4,9	15	30	11,14 20	8, 14	2,2	14,6	17	13,7	20,3

* Partial feint.

In three cases, stimulated by pinching with forceps while lying on their backs, it was found that the insects would draw up their legs to the feigning attitude, but relaxed them and resumed their struggles on being released from the forceps.

In the case of ether the results were different. A longer succession of feints could be obtained, but the ether had the

effect of reducing the duration of the feints.   While the number of successive feints was higher than was the case under the effect of chloroform it was not as high as was obtained under normal laboratory conditions.   Only one individual feigned sufficiently often to be killed by the fumes of the ether.

TABLE IV

SHOWS THE AVERAGE DURATION IN SECONDS OF THE FIRST FEINT IN A LARGE NUMBER OF INDIVIDUALS UNDER NORMAL CONDITIONS AND UNDER THE INFLUENCE OF PHYSICAL AND CHEMICAL AGENTS

Normal	Heat	Cold (near 0° C.)	Chloroform	Ether
14.2	0	2020	13.3	5

The Nature of the Death Feigning Instinct.   The death feigning instinct occurs in many widely different animals, even among certain birds and mammals.   The advantage of the instinct to the possessor is a doubtful one.   In the case of insects and other animals, the color of which resembles that of the natural environment, the power of feigning death is an additional safe-guard against the prying eyes of the enemy.   But in many cases the death feint is not only useless but may be positively injurious, so that the instinct cannot wholly be regarded as an advantageous adaptation, nor can its origin and subsequent evolution be accounted for on the grounds of usefulness to its possessor.

The instinct undoubtedly has its roots in some fundamental physico-chemical reaction of zooplasm.   Holmes believes that in the amphipods the death feigning instinct has its foundation in the thigmotactic reactions common among these animals. The Severins also advance the theory that the reaction in *Nepa* and *Belostoma* is thigmotactic in nature.   The results obtained with *Tychius picirostris*, in the writer's opinion, corroborate the theory that the physico-chemical reaction responsible for the manifestation of the death feint is of the same nature as that which calls forth the thigmotactic response of many insects and other animals and also of such plants as the *Mimosas* and other " sensitive plants."   It must be borne in mind, however, that the statement that the death feigning instinct is thigmo-

tactic in nature is an explanation which in turn needs to be explained, and a positive explanation is not yet forthcoming. It is probably due, however, to some disturbance in the balance of the metabolic processes causing the excessive elaboration of some substance or substances which incite the contraction of the leg muscles.

The feigning reaction may perhaps be resolvable into two components, one manifested in the flexing of the leg appendages, the other in the quiescence of the insect. The fact that it is possible to induce a partial feint in which the insect is perfectly quiet while the legs are not flexed and, in some cases, after treatment with chloroform, to induce the flexing of the legs unaccompanied by the quiescent state, suggests that these two actions may be the result of separable causes, but the data at hand are too slender for a definite pronouncement on the subject.

Attention should also be called to the fact that the reaction is segmental and not controlled by the supra-oesophageal ganglion. The fact that a decapitated insect will not react at room temperature is in no way antagonistic to this view, because the removal of some of the most important trophic centres must necessarily cause some disturbance in the metabolic processes of the nervous system, and the intensity of the stimulus necessary to bring about a definite reaction will differ from that necessary under normal conditions; in other words, the threshhold of stimulation may be either lowered or raised. One result of this disturbance is manifested in the pendulum and rhythmic movements of the legs of a decapitated weevil, and it it is obvious that this movement cannot coexist with the death feigning reaction as, from their natures, they are mutually exclusive. It will be remembered, however, that cold will so lower the threshhold of stimulation that the decapitated insect will respond readily at low temperature.

THE PHYSIOLOGICAL ANALYSIS OF BEHAVIOR[1]

HARRY BEAL TORREY

Reed College

I

The facts of behavior make a manifold appeal. Among them all, those which seem especially to attract us pertain to the intricate game of human relations. Whether they take the form of premeditated words or unconscious deeds, elaborate rhetorical statements or direct emotional reactions, whether they suggest a soaring or a grovelling imagination, they challenge our powers of interpretation; they entice us into a search for their meaning. Attentive to their significance for us, we set up social standards, we develop moral codes, and we encourage a science of conduct that shall help us to formulate the courses of action we call ideals. We do all this that we may be the gainers thereby, somehow, somewhere, in the immediate present, the near or the distant future. Our motive is personal. We follow an impulse to self-preservation which reveals itself in all the races of mankind. Few individuals, indeed, are so thriftless as to fail to take some such thought, crude and sporadic though it may be, for the morrow. Explanations of some sort all but this exceptional and degenerate few must have. For primitive man, spirits and demons, naive myths and legends built on accidental circumstance suffice. For the children of civilization in large part, they suffice also. Nothing more dramatically proclaims the essential similarity of the peoples of the earth, however diverse in degree of savagery and sophistication, than the conservatism of their mythologies. It is but a few years since a most distinguished British statesman solemnly defended against scientific criticism the authenticity of the unclean spirits that entered into the Gadarene swine. Today whole nations are passionately associating their Gods and all the angels with their several contributions to the inconceivable violation of civilization that is now debauching Europe.

[1] Read at Berkeley, California, before Section F, A. A. A. S., August 3, 1915.

II

These strange anachronisms are in striking contrast with current biological theory. Darwin's masterly argument for natural selection as a mechanical theory of adaptation banished forever from scientific speculation the doctrine of special creation according to Design, and established in its place an interest in the genesis of organic forms and functions according to natural law that has been of inestimable value in the interpretation of the world as we find it. With the publication of the "Origin of Species" appeared new aspects of fitness, new conceptions of conduct, a new and more practical ethic. The problems of behavior gradually assumed new forms under the influence of the comparative method. New light was thrown on questions of human right and wrong by investigations of the behavior of the lower organisms. Objective studies made head against pre-Darwinian types of speculation and the doctrine of natural selection was applied with increasing freedom to the elucidation of all sorts of organic response.

The adoption of a mechanical substitute for the crude teleology which natural selection displaced, marked an enormous advance in methods of investigation at the same time that it gave new meaning to problems of behavior. No mechanical theory of selection, however, is competent to explain the origin of the differences between organisms, their parts, or their actions, on which selection must be based. Such a mechanism of survival is insufficient because it represents results rather than processes. Even in the extreme form in which it appears in the theory of germinal selection, it remains external to the units selected. It is a logical, not a physiological mechanism.

III

It is to the analysis of physiological mechanisms that we turn, then, for further light upon the problems of behavior. At once questions of meaning take a new form. The significance of behavior, and its development, cease to be of immediate concern. For the objective of the physiologist is control of physiological processes, which is at once the pragmatic test of understanding and a practical necessity for the righteous life.

It is as a physiologist, then, that I invite your further atten-

tion to the problems of behavior. That we may see the fruits
of physiological analysis against a background which will throw
them into significant relief, it will be desirable first of all to
consider the influence of selection theory on the physiological
field.

Allusion has already been made to Weismann's application
of selection theory to the problem of variation, which as the
theory of germinal selection marks its extreme development in
this direction. In the field of behavior it has appeared in its
most extreme form in connection with the interpretation of the
activities of the lower organisms. Here it is found in signifi-
cant association with the method of trial.

The method of trial was first used in this field as a measure
of the learning capacity of the higher animals. As such it has
been eminently successful. In the obscure and baffling field of
psychology it has encouraged the establishment of objective
standards and the prosecution of vigorously scientific investiga-
tion. With its extension to the behavior of organisms in gen-
eral, certain difficulties have arisen that have more frequently
been subjects of dispute than sources of common understanding.
Let me illustrate.

An interesting parallel to the learning process by which a
cat is taught to escape from a puzzle box is the behavior of
Paramecium in the presence of an obstruction in its path. The
unsuccessful trials that accompany the learning process of the
cat are represented in *Paramecium* by the motor reflexes that
follow contact with the obstacle. These reflexes are the means
by which the organism is adjusted to the situation. Passing
the obstruction is evidence of successful adjustment.

To what extent is the behavior of *Paramecium* a key to the
behavior of organisms in general, especially to that peculiar
type in many of the lower organisms that is characterized by
the direction of the reaction with reference to the source of
stimulation ? Is the motor reflex an essential factor in tropic
responses ?

IV

Of the answers which have been given to these questions,
the affirmative alone is of present concern. According to this
view, the final orientation of a phototropic organism to light

is selected from among several positions occupied at random. Not only are individual responses the material for selection, but those individuals also whose initial responses are especially favorable to the rapid attainment of success; that is, the fit survive.

Now there can be no more doubt of the development of types of behavior with the aid of selection than the development of structural variations with similar aid—and no less. Scanty and uncertain as is the experimental evidence for natural selection, I do not wish to deny that it may have had large influence in organic evolution of whatever kind.

This is far from agreeing, however, that the precise responses of organisms to what for the sake of brevity may be called directive stimuli, have been effected, in all or in most cases by selection, whether of individual reactions or of individuals themselves. On the contrary, evidence is accumulating in favor of the view that organisms respond typically without trials; that what have been called, by a figure of speech, trials, are actually definite responses to stimuli that are neglected by the observer; that behavior is the resultant of many stimuli of which the directive stimulus is but one; that, in fact, the tropic response is rigidly determined as to direction by factors which complete analysis may be expected in all cases to bring to light.

V

The serious difficulty with a thoroughgoing application of selection theory to behavior is that it so emphasizes certain types of reaction as to divert attention from others, especially from the analysis of those physiological states on which it is generally recognized behavior depends. Nothing illustrates this fact more clearly than the criterion of stimulation that was introduced into studies of behavior with the method of trial.

Let us return again to *Paramecium*. How shall we determine when this organism is under stimulation ? It is obvious that our criterion will depend on our reason for ascertaining the fact. If we are interested primarily with selection among such motor reflexes as *Paramecium* executes upon contact with obstructions, a sufficient criterion for our purpose might well be the reflex itself, however pronounced, that would bring the organism into a recognizably new position with reference to

the source of stimulation. And it would continue to be suffi-
cient regardless of the agency of stimulation—whether contact
or chemical, light, gravity, galvanic electricity—provided only
that the motive for it remained the same. It has been insisted,
indeed, that in the orientation of the micro-organism *Euglena* to
light, its swervings from the original path are typical evidences
of stimulation, being regarded, in fact, as motor reflexes.

It follows naturally from such a criterion that when organ-
isms such as *Paramecium* and *Euglena*, pursue unswervingly a
direct course, they are in an unstimulated condition. That this
conception, which is entirely compatible with the motive from
which it springs, is quite useless in physiological analysis, will
not be difficult to show, if it is perhaps not already apparent.

It is characteristic of the reaction of *Paramecium* to a con-
tinuous galvanic current that it moves toward the cathode, or
anode, as the case may be, along a line of force, under very
obvious compulsion. From beginning to end of its course toward
the cathode, for instance, the cilia at the cathodal end of the
organism beat constantly in a direction the reverse of that in
which they beat when swimming freely in the absence of the
galvanic current. It is as obvious that they are being subjected
to constant stimulation as it is that the organism maintains a
constant course. How can such behavior be reconciled with the
criterion of stimulation established for the use of the selectionist?

It cannot. But the difficulty may be composed by disre-
garding it; by asserting, in fact, that since galvanic electricity
has never been experienced by *Paramecium* in a state of nature;
since it has never either directly or indirectly provided material
for selection; the galvano-tropic response is of no serious im-
portance to the student of behavior who is busy with problems
of genesis and survival.

Such a procedure avoids still another embarrassment, namely,
the radical modification of the definition of stimulus that served
well enough for the reactions of various organisms to sudden
changes in the intensity of what may be called the stimulating
medium. When *Stentor* passes from a shaded to a brightly
illuminated area, it executes a motor reflex at the boundary of
the shadow much as it would react to contact with a solid
object. Reactions of this type have long been recognized and
ascribed to a capacity of the organism commonly known as

unterschieds empfindlichkcit or differential sensibility. They are of the nature of trigger effects, depending on the release of internal energy by a sudden change of potential in the stimulating medium. It is this change in potential or intensity rather than any addition of energy from without that represents the stimulus in all such cases. Can this conception of stimulus be applied to tropic responses as well?

It is noteworthy that probably the most typical reactions of this type are executed by various organisms when subjected to sudden changes of potential in the galvanic current. *Paramecium*, for instance, responds to the making and breaking of the current by characteristic motor reflexes. And this is quite regardless of the fact that the galvanic current is unknown to *Paramecium* in a state of nature and could have played no part in the evolution of its behavior.

The responses of *Paramecium* to the galvanic current are, accordingly, of two types. And these it is quite impossible to reduce to the common denominator of the motor reflex. How is it then with the responses of photosensitive organisms to light, which fall similarly into two groups? For light, unlike the galvanic current, belongs to the world of nature. It is only exceptionally a laboratory product. Hence its influence on the behavior of organisms cannot be disregarded. Can these two types be reduced to one whose key is the motor reflex in one form or another? Are the remarkably direct and precise turning movements that characterize tropic reactions resultants of the selection of random movements of this type? Or are they compelled by the constant application of energy, as is *Paramecium* in the constant galvanic current?

There can be no doubt that a successful attempt to resolve the difference here presented, in terms of a single fundamental factor, would greatly simplify the problem. But, assuming the existence of such a factor, the view that its application to tropic responses would involve selection of random movements does not square with the fact that various organisms, among them *Euglena*, the earthworm (*Allolobophora*), the sow bug (*Porcellio*), and house fly larvae have exhibited unmistakable evidence of responding to light by reactions whose direction can be definitely *predicted*.

VI

The crux of the matter, however, for the physiologist, lies in the third question. Here the problem appears under a purely physiological guise. It is formulated in physiological terms. It invites attack from the side of physics and chemistry. It suggests a measure of energy transformations.

If there is a definite relation between the application of energy to an organism and its behavior, it might be expected to appear in an examination of the evidence for constant stimulation. For the sake of brevity but a few of the recent contributions to this end will be considered, including certain results as yet unpublished. They have been chosen so as to outline the gradual emergence of demonstrable fact from a crowd of observations whose real significance could only be surmised in the absence of later experimentation. We may begin with the phototropic behavior of *Euglena*.

It has frequently been observed that when *Euglena* is exposed to light from two sources the direction of its locomotion may be most delicately adjusted to their intensity as well as to their position, and experimentally controlled with remarkable precision by modifying these two factors. These facts have been interpreted in various ways. To some they strongly suggest, though they do not demonstrate, the presence of constant stimulation.

Two years ago, experiments that involved the most careful and detailed observations of the behavior of *Euglena* that have ever been published, led Bancroft to the conclusion that the reactions of this organism to light are not only of two distinct types but governed by two distinct mechanisms. Of especial significance was the observation, which has been confirmed in my own laboratory, that when *Euglena* swims directly toward the source of light in its characteristic spiral path, the width of the spiral changes with the distance of the organism from the light. In this orientation, the photosensitive area is presented constantly to the source of light, not intermittently as would be the case were the light falling on the organism from one side. Constant illumination produces a constant response. The variation of the width of the spiral with the intensity of

the light thus constantly playing upon the photosensitive area leaves no room to doubt that the organism is as surely in a condition of constant stimulation as is *Paramecium* when exposed to a constant galvanic current. Its orientation is forced.

Can the relation between the photic energy applied to the organism and the reaction of the latter be expressed in quanti-. tative terms ? Though this has not yet been accomplished for *Euglena*, experiments have shown that the relation can be expressed for several other organisms in terms of the law originally offered by Bunsen and Roscoe as a formulation of the effect produced by light upon silver chloride. According to this law, stated in more general terms than those originally employed, the effect of the light radiation is proportional to the product of the intensity of the light and its duration, that is, to the total amount of photic energy supplied.

The first application of the Bunsen-Roscoe law to biological phenomena appears to have been made by the plant physiologist Blaauw. The results of his investigations on oat seedlings (*Avena*) and a fungus (*Phycomyces*) published in 1909, are in striking conformity with the theoretical expectation. It will not be possible here to consider either the details of his experiments or their technic. It must suffice to say that in a series of twenty-six experiments on *Avena*, he varied the duration of the light from 1-1000 of a second to 43 hours, and its intensity in inverse ratio so that the energy delivered should be a constant quantity; and that in spite of this enormous range in the values of these factors, the extreme experimental variation from the average among the entire twenty-six measurements, was but 28 per cent. When it is remembered that the response of an organism to a given stimulus is necessarily complicated by the influence of various other stimuli whose effects may not even be recognized, much less accurately determined, I believe we shall be willing to admit that Blaauw's experimental results demonstrate the applicability of the Bunsen-Roscoe law to the phototropism of plants.

Later experiments have shown the applicability of this law to the phototropism of animals also. Loeb has obtained evidence of its existence in a hybroid (*Eudendrium*). Ewald has found it to apply to the eye movements of *Daphnia* under appropriate

stimulation. According to Patten there is evidence of it in the behavior of blowflies. And one of my students, G. P. Hays, appears to have demonstrated that the phototropism of the fruit fly *Drosophila* conforms to it also. This case will be briefly sketched.

The imagoes of *Drosophila* are positively phototropic. The method of experimentation consisted essentially in subjecting a given number confined in a large test tube, to diffused light from a source whose area could be readily controlled by diaphragms. The flies were first aggregated at the end of the tube away from the light, and then exposed to it, from darkness, for a given number of seconds. The number of flies entering during that time the fifth of the tube which lay nearest the light was adopted as the criterion of the effect of the light. *Drosophila* is so sensitive to light that it was found necessary to use very low intensities in order that the responses obtained at different exposures might be determined with a sufficient degree of accuracy.

Five intensities, multiples of 1, were used, with exposures, varying from 16 to 80 seconds, calculated to deliver the same quantity of photic energy in all five cases. Every day ten trials were made at each intensity, and the average number of flies affected was computed. This was repeated on five successive days with five different sets of flies and the results averaged. These averages agree excellently with Blaauw's figures, varying from 1.44 to 2.1. Under the conditions, this is a satisfactorily constant result. I do not see how it can be interpreted on any theory that neglects the quantity of photic energy involved.

If it appears from the facts that have been thus hastily summarized that tropisms are not interpretable in terms of random movement and selection processes, must we then conclude that they possess no fundamental characteristics in common with reactions of the non-directive type ? By no means. The essential relationship of these superficially different kinds of reflexes is to be found in the physiological processes that they represent, processes that are evident also in the phenomena of growth, development, differentiation, and all other manifestations of life. As physiological reflexes, tropisms exercise their fascination for

the general physiologist, because they offer certain peculiarly favorable opportunities for physiological analysis. And I think we may say that all reflexes must be thus analyzed if they are to be subject to the control that is demanded by human beings for whom conduct is the one problem of perennial interest and concern.

NOTES ON THE FEEDING BEHAVIOR AND OVIPOSITION OF A CAPTIVE AMERICAN FALSE SPIDER

(*Eremobates formicaria* Koch)

C. H. TURNER

Summer High School, St. Louis, Mo.

INTRODUCTION

Eremobates formicaria is a false-spider, a member of a peculiar group of Arachnids (*Solpugidae*), in which there is a ten-jointed abdomen and a segmented thorax, and in which the first pair of legs is modified to serve as feelers, so that each individual seems to have three pairs of legs and two pairs of pedipalpi. These are rare invertebrates and are found only in the warmer parts of the world. In our country they occur only in the southern and western portions. We know almost nothing about the habits of our indigenous forms. During the past quarter of a century no original observations upon the behavior of our American forms have appeared. All that has been published upon their activities prior to that time has been condensed by Putnam (16) in the following quotation:—

" Regarding the habits of the American Solpugidae comparatively little is known. I have myself collected five individuals of *D. pallipes* in different parts of Colorado. They were always found, one at a time, in a small cavity in the earth, under a stone or ' buffalo chip.' No other animal life was visible in their vicinity, and they appeared to be quite pugnacious. In my haste to transfer them to alcohol I failed to make any particular observations upon their behavior and mode of life.

" At the meeting of the Academy of Natural Sciences of Philadelphia, held November 7th, 1871, Prof. Cope stated, on the authority of Dr. Gerhung, that it (*pallipes*) was common in (Denver) houses, and was an enemy and destroyer of the *Cimex lectularius* (bed-bug). In captivity it showed a preference for them as food, and crushed them in its short chelae preliminary to sucking their juices.

" Upon sending me two specimens of *D. Californicus*, Mr. D. Cleveland wrote that they were found at San Diego, in October, under a board near together in a small, funnel-shaped sand hole, with nothing else near them in the way of life, and that they were belligerent. Rev. Green writes that one morning at Silver City, New Mexico, he found a small *Galeodes* dead and half buried away on the top of his candle. On another occasion, while lying on his bed one very hot night, a large *Galeodes* ran across his body and down one of his legs, but escaped before he could capture it. Regarding the Texas species (*D. sulfurea* and *C. geniculata*), Mr. G. W. Belfrage writes as follows: ' They are true nocturnal species, running

with great activity about houses at night, and are attracted by the light, and some-
times to sugared trees. They are rare, but appear more common in rainy seasons,
and only in dark and damp nights. They are probably solitary, and although
I have examined everything in the locality where they have been taken for years,
I have never found a single one in the day time. When attacked they raise and
swing their formidable palpi and show fight, but they are perfectly harmless.'

"From Guanajuato, Mexico, Dr. Eugene Duges writes as follows: 'Here there
is a *Gluvia* which the vulgar call *Genisaro*, and make out to be excessively ven-
omous, which it is not the least in the world.'

"Dr. Edward Palmer, speaking of the specimens collected by him in Mexico,
says: 'The *Solpuga* marked San Louis Potosi was running in a garden, the one
from Bledos was taken out of my bed in the night, while the other was found under
a piece of volcanic rock.'

"Dr. R. A. Phillippi, writing from Santiago, Chili, and speaking of the two
species described by Gervais (*C. morsicans* and *M. variegata*) says: 'They are
very common in the streets of Santiago, running with great swiftness in the sun,
so that they are called 'aranas del sol,' (spiders of the sun); their bite is said to
be very painful, but I know of no personal experience of my friend or my own,
unless one case when a young daughter of mine having been bitten in the finger,
experienced severe pain, fever, and had the whole forearm swollen for two days,
but I do not know whether she was bitten by a *Galeodes* or by *Lathrodectus
formidabilia.*'"

Meager as these accounts are, so far as I have been able to
ascertain, they contain all of the first-hand knowledge we have
of the habits of the American false-spiders.

THE BURROW*

Knowing that the female of an Indian false-spider (17, 11)
burrows into the ground to lay her eggs, I confined my captive
in a glass jar containing about four inches of dry, compact soil.
Although it was broad daylight, she proceeded at once to exca-
vate a burrow. With her jaws (chelicerae) and her second pair
of legs, she dug out the soil and scraped it backwards. When
a pile of dirt had been thus accumulated beneath her body,
she shoved it away in the following manner. The ventral sur-
face of each chelicera is flat and on a level with the equally
flat ventral surface of the thorax (Figs. 2 and 3). The jaws
are on the upper anterior (dorso-anterior) portion of each cheli-
cera (Fig. 1) and the lower anterior (ventro-anterior) surface
of each chelicera is almost truncate (Fig. 3). With the body
appressed against the ground and the ventro-anterior surface
of the chelicerae pressing against the pile of dirt and the blades
of her jaws above it, the solpugid moved forward, pushing the
dirt ahead of her. These movements were repeated over and
over again until the burrow had been completed.

*The false spider which supplied the data for this paper was sent to me alive,
from New Mexico, by Mrs. Maud Tanter.

The floor of the completed burrow sloped inward, forming an inclined plane of about thirty degrees. Having completed her burrow she plugged the opening with soil and remained therein the remainder of the day. This false-spider is nocturnal in her habits. Each night she constructed a new burrow, in the manner mentioned above; but there were variations in both the direction of the burrow and its length. Sometimes, after reaching the bottom of the jar, the cavity turns and continues upward almost to the surface; at other times, by means of an elbow, the burrow is extended in some other direction. At night, on leaving the burrow to forage, she usually closes the mouth with dirt. In about seventy per cent of the cases the burrow was closed during the day. In its habit of excavating a new burrow each night, our New Mexican *Eremobates formicaria* differs from the Indian species of *Galeodes* studied by Hutton (11), which occupies the same burrow throughout the breeding season.

<div align="center">FEEDING ACTIVITIES</div>

Daily a large number of live insects were placed in the jar of this solpugid. At night, after closing her burrow, she would proceed to slay and eat. She is, indeed, voracious; feeding ravenously and almost indiscriminately upon small moths, small beetles, nymphal locusts, small locusts and grasshoppers, lace-wing flies, crickets, small bugs, caterpillars, flies, gnats, etc. Some she chases down; others she captures by resting quietly until they come within striking distance of her jaws. On the evening of July 30th, between half past nine and half past ten, she captured and devoured four moths, four small beetles, one lace-wing fly and several gnats. When I left at half past ten, she was lying in wait for other prey. With the exceptions mentioned later on, this greediness was exhibited nightly.

In 1843, Hutton (11), in discussing a large false-spider (*Galeodes*) which he captured in India, says: "This species is extremely voracious, feeding at night upon beetles, flies and even large lizards. * * * A lizard three inches long, exclusive of the tail, was entirely devoured. * * * The only parts uneaten were the jaws and parts of the skin." J. H. Comstock (6) doubts the correctness of this statement. In 1911 he replies: "Captain Hutton states distinctly that the *Galeodes* observed by him con-

FIG. 1. Dorsal view of the cephalothorax of the false-spider *Eremobates formi-caria*, Koch. Each division of the scale shown at the bottom is one millimeter.
FIG. 2. Ventral view of the cephalothorax of the false-spider *Eremobates formi-caria*, Koch. The scale is the same as in figure 1.
FIG. 3. Lateral view of the cephalothorax of the false-spider *Eremobates formi-caria*, Koch. The scale is the same as in figure 1.
FIG. 4. Eggs of the false-spider *Eremobates formicaria*, Koch, photographed twenty-four hours after they were laid.

sumed an entire lizard except the jaws and parts of the skin. Other instances in which solpugids are supposed to have eaten their prey are given by Rev. J. J. Wood, in his ' Natural History Illustrated,' and quoted by Murray.   Still it is believed that solpugids take only liquid food, which they suck from the bodies of their victims.''

Since the jar in which my solpugid was confined is only five inches in diameter, frequently the arachnid captured her food near enough to the side of the jar for me to focus my hand lens upon her jaws.   Evening after evening, magnifying glass in hand, I have watched those jaws while the false-spider devoured insect after insect.   And then, when the arachnid had cast the remains aside, I have fished them out with a crooked wire. Our *Eremobates formicaria* is not a mere imbiber of juices; she consumes all of her victims except the hard chitin.

· Her first pair of large appendages are powerful chelae, each blade of which is armed with stout teeth (Fig. 3).   These cheli- cerae are so articulated to the head that, as the blades move dorso-ventrally like those of scissors, the chelicerae move for- ward and back with a saw-like movement.   While the right chelicera is moving forward the left is moving backward.   When a small insect is captured by the chelicerae, this scissors-saw- like movement of the jaws soon reduces it to a shapeless mass of chitin, while the contents of its body are being consumed. When the *Eremobates formicaria* encounters a large insect, it usually grabs it, on the ventral side, just back of the head. Once the jaws have secured a hold, the creature is usually doomed.   The insect may squirm and struggle and jump, but the false-spider retains its hold.   I have seen a locust jump back and forth across the jar several times without getting rid of its antagonist.   In a comparatively short time the scissors- saw-like movements of the jaws make a breech in the integu- ment of the victim.   If the thorax is large enough, the jaws are inserted and their scissors-saw-like movements enable the arachnid to soon pulpify and devour much of the contents of the body.   After the removal of all of the contents that can be secured in this manner, the lower blade of each jaw is placed on the outside and the upper blade on the inside of the body of the victim, and the scissors-saw-like movements continue. At the same time the carcass is moved from side to side and

back until the chitin has been scraped clean. When the thorax is too small for the jaws to be inserted, from the beginning, the lower blade of each jaw is placed on the outside and the upper on the inside of the body. After the body has been disposed of, the fleshy parts of the legs and even the bases of the wings are subjected to these scissors-saw-like movements of the jaws and passed from side to side between them, until all edible parts have been removed. If the false-spider is not disturbed while eating the carcass left behind is usually nothing but a shapeless mass of chitin. Even when disturbed the result is often the same.

Normally this false-spider feeds only on living prey. With dead insects on all sides, I have seen it rest quietly for more than an hour, waiting for living prey. However, it is possible to induce it to eat recently killed insects, if they are properly manipulated. Two large crickets that had been dead about an hour were placed in the jar with the solpugid. One of these was manipulated in such a manner that it moved about and occasionally touched the false-spider. The movements did not resemble in the least those of a living cricket; they were simply jerky and somewhat gentle. Finally the false-spider grabbed the cricket by its posterior end (which end was moving forward) and devoured it in the manner mentioned above. In due time nothing was left but one leg and a shapeless mass of chitin. Although she came in contact with the other dead cricket several times, never once did she even attempt to eat it.

I found two living things that my specimen would not eat: hairy caterpillars and spiders. When first confronted with a hairy caterpillar, she sprang to the attack, snapping viciously. At each snap she secured a jaw full of hairs, but the larva was unhurt. She then wiped her chelicerae on the soil, as though trying to clean them. After the first few nights she no longer snapped at hairy caterpillars, but, when they came near her, she would back or rush away. Along with the insects obtained by sweeping I placed live spiders in the jar. She never touched one of them in my presence. Each morning I found practically all of the spiders alive. Whether this immunity of the spiders is due to their elusiveness or to an inherited bias against them on the part of the solpugid is uncertain.

Although these false-spiders are nocturnal in their habits and spend much of the day asleep—reclining on either the side,

the back, or the sternum—if food strays near them, they rise, slay and eat. Occasionally the burrow was left open in the day-time. On such occasions, on dumping live insects into the jar, some were sure to fall into the burrow. Immediately the false-spider would begin to eat.

THE EGGS

On the twenty-sixth of July the burrow of this false-spider was built against the glass of the jar in such a manner that practically all of the interior was visible. That evening the solpugid did not come out to forage, and on the following morning she was resting quietly in the bottom of the burrow. Sometime during the day she laid a batch of milk-white, spherical eggs (Fig. 4). Each egg was about 1.7 millimeters in diameter. At six on the evening of the twenty-seventh the eggs were in the bottom of the burrow and the false-spider was resting about halfway between them and the mouth of the burrow. At nine that evening she was busy plugging the mouth of the burrow with soil, taking pains not to include dead insects. Off and on several dead moths got into the dirt she was shoving into the burrow. Each time she caught the moth in her chelicerae and dragged it, backwards, away from the burrow. Later in the night, after having gluttonized, she excavated a new burrow in another part of the jar. For the next two weeks she excavated a new burrow each night.

On August the eighth no part of her burrow was exposed, hence it was impossible to see what was transpiring inside. Up to a few minutes after nine that evening she had not appeared on the surface. This was past her usual time of appearing, and since for several days I had been expecting her to lay again, I began to wonder if she were ovipositing. Little by little the soil was carefully removed until the solpugid was exposed in her burrow. She had not laid. Soon after this disturbance she crawled to the surface and moved about sluggishly; but did not feed. I watched her until about eleven o'clock and then went to bed. By the next morning she had oviposited. There were a few milk-white, spherical eggs in the bottom of an exceptionally short burrow; and many more were strewn on the ground near to and on its closed mouth. In the course of a

few days a few of these eggs had turned yellow and had begun to shrivel into angular shapes.

The night following the laying of these eggs, the false-spider came to the surface and fed. The next morning she was resting in a depression of the ground. For several nights thereafter she fed as usual; but did not construct any more burrows. She spent the day in some depression of the ground. On the night of the twelfth she fed heartily; on the morning of the thirteenth she was dead.

In both color and size the eggs of our American *Eremobates formicaria* are similar to those of the Indian *Galeodes* studied by Hutton (11, 15), but the habits of the mothers are not identical. After laying her eggs in the burrow, the Indian *Galeodes* rests quietly among them. After they have hatched, she guards the burrow and prevents any intruder from harming her children. Our American *Eremobates formicaria* digs a new burrow each night, and lays a second batch of eggs before the first has had time to hatch. Nothing in her behavior suggests that she guards her young from danger.

CONCLUSIONS

1. The American *Eremobates formicaria* constructs its burrow in the same manner as does the Indian *Galeodes* studied by Hutton; but instead of using a common burrow throughout the breeding season, the female constructs a new one almost every night.

2. The female of this species is nocturnal in her habits, remaining in her burrow all day. On retiring to her burrow and in departing therefrom, she usually closes the mouth with dirt.

3. She feeds voraciously upon a large variety of insects, which she secures by chasing them, or by lying in wait until they come to within striking distance of her powerful jaws.

4. Like the Indian *Galeodes* studied by Hutton, this false-spider eats solid food. Aided by the scissors-saw-like movements of her powerful jaws she pulpifies and devours all parts of the captured insects except the chitin.

5. Normally this species feeds upon live insects; but she may be enticed to feed upon recently killed insects that are artificially induced to move. Ability to move seems the main

attribute by means of which she distinguishes the living from the not-living.

6. Like the Indian *Galeodes* she deposits her milk-white, spherical eggs in the bottom of a burrow; unlike the Indian species she closes the mouth of the burrow and leaves the eggs to their fate.

7. She lays, at intervals, more than one batch of eggs a season.

8. Judging from the mother's behavior in captivity, the young are allowed to shift for themselves; the Indian *Galeodes* described by Hutton protects her young.

REFERENCES*

1. BANKS, N.   Synopsis of American Invertebrates.   IX. The Scorpions, Sol-
        1900.   pugids and Pedipalpi.   *Amer. Nat.*, XXXIV, 421-427.
2.   1902.   Papers from the Hopkins Stanford Galapagos Expedition, 1898-
                1899.   VII. Entomological Results.   (6) Arachnida with Field
                Notes by Robert E. Snodgrass.   *Proc. Washington Acad.*, IV,
                49-86, pls. I-III.
3. BERNARD, H. M.   Are the Solpugidae Poisonous?   *Nature* XLVI, 223.
        1892.
4.   1897.   Wind Scorpions.   A Brief Account of the Galeodidae.   *Science Pro-
                gress, New Series*, I, 317-343.
5. BIRULA, A.   Bemerkungen ueber die Ordnung der Solifugen.   *Annuaire Mus.*
        1903.   *St. Petersb.*, VIII, 391-416.
6. COMSTOCK, J. H.   The Spider Book, pp. 32-39.
        1911.
7. COOK, A. J.   Nature and Habits of Pliny's Solpuga.   *Nature*, LVIII, 247
        1898.   and 320.
8. FAUSSEK.   Defensive Attitudes of Scorpion and Soufugid.   *Biol. Untersuch-
        1906.   ungen in Tramskaspien. St. Petersburg, Zap. Russ. Georg. Obsc.*,
                XXVII, 1+1-192+1, 4 Taf.   (In Russian.   I have not seen
                this article.)
9. FISCHER.   Habits of Galeodes.   *Bombay Nat. Hist. Soc.*, XX, 886.
        1911.
10. HEYMONS, R.   Biologische Beobachtungen an Asiatischen Solifugen nebst
        1901.   Beitragen zur Systematik derselben.   *Abh. Ak. Berlin*, Anh. i,
                65 pp.
11. HUTTON, CAPTAIN THOMAS.   Observations on the Habits of a Large Species
        1843.   of Galeodes.   *The Ann. and Mag. of Natural History*, XII,
                81-85.
12. LÖNNBERG, E.   Some Biological Observations on Galeodes and Buthus.   *Ofv.*
        1899.   *Ak. Forh.*, LVI, 977-983.
13. LUCAS, H.   On the Eggs of Galeodes.   *Bull. Soc. Ent. Fr.*, X, LVII-LVIII.
        1891.
14. MARX, G.   Contributions to the Knowledge of the Life History of Arachnida.
        1891.   *P. E. Soc. Wash.*, II, 252.

* In this list an attempt has been made to include all papers that have been written upon the habits and life-history of American Solpugidae; and papers on the habits of foreign forms that have appeared during the past twenty-five years. References to earlier papers will be found in Putnam's (16) article.

15. Pocock, R. I.   On the Genera and Species of Tropical African Arachnida
    1897.   of the Order Solifugae, with Notes Upon the Taxonomy and
                Habits of the Group.   *Ann. Nat. Hist.*, XX, 249-272.
16. Putnam, J. D.   Solpugidae of America.   *Davenport, Iowa, Proc. Acad. Sci.*,
    1883.   III, 249-310.
17. Pocock, R. I.   The Nature and Habits of Pliny's Solpuga.   *Nature, London*,
    1898.   LVII, 618-620.
18. Say, Thos.   Account of Expedition from Pittsburgh to the Rocky Mountains
    1823.   in 1819-20, under command of Major Stephen H. Long,   Phila-
                delphia, vol.II.

VISUAL PATTERN-DISCRIMINATION IN THE VERTEBRATES—III

EFFECTIVE DIFFERENCES IN WIDTH OF VISIBLE STRIAE FOR THE MONKEY AND THE CHICK

H. M. JOHNSON

Nela Research Laboratory, National Lamp Works of General Electric Company

In an experiment reported some time ago[1] I determined the width of the individual members of a regular system of striae necessary to enable three animals to distinguish the field as striate at a given distance and under the experimental conditions prescribed. The work reported in this paper was done on the same animals, in an attempt to ascertain what difference in width of the members of two regular systems of striae, both of which the animals can distinguish as such, is necessary to effect discrimination between the two systems. The discriminands are two interchangeable circular fields, 6 cm. in diameter and equal in brightness and color. The distribution of energy through the visible spectrum approximated that of a tungsten lamp operated at a specific consumption of 1.25 watts per candle. In the work on the chickens the mean brightness of the fields was 12.24 candles per square meter; in the work on the monkey, 6.67 candles per square meter; and in a supplementary test made on two human subjects, 6.24 candles per square meter. The striae composing the system on the positive field are coarser and fewer in number than those composing the system on the negative field. The animals were fed in the food-compartment

---

[1] Johnson, H. M. Visual pattern-discrimination in the vertebrates. II. Comparative visual acuity in the dog, the monkey and the chick. This journal, vol 4, 1914, pp. 340-361.

indicated by the positive field, and were punished by an electric shock for attempting to enter the food-compartment indicated by the negative field.   In an earlier communication[2] I described at some length the optical instruments used, and the methods of preparing the stimuli and of training the animals.[3]   I followed these methods rigidly in the present work except in three particulars.   It became necessary, when the differences in width between the members of the two systems of striae became small, to make the adjustments by hand, employing the micrometer screw for the purpose, instead of using the string and pulley mechanism.   Further, in this work it is unnecessary that each animal be required to compare the test-fields at the same minimal distance as that prescribed for another animal, in order to make the results comparative.   I therefore eliminated the stops in front of the alleys A[1] and A[2] of the Yerkes box (shown in figure 6 of the last article cited) which I had used in the work on the chicks.   This reduced to 50 cm. the minimal distance at which comparison could be made without a choice being registered. The actual distance usually employed by the birds seemed to be between 50 cm. and 60 cm.   If the difference in width of the members of the two systems was large as compared with the least effective difference for the individual, the animals tended to choose without comparing except possibly from the position they happened to occupy in the home-compartment when the exit-door was raised and the test-fields exposed.   I retained the plate glass partition formerly used in the work on the monkey, in order to limit his movements.   In this work he occasionally thrust his head into one opening in this partition and withdrew it without choosing that alley.   Such behavior was relatively infrequent, and in such cases I did not exclude the responses. In practically all the presentations in which he compared the two fields before choosing, he inspected them successively with

[2] Johnson, H. M.   Visual pattern-discrimination in the vertebrates.   I. Problems and methods.   This journal, vol. 4, 1914, pp. 319-339.

[3] The original drawing for Figure 1 in that article was lost or destroyed after it had been mailed to the printer.   A second drawing had to be prepared hastily and was used.   It contains an error which I beg the reader, in the interest of clearness, to correct.   The acute angle I, II, in the figure should be lettered o, and the obtuse angle I, II, should be lettered o^1 instead of o.   The system of right lines bisecting the obtuse angle should be lettered III.   On page 330, in the phrase, " the lines III bisect the angle I, II (o)," the symbol o^1 should be substituted for the symbol o.   My responsibility for the error is limited to carelessness in copy and proofreading.

his eyes in or quite near the plane of the windows in the parti-
tion—60 cm. from the test-field. In all cases I recorded as the
alley "chosen" the one into which the animal first stepped.
The animals automatically and instantly registered their choices
by breaking the circuit through a signal lamp as they stepped on
to the floor of the alley. The third change is the introduction
of a shallow copper tray into the Yerkes box, between the exit-
door and the alleys A^1 and A^2. This tray contained a moist-
ened felt pad[4] on to which the animal had to step before he
could enter the alley. This tended to minimize the variability
of the resistance of the animal's feet. It is somewhat more
satisfactory than the means employed in my earlier work—that
of soaking the animal's feet before beginning the daily series
of trials.

RELATIVE EASE OF LEARNING FOR INDIVIDUAL ANIMALS

The animals used were a young male Capuchin monkey and
two Indian gamecocks. They were described in paper No. 2
of this series, and designated severally as Monkey 2 and Chicks
1 and 2. Since that report was published, Dr. P. W. Cobb
refracted the eyes of the birds by skiascopy. The static error

---

[4] Breed had used a similar device in his work on the chick. Some such precau-
tion is indispensable to good results if punishment with electric shock is employed.
The resistances of dry feet and moist feet are of different orders of magnitude. If
an animal is put into the box with dry feet and hands, and if during the series the
latter become moist, as from perspiration or contact with urine or wet food, the
increased effect of a steady line current may work great disturbance. In my work
on audition in dogs I found this factor troublesome. Miss E. M. Smith reports
a similar experience. The unsatisfactory results reported by some other experi-
menters may be partly due to failure to take this precaution. Watson (Behavior,
p. 60) asserts that some animals "are extremely resistant even to fairly high cur-
rents. The rabbit is not disturbed in the smallest degree by a current which is
unbearable to the human being." It should be remembered that thick tufts of
long hair cover the soles of the rabbit's feet, forming an excellent insulation when
dry. When moistened, the water acts as a conductor. The rabbit will then react
violently to a current which is not unpleasantly strong when received by the
human subject through the moistened finger-tips. I recently demonstrated this
fact in a simple experiment on the rabbit. However, even with the best attempts
to keep the resistance of the animal's feet constant, the variability is fairly large—
as great, I have been told, as 25%. It is impossible to keep the animal's feet free
of dirt and grease, which interfere with good contact with the electrodes. It there-
fore seems unnecessary to use such extreme care to control the steadiness of the
line current as some students have done. I have obtained satisfactory results
by passing A.C. from the city circuit through the primary coil of a Zimmermann
inductorium, connecting a bank of lamps in series with the coil and in parallel
with each other. Small changes in intensity of shock can be made by changing
the position of the secondary coil with reference to the primary. This method
has one advantage over the use of D.C. with an interrupter, in that the noise of
the latter, which is often a source of disturbance, is dispensed with.

under mydriasis for Chick 1 was 0.75 D. hyperopia in the right
eye and 1.25 D. hyperopia in the left eye. For Chick 2 the
error was between 0.25 D. and 0.50 D. hyperopia in both eyes.
No astigmatism was discoverable in either bird. After the ani-
mals had recovered from mydriasis, Dr. Cobb repeated the
tests, but, since the birds were continually changing their ac-
commodation, the results were quite indefinite. In the emme-
tropic human eye an hyperopia as great as that found for Chick
2 usually exists during mydriasis, owing to lack of tone in the
ciliary muscle. It seems fair, therefore, to regard this bird's
eyes as practically emmetropic, since no error was discoverable
without mydriasis.

Chick 1 failed to establish a perfect or highly accurate habit
in 300 trials, although the width of the members of the positive
system of striae was three times as great as that of the members
of the negative system. At this point I abandoned the attempt
to train him. Later on I gave him the problem of discriminat-
ing between two regular systems of striae the members of which
were equal in width, but differed in direction by 90°. He failed
to learn this problem also. When I introduced a 2 to 1 differ-
ence in width in addition to the difference in direction, he estab-
lished a perfect habit in 150 additional trials, and maintained
discrimination until the relative width of the members of the
two systems was reduced to a 5 to 4 relation. The bird's record
over 1100 trials indicated that a difference in either width or
direction is ineffective if it is presented alone, but that either
difference is effective if it is made sufficiently large and is pre-
sented with a maximal difference in the other characteristic.
This fact raised some questions of great interest, which I was
prevented from studying by an injury to the bird's left eye.
I shall, therefore, omit a detailed report on the work done on
Chick 1.

Chick 2 and Monkey 2 learned the problem in less than 100
trials each.

BASIS OF DISCRIMINATION

In attempting to train an animal to respond to a difference
between two stimuli either of which may be made the variable,
it is important to know whether the animal is reacting on the
basis of relative difference, or by choosing or rejecting a familiar
stimulus. If in work on this problem, the animal can be trained

invariably to compare the test-fields and choose the coarser system regardless of the absolute width of its members, it would seem feasible to adopt the method of right and wrong cases, presenting in haphazard order large and small differences in both directions from the standard, and to treat the results statistically. The advantages of using such a method in preference to the cruder methods on which we have thus far had to rely are obvious.

TABLE 1

DAILY RECORD OF CHICK 2

Date 1914		Width (mm.) of striae on		Number of		Remarks
		Positive field	Negative field	Trials given	Correct responses	
Feb.	13	2.23	0.92	10	8	Not worked on days for which
"	14	2.23	0.92	10	10	no record is given
"	15	2.23	0.92	10	9	
"	16	2.23	0.92	10	9	
"	17	2.23	0.98	10	8	
"	18	2.23	0.98	10	8	
"	19	2.23	0.98	10	9	
"	20	2.23	0.98	10	8	
"	21	2.23	0.98	10	8	
"	22	2.23	0.98	10	9	
"	23	2.23	0.98	10	9	
"	24	2.23	0.98	10	10	
"	25	2.23	0.98	10	10	
"	26	2.23	0.98	10	10	
"	27	2.23	1.00	10	10	
"	28	2.23	1.02	10	8	Disturbed by punishment
Mar.	1	2.23	1.02	10	10	
"	2	2.23	1.08	10	8	
"	3	2.23	1.08	10	10	
"	3	2.23	1.11	10	9	
"	4	2.23	1.11	10	9	
"	5	2.23	1.11	20	15	Greatly excited by punish-
"	9	2.23	0.11	10	10	ment
"	11	2.23	0.11	10	10	Responses very slow
"	12	2.23	0.11	10	10	Responses very slow
"	13	2.23	0.11	10	10	More active
"	14	2.23	0.11	10	10	Active
"	15	2.23	0.11	10	10	Active
"	16	2.23	0.11	5	5	
"	16	2.23	1.04	5	5	
"	16	2.23	1.11	10	10	
"	17	2.23	1.08	5	4	
"	17	2.23	1.11	5	5	
"	17	2.23	1.15	10	10	
"	18	2.23	1.11	5	5	
"	18	2.23	1.15	5	5	
"	18	2.23	1.18	20	18	
"	19	2.23	1.15	5	5	
"	19	2.23	1.18	5	4	

TABLE 1—*Continued*

Date 1914		Width (mm.) of striae on		Number of		Remarks
		Positive field	Negative field	Trials given	Correct responses	
Mar.	19	2.23	1.22	20	16	
"	20	2.23	1.15	5	4	
"	20	2.23	1.22	5	5	
"	20	2.23	1.28	20	11	Taken as threshold
"	20	2.23	0.92	10	10	Given as test of bird's condition
"	21	2.23	1.11	10	10	
"	21	4.33	2.23	10	3	{Chose familiar field against
"	22	4.33	2.23	10	4	{ punishment
"	23	2.23	1.11	10	8	
"	23	4.33	2.23	10	4	{Chose familiar field against
"	24	4.33	2.23	10	2	{ punishment
"	25	2.23	0.92	10	9	
"	25	1.95	0.92	10	10	
"	25	1.73	0.92	10	8	
"	26	1.95	0.92	5	5	
"	26	1.73	0.92	5	5	
"	26	1.56	0.92	5	5	
"	26	1.42	0.92	10	7	
"	27	1.56	0.92	10	9	
"	27	1.42	0.92	5	5	
"	27	1.30	0.92	10	7	
"	28	1.42	0.92	5	5	
"	28	1.30	0.92	10	5	Taken as threshold
Apr.	5	2.60	0.98	10	9	
"	6	2.60	1.04	10	9	
"	7	2.60	1.04	10	8	
"	7	2.60	1.11	10	9	
"	8	2.60	1.11	5	5	
"	8	2.60	1.20	5	5	
"	8	2.60	1.30	10	9	
"	9	2.60	1.39	5	4	
"	9	2.60	1.44	5	4	
"	9	2.60	1.53	10	10	
"	9	2.60	1.73	10	6	Taken as threshold
"	15	3.12	1.04	10	10	
"	16	3.12	1.04	10	10	
"	17	3.12	1.04	10	10	
"	18	3.12	1.11	5	5	
"	18	3.12	1.20	5	5	
"	18	3.12	1.30	5	5	
"	18	3.12	1.42	5	4	
"	19	3.12	1.42	10	10	
"	20	3.12	1.42	5	5	
"	20	3.12	1.56	10	8	
"	21	3.12	1.56	10	8	
"	30	3.12	1.56	20	15	
May	1	3.12	1.56	10	8	
"	2	3.12	1.56	10	8	
"	3	3.12	1.56	10	9	
"	3	3.12	1.73	10	8	
"	4	3.12	1.30	5	5	
"	4	3.12	1.81	10	7	Taken as threshold
"	5	3.12	1.30	5	5	

TABLE 1—*Continued*

Date 1914		Width (mm.) of striae on		Number of		Remarks
		Positive field	Negative field	Trials given	Correct responses	
May	5	3.12	1.90	10	6	
"	5	3.12	1.04	5	5	
"	5	2.60	1.04	5	5	
"	6	2.23	1.04	5	5	
"	6	1.95	1.04	10	6	Greatly excited by punish-
"	7	2.23	1.04	10	8	Still excitable [ment
"	11	2.23	1.04	10	9	
"	12	2.23	1.04	10	10	
"	12	1.95	1.04	10	10	
"	12	1.73	1.04	10	8	
"	13	1.73	1.04	5	5	
"	13	1.56	1.04	10	8	
"	13	1.44	1.04	10	6	Taken as threshold
"	13	3.12	1.04	5	5	Taken as test of bird's con-
"	14	1.30	0.74	10	10	dition
"	14	1.20	0.74	20	16	
"	14	1.11	0.74	10	8	
"	15	1.30	0.74	10	10	
"	15	1.04	0.74	10	6	Taken as threshold

TABLE 2

DAILY RECORD OF MONKEY 2

Date 1914		Width (mm.) of striae on		Number of		Remarks
		Positive field	Negative field	Trials given	Correct responses	
June	7	1.561	0.780	10	6	Very inactive
"	8	1.561	0.780	10	4	
"	9	1.561	0.780	10	7	
"	10	1.561	0.780	10	7	
"	11	1.561	0.780	10	8	Compared in 9 trials
"	12	1.561	0.780	10	9	
"	13	1.561	0.780	10	10	
"	14	1.561	0.780	10	10	
"	16	1.561	0.780	10	10	Not worked on days for
"	17	1.561	0.822	10	10	which no record is given
"	18	1.561	0.867	10	10	
"	19	1.561	0.908	10	10	
"	20	1.561	0.976	10	10	
"	21	1.561	1.041	10	10	
"	22	1.561	1.115	10	10	
"	23	1.561	1.201	10	10	
"	24	1.561	1.301	10	10	
"	27	1.561	1.301	10	9	
"	28	1.561	1.301	10	4	
"	29	1.561	1.301	10	7	
"	30	1.561	1.301	10	7	
July	1	1.561	1.301	10	5	
"	1	1.561	0.976	5	5	
"	2	1.561	0.976	5	5	
"	2	1.561	1.115	5	5	

TABLE 2—*Continued*

Date 1914		Width (mm.) of striae on		Number of		Remarks
		Positive field	Negative field	Trials given	Correct responses	
July	2	1.561	1.301	10	8	Taken as threshold
"	3	2.602	1.561	10	6	
"	4	2.602	1.561	10	7	
"	5	2.602	1.561	10	8	
"	6	2.602	1.561	10	10	
"	7	2.602	1.561	10	10	
"	8	2.602	1.561	10	10	
"	9	2.602	1.561	10	10	
"	10	2.439	1.561	10	10	
"	11	2.439	1.561	10	10	
"	12	2.296	1.561	10	10	
"	13	2.296	1.561	10	10	
"	13	2.168	1.561	10	10	
"	14	2.168	1.561	10	9	
"	14	2.001	1.561	10	10	
"	15	1.904	1.561	10	9	
"	16	1.904	1.561	20	19	
"	17	1.904	1.561	10	9	
"	17	1.815	1.561	10	10	
"	18	1.815	1.561	10	10	
"	18	1.734	1.561	10	6	
"	19	1.815	1.561	10	9	
"	20	1.815	1.561	10	9	
"	21	1.774	1.561	10	7	
"	24	1.774	1.561	10	7	Taken as threshold
Aug.	10	0.780	0.446	10	6	In bad condition since July
"	11	0.780	0.446	10	4	Refused food [24
"	12	0.780	0.446	10	9	
"	13	0.780	0.446	10	7	
"	14	0.780	0.446	10	10	
"	15	0.780	0.446	10	10	
"	16	0.780	0.446	10	10	
"	17	0.780	0.520	10	9	
"	18	0.780	0.520	10	9	
"	19	0.780	0.538	10	10	
"	20	0.780	0.558	10	10	
"	21	0.780	0.578	10	8	
"	22	0.780	0.520	3	3	
"	22	0.780	0.578	2	2	
"	22	0.780	0.600	10	10	
"	23	0.780	0.520	2	2	
"	23	0.780	0.558	3	3	
"	23	0.780	0.624	10	10	
"	24	0.780	0.520	2	2	
"	24	0.780	0.558	3	3	
"	24	0.780	0.650	10	10	
"	25	0.780	0.520	2	2	
"	25	0.780	0.558	3	3	
"	25	0.780	0.679	12	7	
"	26	0.780	0.520	1	1	
"	26	0.780	0.558	2	1	
"	26	0.780	0.600	5	5	
"	26	0.780	0.650	3	3	
"	26	0.780	0.655	10	8	

TABLE 2—*Continued*

Date 1914	Width (mm.) of striae on		Number of		Remarks
	Positive field	Negative field	Trials given	Correct responses	
Aug. 27	0.780	0.600	10	9	
" 27	0.780	0.661	10	9	
" 28	0.780	0.600	10	9	
" 28	0.780	0.667	10	10	
" 29	0.780	0.600	10	10	
" 29	0.780	0.673	10	5	Taken as threshold
" 30	1.040	0.780	10	10	
" 31	0.918	0.780	10	10	
Sept. 1	0.918	0.780	10	10	
" 1	0.909	0.780	10	9	
" 2	0.918	0.780	10	10	
" 2	0.897	0.780	10	10	
" 3	0.918	0.780	10	9	
" 3	0.890	0.780	10	7	Taken as threshold
" 4	0.650	0.520	10	10	
" 5	0.624	0.520	10	10	
" 6	0.624	0.520	10	10	
" 6	0.615	0.520	10	8	
" 7	0.624	0.520	10	8	
" 7	0.610	0.520	10	7	Taken as threshold
" 8	0.624	0.520	10	9	
" 8	0.605	0.520	10	7	
" 9	0.520	0.390	10	9	
" 10	0.520	0.400	10	9	
" 11	0.520	0.411	10	10	
" 13	0.520	0.422	10	9	
" 13	0.520	0.434	10	10	
" 15	0.520	0.446	10	9	
" 15	0.520	0.459	10	7	
" 16	0.520	0.446	10	8	
" 16	0.520	0.467	10	8	
" 17	0.520	0.434	10	8	
" 17	0.520	0.473	10	9	
" 18	0.520	0.434	10	10	
" 18	0.520	0.479	10	7	Taken as threshold
" 19	0.520	0.434	10	10	
" 19	0.520	0.488 ·	10	6	
" 20	0.459	0.390	20	17	
" 21	0.459	0.390	10	10	
" 21	0.446	0.390	10	8	
" 22	0.459	0.390	10	10	
" 22	0.441	0.390	10	8	
" 23	0.459	0.390	10	10	
" 23	0.436	0.390	10	9	
" 25	0.459	0.390	9	9	
" 25	0.431	0.390	11	10	
" 27	0.459	0.390	10	10	
" 27	0.427	0.390	10	7	
" 28	0.459	0.390	10	10	
" 28	0.422	0.390	10	10	
" 29	0.459	0.390	10	10	
" 29	0.417	0.390	10	9	
" 30	0.459	0.390	10	10	
" 30	0.413	0.390	12	8	Taken as threshold

TABLE 2—*Continued*

Date 1914		Width (mm.) of striae on		Number of		Remarks
		Positive field	Negative field	Trials given	Correct responses	
Oct.	1	0.459	0.390	10	9	
"	1	0.409	0.390	10	7	
"	2	0.390	0.325	10	10	
"	2	0.390	0.339	10	7	
"	3	0.390	0.339	10	9	
"	4	0.390	0.339	10	10	
"	5	0.390	0.339	10	10	
"	5	0.390	0.347	10	9	
"	6	0.390	0.339	10	10	
"	6	0.390	0.355	10	8	
"	7	0.390	0.339	10	8	
"	7	0.390	0.358	10	10	
"	8	0.390	0.339	10	10	
"	8	0.390	0.361	10	7	
"	9	0.390	0.339	10	10	
"	9	0.390	0.365	10	9	
"	10	0.390	0.339	10	10	
"	10	0.390	0.368	10	10	
"	11	0.390	0.339	10	9	
"	11	0.390	0.371	10	7	
"	12	0.390	0.339	10	9	
"	12	0.390	0.371	10	7	Taken as threshold
"	13	0.347	0.312	20	19	
"	17	0.347	0.312	20	15	Distracted by noise outside
"	19	0.372	0.312	10	8	
"	19	0.347	0.312	10	7	
Nov.	11	0.390	0.312	20	17	
"	12	0.390	0.312	20	15	
"	13	0.390	0.312	20	15	
"	14	0.390	0.312	15	12	
"	15	0.390	0.312	15	15	
"	16	0.434	0.312	20	16	
"	17	0.422	0.312	20	20	
"	18	0.411	0.312	10	10	
"	18	0.400	0.312	10	9	
"	19	0.390	0.312	20	17	
"	20	0.381	0.312	20	20	
"	21	0.372	0.312	10	10	
"	21	0.363	0.312	10	10	
"	22	0.354	0.312	10	10	
"	22	0.346	0.312	10	9	
"	23	0.346	0.312	10	10	
"	23	0.339	0.312	10	8	
"	24	0.346	0.312	10	8	
"	24	0.335	0.312	10	9	
"	25	0.346	0.312	10	9	
"	25	0.332	0.312	10	9	
"	26	0.346	0.312	10	9	
"	26	0.328	0.312	10	9	
"	27	0.346	0.312	10	10	
"	27	0.325	0.312	10	10	
"	28	0.346	0.312	10	8	
"	28	0.321	0.312	10	8	
"	29	0.346	0.312	10	9	

TABLE 2—*Continued*

Date 1914		Width (mm.) of striae on		Number of		Remarks
		Positive field	Negative field	Trials given	Correct responses	
Nov.	29	0.321	0.312	10	5	Taken as threshold
"	30	0.312	0.260	20	16	
Dec.	1	0.312	0.260	10	10	
"	1	0.312	0.264	10	10	
"	2	0.312	0.269	10	10	
"	2	0.312	0.274	10	10	
"	3	0.312	0.279	10	10	
"	3	0.312	0.284	10	10	
"	4	0.312	0.289	10	9	
"	4	0.312	0.294	10	9	
"	5	0.312	0.284	10	9	
"	5	0.312	0.298	10	9	
"	6	0.312	0.284	10	10	
"	6	0.312	0.300	10	8	
"	7	0.312	0.284	10	9	
"	7	0.312	0.304	10	8	Taken as threshold
"	8	0.312	0.284	10	10	
"	8	0.312	0.306	10	5	
"	8	0.312	0.284	10	8	⎰Control test to determine
"	8	0.284	0.260	10	10	⎱ basis of choice
"	9	0.244	0.223	10	9	
"	9	0.240	0.223	10	10	
"	9	0.236	0.223	10	9	
"	10	0.244	0.223	6	6	
"	10	0.234	0.223	10	8	
"	10	0.232	0.223	15	11	
"	11	0.244	0.223	10	9	
"	11	0.232	0.223	10	7	Taken as threshold
"	11	0.223	0.199	10	9	
"	12	0.223	0.199	10	9	
"	13	0.223	0.199	10	9	
"	13	0.223	0.200	10	10	
"	14	0.223	0.200	10	10	
"	14	0.223	0.203	10	10	
"	15	0.223	0.203	10	10	
"	15	0.223	0.208	10	9	
"	16	0.223	0.203	10	9	
"	16	0.223	0.210	13	9	
"	18	0.223	0.203	10	10	
"	18	0.223	0.210	10	8	
"	19	0.223	0.203	10	10	
"	19	0.223	0.210	10	8	Taken as threshold
"	19	0.195	0.173	10	9	
"	20	0.195	0.173	10	9	
"	20	0.192	0.173	10	7	
"	21	0.195	0.173	10	8	
"	21	0.192	0.173	10	9	
"	22	0.200	0.173	10	9	
"	22	0.190	0.173	10	7	
"	23	0.200	0.173	10	9	
"	23	0.190	0.173	15	11	Taken as threshold
1915						
Mar.	4	0.780	0.520	20	19	
"	5	0.780	0.538	10	10	

H. M. JOHNSON

TABLE 2—*Continued*

Date 1914	Width (mm.) of striae on		Number of		Remarks
	Positive field	Negative field	Trials given	Correct responses	
Mar. 5	0.780	0.558	10	10	
" 6	0.780	0.577	10	10	
" 6	0.780	0.600	10	10	
" 8	0.780	0.624	10	9	
" 8	0.780	0.650	10	10	
" 9	0.780	0.678	10	10	
" 9	0.780	0.709	10	9	
" 10	0.780	0.709	10	8	
" 10	0.780	0.723	10	8	
" 11	0.780	0.678	10	8	
" 11	0.780	0.729	10	8	
" 12	0.780	0.678	10	9	
" 12	0.780	0.731	10	10	
" 13	0.780	0.678	10	10	
" 13	0.780	0.743	10	8	
" 14	0.780	0.678	10	10	
" 14	0.780	0.750	10	7	
" 15	0.780	0.678	10	10	
" 15	0.780	0.750	10	7	Taken as threshold
" 16	0.975	0.780	10	9	
" 16	0.918	0.780	10	10	
" 17	0.867	0.780	10	9	
" 17	0.848	0.780	10	9	
" 18	0.867	0.780	10	10	
" 18	0.839	0.780	10	9	
" 19	0.867	0.780	10	9	
" 19	0.830	0.780	10	9	
" 21	0.867	0.780	10	10	
" 21	0.822	0.780	10	9	
" 22	0.867	0.780	10	10	
" 22	0.813	0.780	10	10	
" 23	0.867	0.780	10	9	
" 23	0.805	0.780	10	9	
" 25	0.867	0.780	10	9	
" 25	0.805	0.780	10	9	
" 26	0.867	0.780	10	9	
" 26	0.796	0.780	10	6	
" 27	0.867	0.780	10	9	
" 27	0.796	0.780	10	6	Taken as threshold

If the reader will now examine the daily records of Chick 2 and Monkey 2, shown in tables 1 and 2 respectively, he may observe that the chick was usually disturbed when he was required to avoid a field which he had recently been in the habit of choosing. The records for 21 to 24 March, 1914, exhibit this fact strikingly. Monkey 2 tended to respond in this way in the earlier stages of the work, but later overcame the tendency. On December 8, 1914, I made a control test which tends to make the fact clear. In the week immediately pre-

ceding this test I had required him to choose a field each stripe on which was 0.312 mm. wide, and to reject a field each stripe on which was 0.284 mm. wide. He chose correctly in 48 out of 50 trials. In this control test I presented the 0.284 mm. system ten times with a system each member of which was 0.312 mm. wide, and ten times with a system each member of which was 0.260 mm. wide. The animal was required to choose the coarser system at each trial, thus choosing the 0.284 mm. system ten times and rejecting it ten times in the same daily series. The results are shown in table 3.

TABLE 3

	Width (mm.) of striae on		Relative position of positive field	Field chosen by the animal	Remarks
Trial	Positive field	Negative field			
1	0.312	0.284	Right	Right	Compared before choosing
2	0.312	0.284	Right	Right	" " "
3	0.312	0.284	Left	Left	" " "
4	0.284	0.260	Left	Left	" " "
5	0.284	0.260	Right	Right	" " "
6	0.284	0.260	Right	Right	" " "
7	0.312	0.284	Left	Left	" " "
8	0.312	0.284	Left	Left	" " "
9	0.284	0.260	Right	Right	" " "
10	0.284	0.260	Right	Right	" " "
11	0.312	0.284	Left	Left	" " "
12	0.312	0.284	Right	Right	" " "
13	0.312	0.284	Right	Right	" " "
14	0.284	0.260	Left	Left	" " "
15	0.284	0.260	Left	Left	" " "
16	0.284	0.260	Right	Right	" " "
17	0.312	0.284	Right	Left	Chose without comparing
18	0.312	0.284	Right	Left	" " "
19	0.284	0.260	Left	Left	" " "
20	0.284	0.260	Left	Left	" " "

The animal was punished for choices 17 and 18. He had usually shown a preference for the left-food-compartment. In trials 17, 18, 19, and 20 he inspected the left field only. The field presented on that side at these trials was the field which he had correctly chosen in trials 14, 15 and 16. At trials 1 to 16, inclusive, he inspected both fields before choosing, and in every case he selected the relatively coarser system, regardless of the absolute width of its members. I believe that this animal could have been adapted by training to study by the standard method of right and wrong cases. Chick 2 gave no such promise.

The tendency of Chick 2 to respond by choosing or rejecting the familiar stimulus differs from the behavior of some birds used by Bingham,[5] which chose the larger of two circles and avoided the smaller without regard to the absolute size of the larger, and without regard to its previous association with reward or punishment. The comparison is worthy of mention as it seemingly points to an individual difference.[6] Bingham, however, gives no details which indicate how nearly unanimous or how consistent his birds were in manifesting this form of behavior.

AN INCIDENTAL OBSERVATION

One incidental feature of the behavior of Monkey 2 seems deserving of special mention. As was remarked above, I used a plate glass partition across the entrances of Alleys A[1] and A[2] of the Yerkes box. This partition contained two rather small holes through which the animal had to squeeze himself in order to enter the alley. On two occasions—June 16, 1914, and March 14, 1915, I neglected to insert this partition before giving the first trial of the daily series. On each occasion the animal refused to enter either alley. When I looked into the box to ascertain the cause of his delay in responding I found him groping in large semi-circles with his hands near the plane in which the glass partition belonged, and uttering frequent vocal exclamations. It was necessary to recall him to the home-compartment and insert the partition. It appeared from this behavior that he had become habituated to disregarding the partition as a visual object.

RELATIVE EASE OF DISCRIMINATION

In tables 4 and 5 I have summarized the values taken as "thresholds" for the two animals. The reader may see how these values were obtained by referring to tables 1 and 2, in which the animals' daily records appear. Whenever there

[5] Bingham, H. C. Size and form perception in *Gallus domesticus*. This journal, vol. 3, 1913, pp. 65 ff.

[6] Watson (Behavior p. 367) refers to the difference between the behavior of my chick and those of Bingham's as indicating that " this (Bingham's) observation cannot be confirmed." This interpretation is not mine. Had all the birds been worked on the same problem I should not have considered that the behavior of one bird was predictable from the behavior of a few others. But the two problems are so different that there is little basis for comparison.

seemed room for doubt whether the animal's errors were due to the magnitude of the stimulus-difference or to disturbance from some other cause, I presented a larger difference at a number of trials in the same daily series with the smaller difference. If all or most of the incorrect choices were made at the small stimulus-difference, I concluded that discrimination at that stimulus-difference was becoming difficult; if the animals' percentage of correct choices was low for the large stimulus-difference as well, I assumed that the source of disturbance was extraneous.

The values obtained on the two animals are not strictly intercomparable. In work on the monkey I reduced the stimulus-difference by smaller gradations than I could use in the work on the chick, owing to a limitation of the optical instrument by which the field was formed. As the angle of rotation of the gratings over each other becomes very small, as is the case where the width of the visible stripes thus formed is large, a very slight change in the angle of rotation makes a large difference in the width of the visible stripes. In the work on the monkey a larger angle and smaller gradations could be employed, since he was sensitive to much smaller widths than was the chick under similar conditions. I took for "threshold-differences" for the monkey the differences at which his average percentage of correct choices most nearly approximated 75. For the chick I took the stimulus-difference at which the first breakdown of discrimination not apparently due to disturbance from other causes occurred. This procedure is open to criticism in that I did not ascertain to what extent the bird could be made to overcome his uncertainty by continued training. At the time, however, this bird did not react well under punishment. As soon as the stimulus-difference became relatively small he usually refused to inspect both fields and adopted a position-habit. I recognized this defect in the procedure, and in a later piece of work attempted to settle the question.[7] I found that this bird could be made to improve to a limited extent after very long continued training. The degree of improvement which I was able to elicit is not sufficiently large to invalidate the results herein presented as the rough approximations of the

---

[7] Johnson, H. M. Visual pattern-discrimination in the vertebrates. IV. Effective differences in direction of visible striae for the monkey and the chick. To appear in this journal.

limits of the bird's discriminative ability which I regard them as being. It will be seen that the threshold-values for the chick vary irregularly from 33% to 42% of the width of the striae on the standard field. The variations may be explained by assuming that discrimination was difficult throughout this region of stimulus-differences. If the bird received punishment several times in close succession shortly after the difference approached this region, he "gave up" earlier, and yielded a larger "threshold" than if his errors were more widely distributed.

Table 5 also shows a great disparity between the "upper" and the "lower" threshold values given by the monkey when the width of the striae on the standard field was 0.520 mm. This fact pointed to a large effect of practice. The magnitudes of the thresholds obtained at the smaller values of the standard stimulus are so much lower than those obtained in the earlier stages of the work at the larger stimulus-values, that it was necessary to make a control test to discover if these differences were not due to the effect of training, instead of being a function of the absolute width of the striae. This test was made between March 4, 1915 and March 27, 1915. It shows quite clearly that the differences were due to the effect of training. The results suggest strongly that if training had been continued sufficiently long after the full effect of practice had been obtained, the values for all the difference-thresholds where the striae on the standard field were over 0.3 mm. wide would have borne a relation to the absolute width of the members of the standard system analogous to Weber's law for brightness. This relation probably does not hold for absolute widths below 0.2 mm., under these experimental conditions, since such fine systems become increasingly hard for the monkey to distinguish as striate. Due to pressure of other work and the small likelihood of Monkey 2 living through many more months, I did not feel justified in carrying this exploratory study farther at the time. Should a similar study ever be made, it would seem advisable to select fewer points at which to determine the animal's threshold, and to give a large number of presentations—several hundred, at least—of a number of differences in either direction from each point. In work on another problem with this animal I found such procedure quite fruitful.

TABLE 4

THRESHOLD CONDITIONS FOR CHICK 2

Width of striae on		Difference per cent width on standard field	Mean of upper and lower thresholds	Remarks
Positive field	Negative field			
*2.23 mm.	1.28 mm.	42	. . .	
1.30 "	*0.92 "	41	. . .	
*2.60 "	1.73 "	33	. . .	
*3.12 "	1.81 "	42	. . .	
1.44 "	*1.04 "	38	. . .	
1.04 "	*0.74 "	40	. . .	

TABLE 5

THRESHOLD CONDITIONS FOR MONKEY 2

Positive field	Negative field	Difference per cent	Mean	Remarks
1.774 mm.	*1.561 mm.	14		
*1.561 "	1.301 "	17	15.5	
0.890 "	*0.780 "	14		
*0.780 "	0.673 "	14	14	
0.610 "	*0.520 "	17		
*0.520 "	0.479 "	8	11.5	Note training-effect
0.413 "	*0.390 "	5.9		
*0.390 "	0.371 "	4.9	5.4	
0.321 "	*0.312 "	2.9		
*0.312 "	0.304 "	2.6	2.8	
0.232 "	*0.223 "	4		
*0.223 "	0.210 "	5.8	4.9	
0.190 "	*0.173 "	9.8	. . .	
0.796 "	*0.780 "	2		
*0.780 "	0.750 "	3.8	2.9	Note training-effect

* Standard stimulus.

COMPARISON WITH HUMAN SUBJECTS

A comparison of the relation between the absolute stimulus-value (expressed in terms of width of striae on the standard field) and the minimal effective differences for the animals with that obtained for human subjects is of some interest. Accordingly I determined this relation for two human subjects by means of the method of limits, using the same visual conditions as for the animals. The magnitudes of the thresholds obtained on the human subjects by the method of limits are not to be compared with those obtained by the discrimination-method on the animals. A threshold-value obtained by the method of limits

is generally smaller than one obtained under the same conditions by the method of right and wrong cases, of which the discrimination-method is a special and rough adaptation. The relation between the absolute value of the standard stimulus and a series of thresholds obtained by either method ought to vary in the same way. This comparison between the two sets of data is the only one which I wish to be made directly, although the values obtained for the monkey and for the human subjects indicate that their sensitivities are of the same order. The two human subjects were Dr. A. G. Worthing (W), a member of the research staff of this laboratory, and Mr. B. E. Shackelford (S), of the University of Chicago, late Brush fellow in this laboratory. Both observers are physicists possessed of a high degree of skill in optical pyrometry—one of the most difficult types of photometric measurements. Perhaps it should be remarked that both observers considered the visual conditions in the present experiment quite trying. An hour or more was usually required for making ten paired readings, which constituted a single sitting. The results are summarized in table 6.

TABLE 6

Width of striae on standard field (mm.)		Upper threshold in mm.	Lower threshold in mm.	Mean threshold per cent standard	Mean variation per cent mean threshold	Mean threshold for the two observers
0.780	W.	0.026	0.020	3.0	58	2.6
	S.	0.019	0.012	2.1	45	
0.390	W.	0.007	0.009	2.1	28	2.8
	S.	0.014	0.013	3.5	35	
0.260	W.	0.009	0.008	3.3	40	3.0
	S.	0.006	0.008	2.7	27	
0.195	W.	0.006	0.006	3.1	49	3.9
	S.	0.009	0.008	4.7	34	

The relation between absolute width and magnitude of the threshold for the animals and the two human observers is shown graphically in the accompanying figure. The average threshold for the two observers at each stimulus-value was taken merely for convenience in plotting on the scale selected.

SUMMARY

A very large effect of practice was found in the work on the monkey, which indicates the desirability of modifying the discrimination-method for use on the higher mammals.

When the full effect of practice has been obtained, Monkey 2, under optimal conditions, can distinguish differences in width of striae of less than 3%. These values are of the same order of magnitude as those obtained by the method of limits on two human observers possessed of unusual skill in photometry. Chick 2 ceased to discriminate when the difference in width of striae was reduced to a value between 33% and 42%. The relatively poor results of the chick were not due to errors of refraction, as both his eyes were emmetropic.

The discriminative ability shown by the monkey is on the average roughly ten times as great as that shown by Chick 2. His visual acuity, however, is only four to five times as good as that of the same bird. This disparity suggests that difference of width between two systems of visible striae constitutes a more difficult basis of discrimination for the chicken than the mere presence or absence of the striae. The fact that Chick 1 did not learn the problem, although width-difference was effective for him when presented with an ineffective difference in direction, lends support to this belief.

Nothing in the above work indicates that Chick 2 might not have yielded a lower threshold had training been sufficiently prolonged. A later experiment, however, indicates that the chick's susceptibility to improvement under prolonged training is not sufficiently large to affect the order of difference between his results and the monkey's which appears in this work.

For all the subjects, both human and animal, the relation between absolute size of detail and effective difference in size approximates an analog of Weber's law.

For the chick, familiarity was a more effective stimulus-characteristic than relative size of detail, and the bird never overcame the tendency to respond on that basis without continued retraining. The monkey eventually learned to respond on the basis of relative size. His results suggest that he is adaptable to study by a method of much greater precision than the method which was actually employed.

In conclusion I wish to thank Dr. P. W. Cobb for the work of refracting the eyes of the animals, and for making the photometric determinations for me; also, Dr. A. G. Worthing and Mr. B. E. Shackelford for their cheerfulness in undertaking the tedious observations.

H. M. JOHNSON

Least effective difference per cent standard

Width of striae on standard field (mm.)
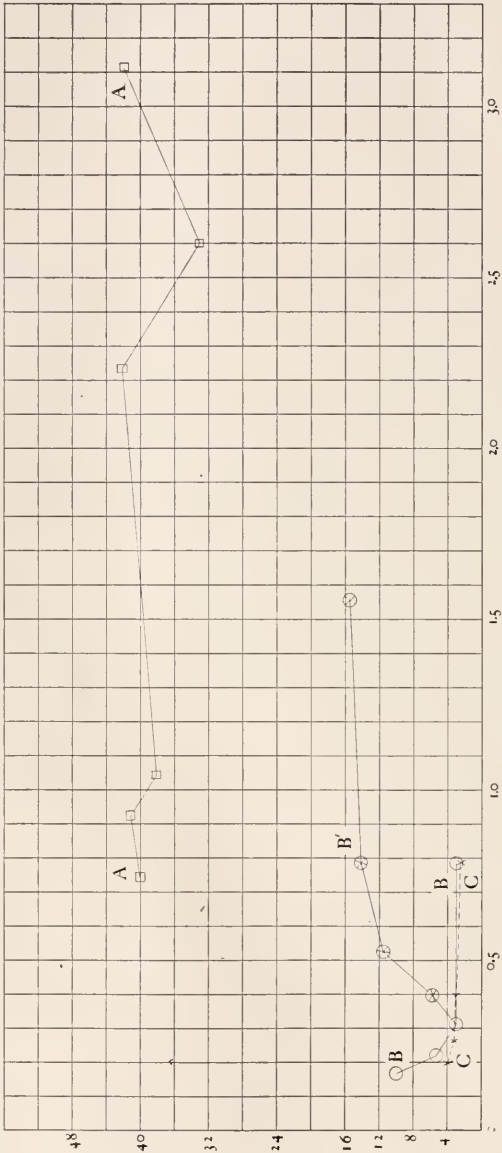
Curve A: Threshold values for Chick 2
Curve B': Mean threshold values for Monkey 2, early stages of training
Curve B: Mean threshold values for Monkey 2, later stages of training
Curve C: Mean threshold values for two human observers

VISUAL PATTERN-DISCRIMINATION IN THE VERTEBRATES—IV

EFFECTIVE DIFFERENCES IN DIRECTION OF VISIBLE STRIAE FOR THE MONKEY AND THE CHICK

H. M. JOHNSON

Nela Research Laboratory, National Lamp Works of General Electric Company

The purpose of the experiments described below was to ascertain how small a difference in direction of two regular systems of visible striae will condition the responses of animals possessing eyes of different types. In this work I used the "discrimination method" described by Yerkes and Watson,[1] feeding the animal in a compartment of the training box indicated by the "positive" test-object, and punishing him for attempting to enter the food-compartment indicated by the "negative" test-object. A detailed description of the method of training and of preparing the stimuli has appeared in an earlier report.[2] In the present work the discriminands were two circular fields, 6 cm. in diameter and 6.24 candles per square meter in brightness. The energy-distribution in the visible spectrum approximated that of a tungsten lamp operated at a specific consumption of 1.25 watts per candle. Both fields were covered with alternate dark and bright striae equal in width and separation. The chicks and the monkey had previously demonstrated their ability to react with perfect accuracy under the experimental conditions to the presence or absence of the striae from the test-field. The striae on the positive field were horizontal; those on the negative field deviated from the horizontal direction by a definite and variable amount. In the beginning of the training the difference was 90°, and was decreased by small gradations after the animal had formed the habit of invariably choosing the food-box indicated by the positive test-field.

---

[1] Yerkes, R. M. and Watson, J. B. Methods of studying vision in animals. *Behavior Monographs*, vol. 1, no. 2, 1911.

[2] Johnson, H. M. Visual pattern-discrimination in the vertebrates. I and II. This journal, vol. 4, 1914, pp. 319-361.

THE ANIMALS USED

The four animals used in the present study were described in the earlier report just cited, and were therein designated severally as Dog 1, Monkey 2, and Chicks 1 and 2. Dog 1 failed to learn the problem. This experiment is a part of a special study of that animal's vision. His results are interesting only when considered in connection with those obtained in the other work, so I shall reserve them for a separate report.[3] Chick 1 also failed to learn the problem in 800 trials. He had a large refractive error (1.5 D. hyperopia) in the right eye, and was also very easily excited by punishment or by unusual noise, so that he would refuse to work in the experiment-box. Eventually he was blinded in the left eye during a fight, and I did not resume experimentation on him. On account of lack of space I shall not include his daily records in this report. Chick 2, both of whose eyes were emmetropic, had distinguished as striate a system each member of which was 0.78 mm. wide at a distance of 60 cm. from the eye; the width under threshold-conditions for Monkey 2 being 0.163 mm. at the same distance. Chick 2 had also yielded a difference threshold for width of visible striae of 33% to 42%, and Monkey 2, a series of thresholds as low as 3% under optimal conditions.

In the course of the work some serious interruptions occurred. In September, 1914, Chick 2 acquired a severe white diarrhoea, and became greatly weakened. He finally refused to eat, and all the masculine characteristics of his behavior disappeared. I transferred him to an out-door yard where he had plenty of range. He showed improvement in a few days, and made a complete recovery in three months. Meantime his comb grew very large and depended over the left eye, largely occluding the visual field on that side. I amputated the comb March 6, 1915, and resumed retraining on the 10th. On the 20th he became engaged in a fight and was nearly killed. Other uncontrollable conditions then intervened and prevented the resumption of work until June 16, 1915.

Monkey 2—a frail and probably tubercular little animal—also sickened May 21, 1915. He refused food and in two days became too weak to stand alone. I moved him to a room where

---

[3] Johnson, H. M. Visual pattern-discrimination in the vertebrates. V. A demonstration of the dog's deficiency in detail-vision. To appear in this journal.

he could be kept in direct sunlight most of the day, and used forcible feeding on milk and raw eggs for ten days, during which time his condition began to improve rapidly. He became quite wild as a result of such handling, and I dared not resume work with him until June 15, 1915. On August 1 following, he fell from a steam-pipe six feet from the floor and sustained a partial fracture of the right femur and the left tibia. He made a fair recovery, but is still occasionally excited by unusual handling.

While these accidents render the results somewhat ragged in appearance, they occurred after the preliminary training had been completed. They probably do not affect the validity of the results.

RELATIVE EASE OF LEARNING

The daily records for the two animals appear in tables 1, 2-A and 2-B. They show a striking difference in the relative ease with which the animals learned the problem. Chick 2 required 585 trials, distributed over 58 days, to establish a habit of highly accurate choosing. It should be noted, however, that the bird showed consistent improvement in less than 400 trials. The average percentage of correct responses for the 195 trials given between July 12 and August 17 is 87. The monkey, on the other hand, learned the problem in the first daily series of 20 trials, during which he made only two incorrect responses. In learning the first problem—that of plain vs. striate discrimination, the chicken required only 214 trials for establishing a perfect habit, and the monkey required 312.

TABLE 1

RECORD OF MONKEY 2

Width of striae on both fields: 0.780 mm.
Mean brightness of both fields: 6.24 candles per sq. meter
Direction of striae on positive (standard) field: horizontal

Date 1915	Deviation from horizontal of striae on negative field	No. of trials given	No. of correct responses	Remarks
May 18	—90°	20	18	Incorrect choices, trials 1 and 9
" 20	—90°	20	20	Not worked on days for which no record is given
June 15	—90°	30	26	Very inattentive first 10 trials
" 16	—90°	20	20	
" 17	—90°	20	19	

TABLE 1—*Continued*

Date 1915	Deviation from horizontal of striae on negative field	No. of trials given	No. of correct responses	Remarks
June 18	—90°	20	18	
" 19	—90°	20	20	
" 20	—90°	20	20	
" 21	—90°	20	20	
" 22	—90°	10	10	
" 22	—75°	10	10	
" 23	—90°	10	10	
" 23	—60°	10	10	
" 24	—90°	10	10	
" 24	—45°	10	10	
" 25	—90°	10	10	
" 25	—30°	10	10	
" 26	—90°	10	10	
" 26	—15°	10	2	Very inattentive and slow
" 27	—90°	10	10	
" 27	—30°	10	10	
" 28	—30°	10	8	
" 28	—25°	10	10	
" 29	—30°	10	10	
" 29	—20°	10	5	
" 30	—30°	10	9	Up to this series most choices were made without comparison; tendency to compare from today on
" 30	—20°	10	7	
July 1	—30°	10	10	
" 1	—20°	10	9	
" 2	—30°	10	10	
" 2	—20°	10	9	
" 3	—20°	5	5	
" 3	—15°	15	15	Only records from today on are summarized in table 4
" 6	—15°	10	10	
" 6	—10°	10	7	
" 7	—15°	10	10	
" 7	—10°	10	6	
" 8	—14°	10	9	
" 8	—13°	10	10	
" 9	—13°	20	13	
" 10	—13°	20	16	
" 11	—15°	10	9	
" 11	—13°	10	9	
" 12	—15°	20	18	
" 13	—15°	5	4	
" 13	—12°	15	14	
" 14	—15°	5	4	
" 14	—12°	15	15	
" 15	—15°	5	5	
" 15	—11°	13	12	Removed after trial 18
" 16	—15°	5	5	
" 16	—10°	15	14	
" 17	—15°	5	5	
" 17	—9°	15	14	
" 18	—15°	5	4	
" 18	—8°	15	13	

TABLE 1—*Continued*

Date 1915	Deviation from horizontal of striae on negative field	No. of trials given	No. of correct responses	Remarks
July 19	—8°	20	18	
" 20	—8°	5	4	
" 20	—7°	15	15	
" 21	—7°	20	18	
" 22	—7°	5	4	
" 22	—6°	15	13	
" 23	—6°	20	19	
" 24	—6°	5	4	
" 24	—5°	15	12	
" 25	—5°	20	15	
" 26	—10°	5	5	
" 26	—5°	15	9	
" 29	+30°	10	10	Records from today to Aug. 9 inclusive not summarized in table 4
" 29	+25°	10	10	
" 30	+20°	10	10	
" 30	+15°	10	7	
" 31	+15°	20	15	
Aug. 1	+15°	20	14	Sustained severe injury in fall just following this series
" 8	+20°	20	18	Still quite lame; responses slow
" 9	+20°	20	18	
" 10	+20°	10	10	Condition improved
" 10	+15°	10	8	
" 11	+19°	10	10	More active
" 11	+18°	10	10	
" 12	+17°	10	10	
" 12	+16°	10	9	
" 13	+15°	10	8	Active
" 13	+14°	10	9	
" 14	+14°	10	10	
" 14	+13°	10	9	
" 15	+13°	10	10	
" 15	+12°	10	9	
" 16	+12°	10	8	
" 16	+11°	10	9	
" 17	+11°	10	9	
" 17	+10°	10	9	
" 18	+10°	20	17	Very active
" 19	+9°	20	18	
" 20	+8°	20	19	
" 21	+7°	20	14	Was frightened during this test; became wild and remained so for 3 weeks
" 21	+8°	20	17	
" 22	+8°	20	14	
" 23	+8°	20	14	
" 24	+10°	6	4	
" 24	+20°	14	14	
" 25	+15°	10	10	
" 25	+10°	10	7	
" 26	+12°	20	16	
" 27	+12°	20	20	
" 28	+12°	10	10	

TABLE 1—*Continued*

Date 1915	Deviation from horizontal of striae on negative field	No. of trials given	No. of correct responses	Remarks
Aug. 28	+11°	10	9	
" 29	+11°	20	17	
" 30	+11°	10	9	
" 30	+10°	10	7	
" 31	+10°	20	17	
Sept. 1	+10°	20	15	
" 2	+10°	20	19	
" 3	+10°	20	12	
" 6	+10°	22	17	
" 7	+10°	20	14	Retraining considered necessary
" 9	+15°	20	20	
" 10	+15°	20	20	
" 11	+15°	20	19	
" 12	+15°	20	20	
" 13	+15°	20	20	
" 14	+12°	20	19	
" 15	+11°	20	20	
" 16	+10°	10	7	Distracted by noise outside
" 17	+12°	20	15	
" 18	+12°	10	10	
" 18	+10°	10	10	
" 19	+12°	10	10	
" 19	+10°	10	10	
" 23	+12°	20	19	
" 24	+10°	20	20	
" 25	+9°	20	18	
" 26	+9°	20	20	
" 27	+9°	20	17	
" 28	+9°	20	19	
" 29	+8°	20	20	
" 30	+7°	20	19	
Oct. 1	+7°	20	14	
" 7	+7°	20	17	
" 8	+7°	20	15	
" 9	+6°	20	15	
" 10	+6°	20	18	
" 11	+6°	20	18	
" 12	+6°	20	20	
" 13	+5°	20	20	
" 14	+5°	20	18	
" 15	+5°	20	18	
" 16	+5°	20	17	
" 17	+4°	20	16	
" 18	+4°	20	15	
" 19	+4°	20	16	
" 20	+4°	20	15	
" 21	+4°	20	17	
" 22	+3°	20	14	
" 23	+3°	20	12	
" 24	+3°	20	17	
" 25	+3°	20	17	
" 26	+3°	20	16	
" 27	+2°	20	12	

TABLE 1—*Continued*

Date 1915	Deviation from horizontal of striae on negative field	No. o trials given	No. of correct responses	Remarks
Oct. 29	+2°	20	17	
" 30	+2°	20	16	
Nov. 2	+2°	20	16	
" 3	+2°	20	14	
" 4	+1°	20	12	
" 5	+1°	20	11	
" 6	+1°	20	11	
" 7	+1°	20	12	
" 8	+1°	20	15	

TABLE 2-A

RECORD OF CHICK 2

Mean brightness of both fields: 6.67 candles per square meter

Date 1914	Positive field		Negative field		No. of trials given	No. of correct responses
	Width of striae (mm.)	Angular deviation from horizontal	Width of striae (mm.)	Angular deviation from horizontal		
May 21	1.56	0°	1.56	90°	10	5
" 22	1.56	0°	1.56	90°	10	3
" 23	1.56	0°	1.56	90°	10	7
" 24	1.56	0°	1.56	90°	10	7
" 26	1.56	0°	1.56	90°	10	7
" 27	1.56	0°	1.56	90°	10	6
" 28	1.56	0°	1.56	90°	10	7
" 29	1.56	0°	1.56	90°	10	6
June 7	1.56	0°	1.56	90°	10	6
" 8	1.56	0°	1.56	90°	10	7
" 9	1.56	0°	1.56	90°	10	6
" 10	1.56	0°	1.56	90°	10	6
" 11	1.56	0°	1.56	90°	10	7
" 12	1.56	0°	1.56	90°	10	7
" 14	1.56	0°	1.56	90°	10	6
" 15	1.56	0°	1.56	90°	10	5
" 16	1.56	0°	1.56	90°	10	5
" 17	1.56	0°	1.56	90°	10	9
" 18	1.56	0°	1.56	90°	10	9
" 19	1.56	0°	1.56	90°	10	7
" 20	1.56	0°	1.56	90°	10	6
" 21	1.56	0°	1.56	90°	10	5
" 22	1.56	0°	1.56	90°	10	8
" 23	1.56	0°	1.56	90°	10	7
" 28	1.56	0°	1.56	90°	10	4
" 29	1.56	0°	1.56	90°	10	7
" 30	1.56	0°	1.56	90°	10	7
July 1	1.56	0°	1.56	90°	10	7
" 2	1.56	0°	1.56	90°	10	7
" 3	1.56	0°	1.56	90°	10	7

TABLE 2-A—*Continued*

	Positive field		Negative field			
Date 1914	Width of striae (mm.)	Angular deviation from horizontal	Width of striae (mm.)	Angular deviation from horizontal	No. of trials given	No. of correct responses
July 4	1.56	0°	1.56	90°	10	8
" 5	1.56	0°	1.56	90°	10	9
" 6	1.56	0°	1.56	90°	10	7
" 7	1.56	0°	1.56	90°	10	5
" 8	1.56	0°	1.56	90°	10	6
" 9	1.56	0°	1.56	90°	10	8
" 10	1.56	0°	1.56	90°	10	6
" 11	1.56	0°	1.56	90°	10	8
" 12	1.56	0°	1.56·	90°	10	6
" 13	1.56	0°	1.56	90°	10	10
" 14	1.56	0°	1.56	90°	10	9
" 15	1.56	0°	1.56	90°	10	10
" 16	1.56	0°	1.56	90°	10	9
" 17	1.56	0°	1.56	90°	10	8
" 18	1.56	0°	1.56	90°	10	8
" 19	1.56	0°	1.56	90°	5	3
" 21	1.56	0°	1.56	90°	10	7
" 22	1.56	0°	1.56	90°	10	9
" 23	1.56	0°	1.56	90°	10	10
" 24	1.56	0°	1.56	90°	10	8
Aug. 12	1.56	0°	1.56	90°	10	9
" 13	1.56	0°	1.56	90°	10	10
" 14	1.56	0°	1.56	90°	10	8
" 15	1.56	0°	1.56	90°	20	17
" 16	1.56	0°	1.56	90°	10	10
" 17	1.56	0°	1.56	90°	10	9
" 18	1.56	0°	1.56	90°	10	10
" 19	1.40	0°	1.40	90°	10	9
" 20	1.30	0°	1.30	90°	10	10
" 21	1.20	0°	1.20	90°	10	9
" 23	1.11	0°	1.11	90°	10	8
" 24	1.11	0°	1.11	90°	10	7
" 24	1.04	0°	1.04	90°	10	9
" 25	1.56	0°	1.56	90°	6	3
" 25	1.11	0°	1.11	90°	5	5
" 25	0.98	0°	0.98	90°	10	8
" 26	1.30	0°	1.30	90°	3	3
" 26	1.11	0°	1.11	90°	5	5
" 26	0.92	0°	0.92	90°	15	7
" 27	1.30	0°	0.10	0°	5	5
" 27	1.40	0°	0.10	0°	10	10
" 27	1.04	0°	0.10	0°	10	9
" 29	1.30	0°	0.10	0°	10	10
" 29	1.04	0°	0.10	0°	5	5
" 29	0.98	0°	0.10	0°	10	8
" 30	1.11	0°	0.10	0°	5	5
" 30	0.98	0°	0.10	0°	10	8
" 30	0.92	0°	0.10	0°	10	10
" 31	1.04	0°	0.10	0°	5	5
" 31	0.98	0°	0.10	0°	10	9
" 31	0.87	0°	0.10	0°	10	6

TABLE 2-B

RECORD OF CHICK 2

Width of striae on both fields: 1.561 mm.
Mean brightness of both fields: 6.24 candles per sq. meter
Direction of striae on positive (standard) field: horizontal

Date 1915		Deviation from horizontal of striae on negative field	No. of trials given	No. of correct responses	Remarks
June	16	—90°	10	10	Retraining records of 10-19 March
"	17	—90°	20	13	omitted
"	21	—90°	20	18	Not worked on days for which no
"	22	—90°	20	19	record is given
"	23	—90°	20	20	
"	24	—90°	20	17	
"	25	—90°	20	19	
"	26	—90°	10	3	
"	27	—90°	10	9	
"	28	—90°	20	20	
"	29	—90°	20	19	
"	30	—90°	20	16	
July	1	—90°	20	18	
"	2	—90°	20	19	
"	3	—90°	20	18	
"	6	—90°	20	15	
"	7	—90°	20	20	
"	8	—80°	20	20	
"	9	—75°	20	20	
"	10	—70°	20	20	
"	11	—65°	20	16	
"	12	—65°	20,	19	
"	13	—60°	20	17	
"	14	—60°	20	20	
"	15	—55°	20	18	
"	16	—50°	20	18	
"	17	—45°	20	17	
"	18	—45°	20	18	
"	19	—40°	10	6	Removed after tenth trial
"	20	—40°	15	9	Very excitable
"	21	—60°	20	16	
"	22	—60°	15	7	
"	23	—90°	20	14	Very excitable; responses slow
"	26	—90°	20	16	
"	27	—90°	15	14	Very slow
"	28	—90°	20	19	Slow
"	29	—90°	20	17	
"	30	—90°	5	5	
"	30	—60°	15	14	Active
"	31	—60°	20	18	Active
Aug.	1	—60°	10	10	
"	3	—60°	10	9	
"	3	—55°	10	8	
"	6	—55°	10	10	
"	6	—50°	10	8	
"	7	—50°	20	17	
"	8	—50°	10	9	
"	8	—45°	10	7	

H. M. JOHNSON

TABLE 2-B—*Continued*

Date 1915		Deviation from horizontal of striae on negative field	No. of trials given	No. of correct responses	Remarks
Aug.	9	—50°	10	9	
"	9	—45°	10	9	
"	10	—50°	5	5	
"	10	—45°	15	11	
"	11	—50°	10	8	
"	11	—45°	10	10	
"	12	—45°	10	10	
"	12	—40°	10	10	
"	13	—40°	20	18	
"	14	—40°	20	16	
"	15	—45°	5	3	Very excitable
"	16	—45°	10	10	
"	16	—40°	20	12	
"	16	—50°	5	5	
"	19	+90°	20	18	
"	20	+75°	20	19	
"	22	+60°	20	20	
"	23	+55ᶜ	20	19	
"	24	+50°	20	19	
"	25	+50°	20	20	
"	27	+50°	10	9	Rather slow
"	27	+45°	10	10	
"	28	+45°	20	18	
"	30	+45°	30	24	
"	31	+45°	10	8	
"	31	+40°	10	7	
Sept.	2	+40°	20	17	
"	3	+40°	20	19	
"	6	+40°	20	16	Refused to work 4th and 5th trials
"	7	+40°	10	9	
"	7	+35°	10	7	
"	9	+35°	20	18	
"	10	+35°	20	17	
"	11	+35°	20	18	
"	12	+30°	20	13	
"	13	+30°	20	15	
"	14	+30°	20	18	
"	15	+30°	20	18	
"	16	+30°	20	17	
"	18	+25°	20	13	
"	19	+25°	20	15	
"	23	+25°	20	13	
"	24	+25°	20	16	
"	25	+25°	20	14	
"	27	—40°	20	17	
"	28	—40°	20	13	
"	29	—40°	20	16	
"	30	—40°	20	14	
Oct.	7	—40°	20	10	

AN ALTERNATIVE METHOD OF TESTING VISUAL ACUITY

A very convenient measure of an animal's visual acuity is the angle subtended at the eye by a single dark or bright stripe in a system which the animal can just distinguish as striate at a given distance. In the earlier experiments mentioned above, I obtained this value by training the animal to distinguish a striate field from a plain field at a distance of 60 cm. from the eye, and then reduced the width of the striae on the positive field until discrimination ceased. An alternative method consists in training the animal, as I did in the present work, to discriminate between a horizontal and a vertical system of equal width, and then gradually reducing the width of the striae in both systems simultaneously until the animal ceases to discriminate at the given distance. The work of Casteel[4] suggests this possibility, although Casteel did not attempt to control the factor of distance or to ascertain the limits of the animal's sensitivity. A priori, we should not expect the results yielded by the two methods to differ greatly, provided the animal's eyes were free from astigmatism in the vertical or horizontal direction, and provided otherwise that in both cases the animal is responding by choosing the positive field, rather than by rejecting the negative field. If experimental data confirm this expectation, and if the second problem should prove as easy for an untrained animal to learn as the first, the time required for learning the first problem might as well be saved. I decided to test the practicability of this method on Chick 2. The daily results appear in table 2-A, between the dates of August 18 and August 26, 1914. From August 27 to August 31 inclusive I repeated the test by the first method used—that of plainstriate discrimination, which is designated as method No. 1, and the other as method No. 2. In these tests, the minimal distance between test-field and eye at which comparison could be made without a choice being registered was 60 cm. The results are summarized in table 3. The values given under the heading " Width of striae (mm.)" are the widths of striae on the positive field for method No. 1, in which the striae on the negative field were invisibly small, and the widths of the striae on both fields in method No. 2, in which the difference in direction was 90°.

---

[4] Casteel, D. B. Discriminative ability of the painted turtle. This journal, vol. 1, 1911, pp. 1 ff.

TABLE 3

Width of striae (mm.)	Method No. 1		Method No. 2	
	No. of trials given	No. of correct responses	No. of trials given	No. of correct responses
1.56	..	..	106	94
1.40	..	..	10	9
1.30	5	5	13	13
1.20	..	..	10	9
1.11	25	25	30	25
1.04	20	19	10	9
0.98	30	25	10	8
0.92	10	10	15	7
0.87	10	6	..	..

These results indicate that the second method is feasible, and that uncertainty in choosing begins at nearly the same absolute stimulus-value whichever method is used. The relative ease of learning for the chick is decidedly in favor of method No. 1. Chick 1 failed to learn to discriminate when trained by method No. 2, but established a perfect habit in 443 trials when trained by method No. 1, despite numerous disturbing factors. Chick 2 learned by method No. 1 in 214 trials, as against 585 trials for method No. 2. The results given in table 3 should not be taken as indicating with accuracy where the bird's stimulus-threshold lies, as the training was interrupted too soon. I did not wish to risk spoiling the bird by frequent punishment for work on the main problem.

DIFFERENCE-THRESHOLD FOR DIRECTION

The term "threshold" is properly used to designate the mean between effectiveness and ineffectiveness of a stimulus or difference between stimuli, in producing a response. In the present discussion this mean is assumed to have been reached when the stimulus-difference is effective in half the total of a fairly large number of presentations or "trials." If the difference were wholly ineffective, the animal should be expected, on the theory of probability, to respond correctly in 50% of a large number of trials. If the difference were always effective, 100% of the responses should be correct. The stimulus-difference at which the percentage of correct choices is 75 is therefore taken as the animal's "threshold." The accuracy of such a determination is indicated by the consistency of the results. The measure of consistency used herein is the mean variation

of the percentage of correct choices for the daily series of trials from the average percentage of correct responses for the total number of trials at a given stimulus-difference.

In much of the past work on the special senses of animals carried on by means of training methods, the experimenters have trained the animals to respond to a given difference between the stimuli, and have then reduced the difference until the animals cease to discriminate. When a break-down occurs, the experimenters frequently discontinue the training after a few additional trials, and take the stimulus-value or stimulus-difference at the breakdown as the animal's " threshold." In some earlier work I followed this procedure, having observed that in some instances further training confused the animal and caused it to sulk. In the present work I have endeavored to find the degree to which such confusion can be overcome by continued training.[5] The results obtained on the chicken show a training-effect which is important, though not relatively large; while the final results obtained on the monkey yielded a threshold of a different order of magnitude from the stimulus-difference at which the first break-down occurred. As appears in table 1, in the records from August 22 on, the monkey showed a strong tendency to break down at a stimulus-difference of 8° to 10°; but he overcame this tendency after continued training, and eventually yielded a threshold in the neighborhood of 2°. Had I given the monkey a considerably larger number of trials at the stimulus-differences of —13°, —10°, +10°, +8° and +7°, after the full effect of training had been obtained, the average percentages of correct responses could be plotted against the stimulus-differences on a consistent and fairly smooth curve.

The results of Monkey 2 are summarized in table 4, and those of Chick 2 in table 5. In compiling the results for each stimulus-difference, I observed the following procedure: Having obtained the average percentage of correct responses for the total number of trials, I took the average percentage of correct responses for each daily series, and obtained the mean variation of these daily averages from the average for the group. Since 20 trials compose the standard daily series, I weighted the

---

[5] My adoption of this course is the result of an extensive discussion carried on with Professor Knight Dunlap some two years ago, regarding the validity of the discrimination-method, as the latter is usually employed.

variations from the mean of the individual daily averages according to the number of trials in the individual daily series referred to 20 as a basis. The mean variation of the averages of the daily series from the general average is expressed in units of the latter in tables 4 and 5, and it gives an indication of the consistency and hence the reliability of the results.

TABLE 4

RECORD OF MONKEY 2

Width of individual striae on both fields: 0.780 mm.
Mean brightness, both fields: 6.24 candles per sq. meter
Striae on positive (standard) field: horizontal

Deviation from horizontal of striae on negative field	No. of trials given	No. of correct responses	Average percentage of correct responses
—15°	95	89	93.7± 2.9
—14°	10	9	90.0
—13°	60	48	80.0± 7.5
—12°	30	29	96.7± 3.7
—11°	13	12	92.3
—10°	40	32	80.0± 7.5
—9°	15	14	93.3
—8°	40	35	87.5± 1.9
—7°	40	37	92.5± 3.7
—6°	40	36	90.0± 3.3
—5°	50	36	72.0± 6.0
+15°	130	126	96.9± 3.5
+14°	30	29	96.7± 4.3
+13°	20	18	90.0± 0.0
+12°	140	127	90.7± 6.0
+11°	80	73	91.1± 3.0
+10°	228	185	81.2± 8.3
+9°	100	92	92.0± 4.4
+8°	100	84	84.0±11.2
+7°	100	79	79.0± 8.8
+6°	80	71	88.7± 6.9
+5°	80	75	93.7± 6.7
+4°	100	79	79.0± 3.3
+3°	100	76	76.0± 8.8
+2°	100	75	75.0± 8.0
+1°	100	61	61.0± 5.6

TABLE 5

RECORD OF CHICK 2

Width of individual striae on both fields: 1.561 mm.
Mean brightness, both fields: 6.24 candles per sq. meter
Striae on positive (standard) field: horizontal

Deviation from horizontal of striae on negative field	No. of trials given	No. of correct responses	Average percentage of correct responses
—90°	400	345	86.2±10.0
—80°	20	20	100.
—75°	20	20	100.
—70°	20	20	100.
—65°	40	35	87.5± 7.5
—60°	130	111	85.4± 8.7
—55°	40	36	90.0± 3.3
—50°	90	79	87.7± 2.6
—45°	110	94	85.4± 6.4
—40°	195	141	72.3±11.4
+90°	20	18	90.
+75°	20	19	95.
+60°	20	20	100.
+55°	20	19	95.
+50°	50	48	96.0± 2.7
+45°	70	60	85.7± 5.8
+40°	80	68	85.0± 5.0
+35°	70	60	85.7± 4.3
+30°	100	81	81.0± 8.8
+25°	100	71	71 0± 5.2

AN APPARENT EFFECT OF " CONTRAST "

After I had obtained the threshold for deviation in the positive direction for Monkey 2, I gave him 40 trials—20 trials each on the 9th and 10th of November—in which the striae on the positive field were horizontal and those on the negative field deviated from the horizontal by 5° in the negative direction. Only 12 responses out of the 40 were correct, the animal persistently tending to choose the negative field against punishment. In this connection it should be noted that when the difference in direction is small and when the striae on one field are horizontal, if the two fields are regarded simultaneously, the striae on both fields appear to be inclined from the horizontal, but in opposite angular directions. For about six weeks previous to these control tests, the striae on the positive field, although really horizontal, appeared to the human observer to deviate in the negative direction, owing to the influence of the other field, whose striae were inclined slightly in the positive direction. If

we assume a similar "contrast-effect" for the monkey, we have a sufficient explanation of his behavior in these control tests.

SUMMARY

Three animals—a monkey and two chickens—previously trained under comparable conditions, showed a striking difference in their individual ability to acquire a perfect habit of response to difference in direction in two systems of visible striae. The monkey perfected his habit in the first series of 20 trials. One chick failed to learn the problem and another chick required 58 days and 585 trials to perfect the habit.

The work demonstrated the practicability of an alternative method of testing visual acuity, but suggested that for some animals the problem is so difficult as to make the method originally used by the author more desirable.

The monkey's difference-threshold for direction of elements of a pattern lies between 2° and 5°; and the chick's threshold between 25° and 40°. The magnitude of the thresholds within these limits for either individual depends in large part on the effect of training.

The training-records, as well as the final results, suggest that the characteristic of direction in visual objects has much more significance for the monkey than for the chicken.

The relative improvement brought about by training is very much greater for the monkey than for the chicken. This fact suggests that other differential factors than relative development of the sense-organ play an important part in discrimination of this type. The point is emphasized by the fact that the monkey's visual acuity, as shown in an earlier study, is between four and five times as good as that of the chick; while his sensitivity to difference in direction is from eight to twelve times as great.

VISUAL PATTERN-DISCRIMINATION IN THE VERTEBRATES—V

A DEMONSTRATION OF THE DOG'S DEFICIENCY IN DETAIL-VISION

H. M. JOHNSON

Nela Research Laboratory, National Lamp Works of General Electric Company

The experiments reported in this paper grew out of certain questions of especial personal interest to the author. These questions are of minor importance as compared with some general questions which the work involves, but as the former really determined the course of experimentation it seems well to mention them.

In the years between 1910 and 1912 the writer, then working at the Johns Hopkins University, acquired some dogs which had been rendered temporarily blind by having their eyelids scraped at the edges and stitched together during the first week of puppyhood. This operation caused the eyelids, which normally separate at about the ninth day, to grow tightly together; and they remained in this condition until they should be separated by a slight operation.

While these animals were blind[1] I trained each of them to open three "problem-boxes" by a single movement of the head, the teeth or the paw, within a minimal time (two seconds or less) and without making any useless movements. The manner of arranging and conducting these experiments is open to criticism, but the results indicate clearly that the blind dogs became quite as proficient as normal dogs trained under identical conditions, and that the number of trials necessary to the acquisition of skill is not consistently greater for blind dogs (Nos. 7 and 8) than for a normal dog (No. 6) of the same litter and trained in the same way. Also, the blind dogs, as well as the normal dogs, showed practically no loss of skill after sixty days of rest.

---

[1] Johnson, H. M. Audition and habit-formation in the dog. *Behavior Monograph*, no. 8, Cambridge, Mass., Henry Holt & Co., 1913.

After each of the blind dogs had learned to open three boxes in this way, the eyelids were parted by an operation. All the animals except Dog 7 showed an opacity of the cornea, usually slight in degree and extent, but varying in different individuals. Dog 7 did not exhibit an opacity. None of these animals showed marked changes of behavior after the operation. I then required Dogs 7 and 8 to learn three more problem-boxes each. They exhibited slightly greater proficiency in acquiring skill than they had shown while they were blind, but the improvement is due— at least in part—to the effect of practice, and is considerably less than that brought about wholly by practice in the case of the normal dog.[2]

These experiments demonstrated that the dog can get along surprisingly well without vision in making complicated adjustments. Other experiments indicated that even normal dogs did not react to some objects as if the latter were visually perceived, provided the objects were stationary.

While the foregoing experiments suggested that the dog may make little use of vision as we ordinarily think of it, they left the question open as to the kind and degree of vision which the dog may have. In 1911-12, I made an attempt to test the dog's sensitivity to difference of outline in visual objects. I used a single animal, designated as Dog 5 in the report cited. I made the tests in the psychological laboratory of the Johns Hopkins University, under the direction of Professor John B. Watson, using the Yerkes-Watson standard apparatus[3] and the discrimination-method recommended by these authors. The test-objects used were a circle 6 cm. in diameter and its (approximately) equivalent square. The animal was fed at the food-box under the square. He learned in about 1000 trials to choose the square invariably, but its brightness (and hence its luminous intensity) was four times that of the circle. When the brightness-difference was eliminated, the animal immediately ceased to show any preference for the square, and he did not make any consistent improvement in 600 trials. It became necessary to discontinue the work at this point. Shortly afterwards the

[2] The records of dog 6 (normal) and of dogs 7 and 8 (first blind and later with the eyelids separated) are intercomparable. The records of dogs 1 and 2 and of dog 5 are not.

[3] Yerkes, R. M. and Watson, J. B. Methods of studying vision in animals. *Behavior Monograph*, no. 2, Cambridge, Mass., Henry Holt & Co., 1911.

animal was accidentally killed. Meantime I had acquired no information regarding the refraction of his eyes. Consequently I did not feel justified in publishing the report of the work as containing anything decisive or important. It is of some interest when considered in connection with some later experiments described below.

Three years ago I became interested in the question of the relative visual sensitivity of animals possessing different types of retinal structure. The retina of the dog's eye is fairly typical of the mammals below the primates. There is no fovea,[4] rather indefinite "sensitive areas" and numerous opaque nerve-fibers which must be considered as blind spots. Such a retinal structure is characteristic, in the main, of mammals below the primates. It seemed fair to select the dog as a representative of this class. I chose the domestic chicken as representative of animals possessing a definite sensitive area but no fovea, and the Capuchin monkey as representative of animals possessing a fovea centralis, temporal to the entrance of the optic nerve. I also felt impressed by the apparent superiority of stimuli such as Casteel[5] used, over stimuli differing only in outline, for a test of the question in which I was particularly interested. I selected[6] as the stimulus to be chosen by the animal, a circular field, 6 cm. in diameter, covered by a system of horizontal dark and bright stripes of equal width. The number of stripes on the field and the width of each stripe could be varied by insensible gradations. The field to be rejected was covered by a similar system of striae, but the members were so numerous and so fine that the eye would not resolve them at the minimal distance at which the animal could make his choice. The stimuli differed in no other respect. The sensitivity of the animal was to be measured by the angle subtended at the eye by the separation of the upper edge of one bright stripe from the lower edge of the bright stripe just above it. The reader should consult the original report for details of these tests.

The daily results obtained for Dog 1, a pure-bred English

---

[4] Slonaker, J. R. A comparative study of the area of acute vision in vertebrates. *Journal of Morphology*, vol. 13, no. 3, 1897.

[5] Casteel, D. B. Discriminative ability of the painted turtle. This journal, vol. 1, 1911, pp. 1 ff.

[6] Johnson, H. M. Visual pattern-discrimination in the vertebrates. I and II. This journal, vol. 4, 1914, pp. 319-361.

bull-terrier, are shown on page 352 of that report. When the width of each stripe on the "positive" field was 5.2 mm., and the distance from the eye was 60 cm., the animal chose the positive field 36 times in 50 presentations or "trials". In the last 20 trials, 18 choices were correct. Believing at the time that he had learned the problem, I reduced the width of the stripes. On examining his subsequent daily records with these, I became convinced that the improvement was accidental, and due to a change in the animal's "position-preference" as a time when his right-left order of choosing happened to fit the order of presentation quite well. When the width of each stripe was 3.9 mm. the animal chose correctly in 127 cases out of 200; when it was reduced to 3.72 mm., 112 out of 175 choices were correct.[7]

These results did not show anything conclusive regarding the dog, except that working near the limit of the instrument I had not made a stimulus-difference large enough to be effective in 50% of the cases. (This condition would be met when 75% of a large number of responses were correct.)

The general method followed in these experiments had yielded quite definite and positive results in the work on the monkey and the chickens. The individual stripes composing the positive system had subtended a very large visual angle throughout all the work on the dog. The failure to obtain positive results on the dog raised several questions regarding the work.

Early in the training the animal had learned to choose the correct food-box by testing the electrodes at the entrance-alleys for electrical charge. When I eliminated this factor he showed great disturbance. It seemed advisable to use another individual, which had not been thus disturbed during the training. I selected a pure-bred female beagle-hound, four months old, for this purpose. Beginning May 26, 1914, I gave her ten trials daily for 90 days, using the method described in the work on Dog 1, the monkey and the chickens. She showed no consistent preference at any time for the positive field, each stripe on which was 5.2 mm. wide. The minimal distance between test-field and the eye at which a choice could be made was 50 cm. A detailed report of her work would be without value in view of facts which we later ascertained, and which I shall mention below.

---

[7] After the original report was prepared I resumed the work at this stimulus-value, and obtained a lower percentage of correct choices over 150 additional trials.

It now became necessary to determine whether the negative results which the dogs gave were due to the inappropriateness of the conditions under which the latter had worked. The first matter to be settled was that of errors of refraction in the dog's eyes. This examination should have been made before the experiments were begun, as is made evident by the results. My colleague, Dr. P. W. Cobb, was kind enough to make the examination and to assume responsibility for the results. He administered atropin to the animals for about a week, until the pupils ceased to respond to light. He then made a careful skiascopic examination. The results obtained during mydriasis were very consistent. Dog 1 showed about 0.25 to 0.50 D. hyperopia during mydriasis. (This condition is characteristic of the emmetropic human eye.) No astigmatism was discoverable. The examination without mydriasis yielded variable results, but none of them indicated the presence of a refractive error which the animal did not overcome by accommodation or by an analogous process. We assumed, therefore, that this dog's eyes were for practical purposes emmetropic. The correction for Dog 2 was +1.75 D. sphere with +0.75 cylinder, the axis lying in the horizontal meridian. The necessary correction was the same for both eyes. A week later Dr. Cobb attempted to test the animals for extent and range of accommodation, but got no consistently positive results. It seemed useless, therefore, to continue experimentation of Dog 2, since even the best accommodation could hardly have overcome so large a refractive error, and since it was inconvenient to equip her with spectacles.

At this time I was working some other animals on the problem of discriminating between a vertical system of striae and a horizontal system differing from the former only in direction. The problem had proved itself quite easy for some of the animals. I had also found it feasible to test an animal's visual acuity by making the stripes on both fields rather coarse, and training the animal to choose the food-box indicated by the horizontal system. The next step was to reduce the width of the stripes in both systems simultaneously, until the members became so numerous and their width and separation so small that the animal could not distinguish the horizontal system from the vertical system at the given distance. I decided to test Dog 1 by this method.

In this work I used the same experiment-box and test-objects and the same general technique as are described in the former report.[8] The mean brightness of each test-field was 6.2 candles per square meter. The width of each stripe in either system was 3.902 mm. The animal had to choose with the eye 40 cm. or more from the test-field, and he was fed in the food-box indicated by the horizontal system. I gave him 20 trials each day. In 140 trials the animal chose correctly only 75 times, and showed no tendency to improve. There seemed reason to question whether he was capable of discriminating between purely visual objects, and of demonstrating the fact by acquiring a perfect habit. Professor Mast, with whom I discussed the question, urged me to settle the point. On June 24, 1915, I gave the animal 20 trials in which only the positive test-object was presented. He was fed in the box at which it appeared. All 20 choices were correct, and there was no hesitation at any time. On the following day I reintroduced the negative field, but stopped it down, so as to introduce a difference in area in addition to the difference in pattern. Hitherto, each field had been limited by a circular diaphragm 6 cm. in diameter. Over the diaphragm limiting the negative field I now slipped a smaller diaphragm, the opening of which was concentric with that of the former. The animal's daily records for the various differences in area appear in table 1. The results show that the dog is able to discriminate when the difference of area presented is between the ratios of 2.25 to 1 and 1.44 to 1. On July 24, August 1, August 14 and August 31 I made control-tests, in which the width of the striae on both fields was so reduced that the fields appeared of uniform brightness to the human eye. As will be seen in the table, these tests showed that the dog's behavior was not affected by the presence or absence of the stripes. After the animal had ceased to discriminate, when the stimuli was a 6 cm. circle and a 5 cm. circle, I retrained him for six days, beginning August 30, 1915, requiring him to choose the 6 cm. circle and to reject the 3 cm. circle. Both fields were of uniform brightness. His average percentage of correct choices for the 120 trials was 85.8. I then reduced the brightness of the 6 cm. circle by introducing an absorption-

[8] In the present work I placed a copper tray, holding a moistened felt pad, between the exit-door of the home-box and the alleys entering the food-boxes. This tended to reduce the variability of the resistance of the animal's feet to a minimum.

TABLE 1—Record of Dog 1

Date	+field 3.9° 0° No. trials given (1)	−field 3.9° 90° No. correct responses (1)	+field 3.9° 0° No. trials given (2)	−field 3.9° 90° No. correct responses (2)	+field 3.9° 0° No. trials given (3)	−field 3.9° 90° No. correct responses (3)	+field 3.9° 0° No. trials given (4)	−field 3.9° 90° No. correct responses (4)	+field 3.9° 0° No. trials given (5)	−field 3.9° 90° No. correct responses (5)	Remarks
Width of striae (mm.)											Mean brightness, both fields: 6.2 candles per square meter
Deviation from horizontal											
Diameter of field (cm.)											
June 25	20	12									
" 26	20	16									
" 27	20	15									
" 28	20	15									
" 29	20	13									
" 30	20	19									
July 1	20	12									
" 2	20	17									
" 3	20	18									
" 6	20	17									
" 7	20	16									
" 8	20	19									
" 9	20	16									
" 10	20	17									
" 11	20	17									
" 12	20	19									
" 13	20	16									
" 14	20	19			20	13					
" 15					20	13					
" 16					20	14					
" 17					20	16					Not worked on days for which no record is given
" 18					20	18					
" 19											
" 20											

TABLE 1—Record of Dog 1—*Continued*

Mean brightness, both fields: 6.2 candles per square meter

Date	field 1 + 3.9° 0° No. trials given	field 1 − 3.9° 90° No. correct responses	field 2 + 3.9° 0° No. trials given	field 2 − 3.9° 90° No. correct responses	field 3 + 3.9° 0° No. trials given	field 3 − 3.9° 90° No. correct responses	field 4 + 3.9° 0° No. trials given	field 4 − 3.9° 90° No. correct responses	field 5 + 3.9° 0° No. trials given	field 5 − 3.9° 90° No. correct responses	Remarks
July 21			20	18							
" 22			20	19							
" 23			20	18							Considered ready for further control
" 24			20	19							Width of striae reduced to 0.1 mm.
" 25					20	15					Width of striae restored to 3.9 mm.
" 26					20	10					
" 27					20	18					
" 28					20	18					Mr. R. Kerslake present.
" 29					20	16					Dr. A. H. Pfund present
" 30					20	17					Mr. F. W. Chapman present
" 31					20	19					
Aug. 1						20					Considered ready for further control
" 4							20	17			Width of striae reduced to 0.1 mm. Dr. W. E. Burge present.
" 6							20	15			Width of striae restored to 3.9 mm.
" 7							20	17			
" 8							20	18			
" 9							20	15			
" 10							20	16			
" 11							20	16			Dr. L. O. Grondahl present
" 12							20	14			
" 13							20	16			
" 14							20	15			Considered ready for further control
" 15											Width of striae reduced to 0.1 mm.

Width of striae (mm.)....
Deviation from horizontal....
Diameter of field (cm.)....

Date				Notes
" 16	12	20		Width of striae restored to 3.9 mm.
" 17	13	20		
" 19	14	20		
" 20	14	20		
" 22	12	20		
" 23	13	20		
" 24	14	20		
" 25	14	20		
" 27	15	20		
" 28	12	20		
" 29	15	20		Stimulus-difference regarded as subliminal. Width of striae reduced to 0.1 mm. henceforth
" 30			17	20
" 31			16	20
Sept. 2			20	20
" 3			15	20
" 9			17	20
" 10			17	20	Considered ready for further control. Brightness of 6 cm. field reduced to 1.5 candles per square meter henceforth
" 14			9	20
" 15			15	20
" 16			11	20
" 18			12	20
" 19			14	20

screen, to about 25% of its original brightness. This made the areas of the two fields approximately inversely proportional to their brightnesses or, in other words, made them very nearly equal in luminous intensity. I gave the dog 100 trials under this condition, but obtained only 61 correct responses. This indicated that he had been merely choosing the field which sent the greater light-flux into his eye, and had not been affected by the difference in area except in so far as it had occasioned a difference in luminous intensity.

The foregoing results indicate with fair definiteness that the dog did not distinguish the large differences in pattern and in outline presented under the experimental conditions. We are not safe in drawing general conclusions from such evidence, however, as long as there is room for doubt whether a clear image of the test-fields had been formed on the retina. This question hinges on the ability of Dog 1 to accommodate. I have found but few references in the literature bearing on the question of the range of accommodation in the dog. Boden[9] remarks that Würdinger showed in 1886 that the dog has a ciliary muscle, and that the necessary mechanism for accommodation is therefore present. He adds that the question of the extent to which accommodation is actually accomplished is one over which opinions differ widely. He quotes Hensen and Völckers,[10] who worked on the mechanism of accommodation in young dogs, to the effect that the dog possesses a wide range of accommodatory change—as wide at least as the monkey's. On the other hand, he quotes Hess and Heine[11] as having elicited a change of refraction of only 1.0 to 1.5 D. by stimulating the sympathetic fibers electrically. Boden himself refracted the eyes of 100 dogs of both sexes and of various ages and breeds, both before and during mydriasis. In the examination without mydriasis he sometimes observed changes in the diameter of the pupillary opening when the dog appeared momentarily to fixate the mirror used in the examination. Boden suspected that an accommodatory movement accompanied this change, since occasionally the sharp image of the pattern which he projected on to the

[9] Boden, Rudolf. Ueber den Refraktionszustand des Hundeauges. *Arch. f. vergleichende Ophthalmologie*, vol. I, 1909-10, pp. 195-241.

[10] Cited by Hess. Anomalien d. Refraktion und Akkommodation d. Auges. Gräfe-Sämisch, Handbuch, 2 Auflage, p. 230.

[11] Hess and Heine. Gräfe-Sämisch, Handbuch, 2 Auflage, p. 236.

dog's retina would suddenly appear blurred under those conditions. He was unable to establish, however, whether these effects were the result of accommodation or were due to astigmatic refraction in the dog's eye.[12]

Dr. Cobb, in a later and more extensive skiascopic examination of Dog 1, without mydriatic, found occasional fluctuations of refraction, varying from 0.25 to 0.75 D. These fluctuations were seldom sustained for any considerable interval, and could not be elicited by moving the experimenter's fingers, or even food, to and fro before the dog's eye. While the most natural inference is that the fluctuations were due to accommodation, it would also be possible to account for them on other suppositions. It was impossible to control the dog's fixation, and rotation of the eyeball changed the length of the optical path. (This extended from the light-source to the mirror, thence through the comparison lens into the dog's eye and to the retina, thence back through the comparison lens to the experimenter's eye.) This change might be made by difference in angle of incidence at the dog's cornea, by differences in refractive index of the different layers of the dog's lens, and also by unevenness of contour of the dog's retina. It seemed clearly established, however, that parallel rays, or rays proceeding from an object 20 feet or more from the eye, are sharply focused on the retina of

---

[12] I have elsewhere asserted that the dog's mechanism of accommodation is useless unless it serves in some way to change the radius of curvature of the cornea, as is the case in some birds, but, according to Hess, is not true of the mammals. This assertion was based on my acceptance of a reference by an American writer to Freytag's work (Die Brechungsindices der Linse und der flüssigen Augenmedien bei der Katze und beim Kaninchen. *Arch. f. verg. Ophth.*, vol. I, 1909-10). In this reference Freytag is cited as saying that the refractive indices of the lens and of the fluid media of the dog's eye are practically identical, and that several other mammals suffer under the same condition. Since I made the above remark, I have procured a copy of Freytag's original article which before had been inaccessible to me. It appears that Freytag was incorrectly quoted by his reviewer. He actually gives as mean values of the refractive indices in young and old dogs: for the aqueous humor, 1.3349; for the vitreous humor, 1.33483; and for the lens, values ranging between 1.4498 and 1.4666, depending on age. He reports a comparable difference between the refractive indices of the lens and fluid media in all the mammals which he studied.

I am satisfied that some individual dogs make very little use of the mechanism of accommodation. If such is generally true, it would seem that the defect is retinal, rather than in the accommodatory apparatus itself. If it may be assumed that the stimulus to accommodation is indistinctness of the retinal image, it is evident that an animal whose retina is relatively insensitive to detail would have relatively slight stimulus to accommodation.

Incidentally, the solution of a number of extremely interesting problems in the relation between vision and field-behavior must await the determination of the range of accommodation in representative infra-primate mammals.

the unaccommodated eye of Dog 1.   An object 133 cm. distant may be imaged on at least some parts of the retina if the animal accommodates or rotates the eye properly.   In the discrimination work just described, the animal had to choose with the eye less than a meter from the test-fields, and he actually chose, as a rule, with the eye at the minimal distance, which in part of the work was 60 cm. and in the rest, 40 cm.   There was some room for doubt, therefore, whether a clear image had been formed on the retina under the prescribed conditions.   Further work was necessary to determine whether the dog's inability to discriminate was due to retinal insensitivity or to other causes.

I proceeded at once to modify the method so as to insure that a sharp image of the patterns to be discriminated would be formed on the retina of the animal's unaccommodated eye. There are several means by which this could have been accomplished.   We could have mounted the test-objects 20 feet away, so that rays proceeding from each point on them would have reached the dog's eye as nearly parallel rays.   But the test-objects are small, and might not have attracted the dog's attention.   The largest striae which these particular gratings will form subtend a very small angle at 20 feet.   Negative results thus obtained would have been ambiguous.   Of course it would have been possible to project an enlarged image of the patterns on to a distant screen, but in such case modification of the Yerkes experiment-box would have been necessary.   It would also have been possible to equip the dog with spectacles.   Had this course been adopted it would have been necessary to use extreme care to insure that the animal inspected the test-object at a constant distance.   This procedure involved some practical difficulties.   Another course seemed most nearly free from objectionable features.   I took two lenses, each having a free opening of 6 cm. and an equivalent focus of 40.8 cm., and mounted a test-object in the first principal focus of each of these lenses. Each of the two optical systems thus formed was mounted on a photometer bench, so that the face of the lens remote from the test-object was presented at the window (W_1, W_2, fig. 6, p. 338 of the first article of this series) of the Yerkes box.   The axis of each optical system was normal to the plane of the window at which it was presented, and coincided with the center of the latter.   The lenses are achromatised for two points in the visible

spectrum, and are highly corrected for spherical aberration, astigmatism, distortion and curvature of the image. With this arrangement light from all parts of the test-field emerged from the lens in bundles of parallel rays. The eyes of dog 1 being emmetropic, it follows from geometrical optics that if his un-accommodated eye were placed in any part of the cone of light emerging from the lens, a sharp image of the test-field would be formed on the retina, and that the angle subtended by the image of any stripe at the second nodal point of the eye would be the same as that subtended by the stripe itself at the first nodal point of the projection lens.

The stripes on the positive field were horizontal, and each one was 3.902 mm. wide. The distance between the test-field and the first nodal point of the lens was 399 mm.[13] The image of each stripe therefore subtended a visual angle of 33' 32''—an angle larger than is subtended by the sun's disc at the earth. The pattern on the positive field is closely comparable with that of a plank fence, the units in which are 6 inches wide and 6 inches apart, viewed at a distance of 50 feet. The stripes on the negative field were also horizontal, but were only 0.1 mm. wide. They were re-solved by the lens, and may have been resolved by the dog's eye, but being only 1-39 as wide as those on the positive field, an animal capable of distinguishing them as such should have had no difficulty in discriminating between them and the coarser system.

I introduced the dog to this problem 22 September 1915, using the general method already described. The mean bright-ness of both fields was 6.2 candles per square meter—a com-fortable reading condition for the light adapted human eye. The intensity of the electric shock administered for incorrect responses was the same as that used in the immediately preceding experiment, in which it had proved effective and not greatly disturbing. The results of this experiment are shown in table 2. They show that the animal did not discriminate and did not improve in 500 trials. Since this dog was already trained to react in the box, and since he had learned readily to discriminate between other purely visual stimuli, I regard the evidence as conclusive that the dog does not distinguish relatively gross detail in visual objects, and that the deficiency is retinal.

---

[13] I wish to thank Dr. A. G. Worthing and Dr. W. Weniger for making this deter-mination for me.

TABLE 2

RECORD OF DOG 1

Discrimination between plain and striate fields
Width of each stripe on positive field: 3.902 mm.
Width of each stripe on negative field: 0.104 mm.
Mean brightness of both fields: 6.2 candles per sq. meter
(Each test-object mounted in principal focus of lens, 399 mm. from nodal point)

Date	Number of trials given	Number of correct responses		Average percentage correct responses	Remarks
Sept. 22	20	12			
" 23	20	14			
" 24	20	11			
" 25	20	12			
" 26	20	12	1st 100 trials	61±3.4	
Sept. 27	20	11			
" 28	20	13			
" 29	20	10			
" 30	20	13			
Oct. 1	20	11	2d 100 trials	58±5.4	
Oct. 7	20	11			Not worked since Oct. 1
" 8	20	10			
" 9	20	12			
" 10	20	15			
" 11	20	10	3d 100 trials	58±7.6	
Oct. 12	20	10			
" 13	20	11			
" 14	20	9			
" 15	20	7			
" 16	20	13	4th 100 trials	50±8.0	
" 17	20	11			
" 18	20	9			
" 19	20	10			
" 20	20	10			
" 21	20	9	5th 100 trials	49±3.2	
Total...	500	276		55±6.6	

CONCLUSION

Throughout the theories of the most important writers on natural selection and sexual selection it is usually assumed either expressly or implicitly that animals are visually sensitive to certain patterns or markings of the plumage or hair of their own kind, as well as of their natural prey. Theories of protective and warning coloration and marking are built on such an assump-

tion. I hope at some later time to attempt an analysis of some of these theories with reference to this question. In so far as such assumptions are made to apply to animals the structure and function of whose eyes are typified by the dog, I am convinced that the foregoing experiments present at least presumptive evidence to the contrary.

If the dog's eye is not adapted to detail-vision, and if even a 4 to 1 brightness-difference is ineffective, as was indicated by the control tests of 14 September to 19 September, we may seriously inquire what useful purpose his vision serves. Orbeli, Kalischer and Smith have seriously attacked the problem of color-vision. Orbeli[14] used the saliva-reflex method of Pavloff, and attempted conscientiously to control his stimuli. He reports negative results. Kalischer[15] used a food-training method with muscular responses as the criterion. He reports definitely positive results. However, he worked without attempting to exclude certain obvious secondary stimuli, and his own report suggests that it was the latter which were actually effective. Smith's[16] use of colored papers for stimuli is open to fatal criticism, since they reflect a considerable amount of light of all wave-lengths, and since we know nothing as yet of the relative stimulating value of the different wave-lengths for the dog. It is not improbable that the range of effective wave-lengths is comparatively short for the dog, as it evidently is for rodents.[17] Smith seems to have used great care in the training-procedure, and is inclined to draw a positive conclusion from the results. I cannot see that the latter is warranted by the number of trials given and the percentage of correct responses obtained. Regarding the above and other tests of color-vision, it seems well to remark that all of them have been made only with test-fields of large area. In nature, different colors are usually presented as parts of patterns. This is especially true of the markings of plumage and hair. Proof of the existence of sensitivity to dif-

[14] Orbeli, L. A. Réflexes conditionnels du côte de l'oeil chez le chien. *Archives des sciences biologiques* (St. Petersburg), 1909.

[15] Kalischer, O. Weitere Mitteilung über die Ergebnisse der Dressur als physiologischer Untersuchungsmethode auf den Gebieten des Gehör-, Geruchs- und Farbensinns. *Arch. f. Physiol.*, 1909.

[16] Smith, E. M. Some observations concerning color-vision in dogs. *British Journal of Psychology*, vol. 5, 1912-13, pp. 119 ff.

[17] Watson, John B. and Watson, Mary I. A study of the responses of rodents to monochromatic light. This journal, vol. 3, 1913, pp. 1 ff.

ference in wave-length does not necessarily indicate that its possession is useful to the animal, unless there is evidence that his eye will "resolve" the patterns. Leaving the question of color-vision open, it should be remarked that the dog's retina seems well adapted to sensitivity to time-rate of change in intensity. In uncontrolled behavior all the normal dogs with which I have worked attended instantly to moving objects. I have often seen dogs chase the moving shadow of a cloud across the field, and bark at it vigorously. Sensitivity to rate of flicker, of various kinds and at various intensities, in lower mammals, constitutes a problem of great interest and importance. There is good ground for suspecting that such visual sensitivity is the most useful one which the lower mammals possess.

I wish to take this opportunity to acknowledge my indebtedness to Dr. P. W. Cobb for the work of examining the eyes of these animals; also to him and to Professors S. O. Mast and Harvey Carr for criticism which affected the direction and extent of the work. Finally, I should like to thank Mr. Arthur Lawrence, the owner of dog 1, for his generosity in permitting me to keep the animal for several months. It might have been quite difficult to find another dog with emmetropic eyes.

SUMMARY

In an earlier experiment normal dogs showed a surprising lack of superiority over blind dogs in learning to make complicated adjustments. A normal dog gave evidence that he did not depend on vision in making many of his ordinary responses in the field.

In another earlier experiment a 4 to 1 difference in luminous intensity, presented in addition to the difference in outline, enabled a dog to discriminate between a circle and its equivalent square. When the stimuli were equated in luminous intensity. discrimination ceased, and was not reestablished in 600 trials. The factor of refractive aberration was not determined.

In the present work, two chickens and one monkey learned in 300 to 400 trials to distinguish a striate field from a plain field equal to the former in area, outline, color and mean brightness. A dog with two emmetropic eyes failed to learn the problem in over 1,000 trials, although the striae on the positive field were made nearly six times as large for him as for the other animals.

The same animal was later trained in a short time to discriminate between two visual objects. During the training period the stimuli differed in area, pattern and luminous intensity, but only the latter difference was effective. When in a control test it was eliminated, and a 1 to 4 difference in mean brightness was presented with a 4 to 1 difference in area, the animal ceased to discriminate and did not learn to discriminate on the new basis. In this experiment and the one preceding reliance was placed on the animal's (assumed) ability to accommodate, and obtain a clear retinal image. The validity of the assumption could not be established on empirical evidence.

The same animal, continued in training by the same method, was now presented with a field covered with an extremely coarse pattern, to be discriminated from a uniform field of the same area, form and mean brightness. The conditions of the experiment insured the formation of a sharp image of the test-fields on the animal's unaccommodated eye. He failed to learn the problem or to make any improvement in 500 trials.

The cumulative evidence yielded by the above experiments indicates that the dog is very deficient in detail-vision, and that the immediate cause is the relative insensitivity of his retina to differences of distribution of brightnesses over it.

Nela Park, Cleveland, Ohio.

A STUDY OF THE BEHAVIOR OF THE WHITE RAT BY THE MULTIPLE CHOICE METHOD

HAROLD E. BURTT

From the Psychological Laboratory of Harvard University

INTRODUCTION

The multiple choice method of studying ideational and allied forms of behavior has already been described in connection with reports of results.[1] It consists essentially in presenting to a subject of any type, age, or condition a problem "which may be solved by the perception of a certain constant relation or group of relations within the reaction-mechanisms." For instance the subject may be required to operate the right-hand mechanism or the second from the left in a group of mechanisms varying in number from two to nine.

In this way the same *problem* can be presented to widely varied organisms, it being necessary merely to adapt the form of reaction mechanism to the species of animal. For human subjects a simple keyboard suffices,—the sounding of a buzzer as indication of a correct choice proving ample incentive to effort. With crows, pigs, ring-doves, rats and monkeys a series of similar boxes, each with an entrance and an exit door, has been employed, with confinement as punishment for incorrect choices and food as reward for correct choices. The value of this method from the comparative standpoint is obvious.

SUBJECTS

Three outbred and two inbred albino rats were used in the experiments. All were born in the Harvard Psychological Lab-

[1] Yerkes, Robert M. The study of human behavior. *Science,* 1914, **39**, 625-633.

Coburn, Charles A. and Yerkes, Robert M. A study of the behavior of the crow, *Corvus Americanus* Aud., by the multiple-choice method. *Journal of Animal Behavior,* 1915, **5**, 75-114.

Yerkes, Robert M. and Coburn, Charles A. A study of the behavior of the pig, *Sus scrofa,* by the multiple-choice method. *Journal of Animal Behavior,* 1915, **5**, 185-225.

Yerkes, Robert M. The mental life of monkeys and apes: a study of ideational behavior. *Behavior Monographs,* 1916. **3**, whole number 12.

oratory.   Outbred females A and B and male D, all of the same litter, were born February 11, 1915, and were about five months old when they were first used, early in July.   Inbred male J was born March 1, and began work early in August when five months of age.   Inbred female C from another line was younger than the others, being born March 27 and beginning work when about three months of age.

These five subjects were selected from nine rats which were given preliminary training.   They proved readier in forming the food-association and in getting accustomed to the apparatus than the other four, and it therefore seemed possible to bring them to a more uniform state of preparation prior to the actual experiments.

There were, however, very noticeable individual differences from the outset.   A was rather timid, entering the compartments cautiously and with hesitation.   D worked rather slowly and appeared in poor health from the start.   B and C were extremely active and energetic, choosing successive doors with great rapidity and running to the food-dish at full speed.

The rats were not paired, but two or three of the same sex were caged together.

APPARATUS

The experiments were performed in a well lighted attic room at the writer's home in Haverhill, Massachusetts.   A ground plan of the apparatus is shown in figure 1.   It consisted of nine similar compartments, C, C, etc. with a door at each end,—the front door giving access to the reaction-chamber R and the rear door to the back alley A.   The compartments were placed equidistant from the door of the entrance box E, along the arc of a quadrant of a circle.

The various doors, of sheet brass, were arranged to slide vertically and were operated from the experimenter's table by weighted strings passing through screw eyes above the doors. Those doors leading from the reaction-chamber into the nine compartments were arranged to remain 3-16 of an inch from the floor when closed, to avoid pinching the animal's tail.   The entire apparatus was covered with wire netting and the floor was sprinkled with a light layer of sawdust.

From the reaction chamber the animal could enter one of the nine compartments, pass into the back alley, thence to the side

alley and the food-dish F. To facilitate its re-entrance into E, a light wooden door D was hinged to a frame sliding along the wall of the side alley S. Pulling a string caused this door to swing across the alley and then slide along in a transverse position toward the entrance box. This cut off the animal's retreat and, if necessary, pushed it into the entrance box. Another string pulled this device back to its original position.
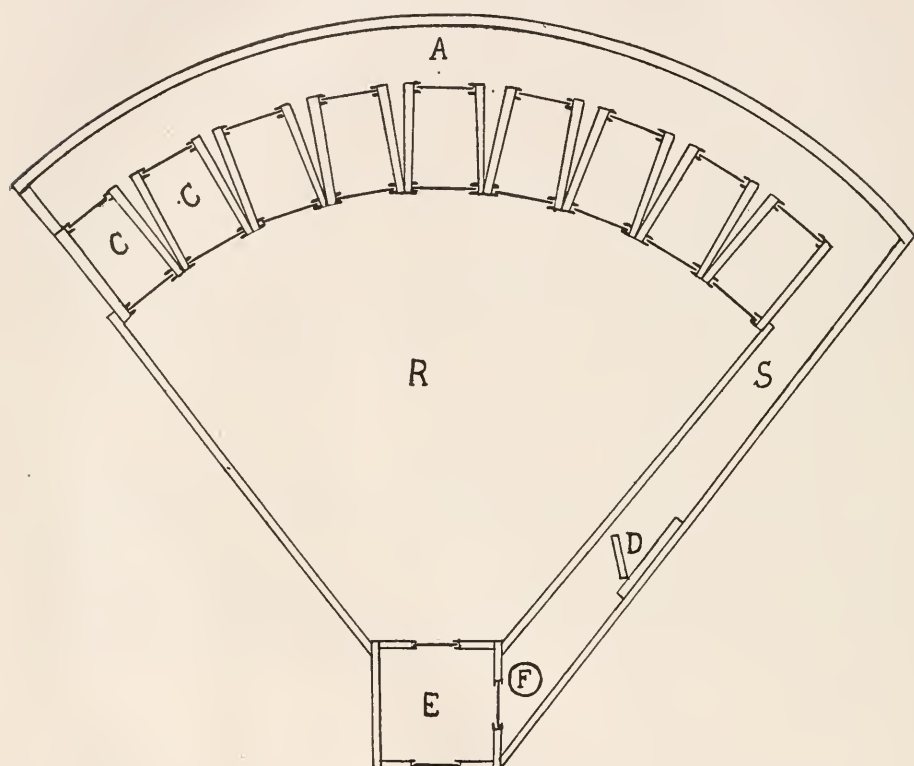
FIGURE 1. Ground plan of multiple-choice apparatus for rats. Scale 1:10
E, entrance-box; R, reaction-chamber; C, reaction-mechanisms; A, back alley; S. side alley; D, sliding door; F, food-dish. The doors (except D) moved vertically and were operated by weighted cords through screw-eyes not shown in the figure.

The interior dimensions of the nine compartments were: width 3 in., length 8 in., depth 4 in. Each front door was 24 in. from the door of the entrance box E. The alleys were 4 in. wide, the entrance box 6 x 6 in. and the entire apparatus 4 in. deep.

The apparatus rested on the floor on the side of the room opposite the only window, with the entrance box nearest the window and the front doors of the compartments directed toward the window. The experimenter sat about 10 feet distant behind a table near the window. A large mirror, hung at an angle of 45 degrees from the wall above the apparatus, illuminated it fairly uniformly and enabled the experimenter to observe the animal in positions that could not be seen directly.

PROBLEMS AND GENERAL METHOD

The first two of the standard problems[2] were presented to the various subjects,—viz. the selection of the first mechanism on the right and the selection of the second mechanism from the left. Below are given the ten settings of the doors which were presented in succession together with the number of the given setting in the series, the number of doors open and the number of the correct door. The doors were numbered from right to left as viewed by the subject.

PROBLEM 1.   First mechanism at the right end of the group

Settings	Doors open	No. of doors open	No. of right door
1	1.2.3	3	1
2	8.9	2	8
3	3.4.5.6.7	5	3
4	7.8.9	3	7
5	2.3.4.5.6	5	2
6	6.7.8	3	6
7	5.6.7	3	5
8	4.5.6.7.8	5	4
9	7.8.9	3	7
10	1.2.3	3	1

Total 35

PROBLEM 2.   Second mechanism from the left end of the group

Settings	Doors open	No. of doors open	No. of correct door
1	7.8.9	3	8
2	1.2.3.4	4	3
3	2.3.4.5.6.7	6	6
4	1.2.3.4.5.6	6	5
5	4.5.6.7.8	5	7
6	1.2.3	3	2
7	2.3.4.5	4	4
8	1.2.3.4.5.6.7.8.9	9	8
9	1.2.3.4	4	3
10	3.4.5.6.7.8	6	7

Total 50

[2] *Cf.* footnote 1.

In most cases the rats were given the ten settings in order in a single series of experiments. In a few of the earlier series it was not feasible to give ten trials in immediate succession.

Both punishment and reward were used as incentives. The punishment consisted of confinement in a compartment after an incorrect choice for 5 (in some cases 10) seconds. The reward consisted of food,—cold boiled potato or green corn proving most satisfactory. The rats were given all the food they wished during the afternoon and evening, but always fasted from 10 p. m. until the middle of the next forenoon when the experimental observations were usually made. If trials were made in the afternoon also, no food was given in the interim.

EXPERIMENTAL PROCEDURE

The usual procedure in a series was as follows. Sufficient food for 10 trials was placed in small bits in the food-dish. The rat was put into the entrance box through the rear door. The experimenter then took his seat at the table ten feet distant and remained there during the entire series. The proper entrance doors of the compartments were raised for the first trial, e. g., in Problem 1 doors 1, 2 and 3 were opened and all the others closed. The door leading from E into the reaction-chamber was then raised and the behavior of the rat was recorded in symbols from its entrance into the chamber until its arrival at the food.

If the animal entered the wrong compartment the door behind it was closed for 5 seconds,—the experimenter counting the tics of the stop-watch. The rat was then allowed to retreat from the compartment and make another choice. This procedure was repeated until the rat entered the correct compartment, whereupon the door behind it was closed and the exit-door opened immediately. The rat then ran along the alley to the food-dish. The experimenter immediately pulled a string closing the door across the alley behind the animal. After a few seconds the door from the alley to the entrance box was raised, and the door behind the rat pulled along until it drove or pushed him into the entrance box. Most of the rats, however, soon acquired the habit of picking up a bit of food, waiting until the door in front of them opened and then going into the entrance box to eat at their leisure. Meanwhile the doors were set for the next

trial and the rat, when ready, was admitted again into the re-
action-chamber for another trial. The time from the entrance
into the reaction-chamber until the arrival at the food was meas-
ured with a stop-watch.

PRELIMINARY TRAINING

The rats were placed in the apparatus in groups of two or
three with all the doors open and with food in the food-dish.
They were left there for three hours. This procedure was re-
peated for three days.

Then with all the entrance doors of the nine compartments
open, a rat was admitted to the reaction-chamber. When he
entered *any* compartment the door was closed behind him and
the exit door immediately raised and he found his way to the
food. He was allowed to eat for a few seconds, then pushed
into the entrance box and readmitted to the reaction-chamber
with all the entrance doors open. This was repeated for half
an hour. Such preliminary training was continued until the
animal made ten choices in half an hour. This necessitated in
most cases only two or three series, of half hour's length, a day
apart.

The following day the rat was given the opportunity to secure
success at each of the nine boxes. No. 1 was the only door
open on the first trial, No. 2 on the second, etc. The next day
this was reversed, No. 9 being the only door open on the first
trial, No. 8 on the second, etc. The rats by this time had the
food-association well formed and appeared to be in a state of
uniform preparation for the regular experiments.

RESULTS OF EXPERIMENTS

As it is essential to present the data for each trial in the series
of experiments, tables I, II, III, IV, V, and VI have been con-
structed after the following manner. At the head of each table
stand the several settings, the letter S serving as an abbreviation
for setting and the number following it designating the place
of the setting in the series. Immediately under the number of
the setting appear the numbers of the doors open, with the one
to be chosen (correct one) in bold face type. The column at
the left gives the date. The second column gives the number
of the various trials in the whole series. Following these num-

bers are the results for the trials indicated,—the figures denoting the numbers of the boxes entered in the order of entrance. The last five columns give the number of correct and incorrect first choices in a given series of ten, the total number of right and wrong first choices on a given day and the daily ratio of right to wrong. At the bottom of the tables for problem 1 appear the results in a check series of ten trials with ten new settings. For example, referring to table I, we see that rat A entered compartment No. 3 on the first trial and after punishment by confinement entered No. 1 which was correct; in the 56th trial she entered No. 8 three times in succession, being punished for each entrance and then entered No. 6 the correct one. The time of the trials, although recorded as a matter of routine is not included in the results.

The tables enable one to obtain quickly information concerning the forms of response and the changes therein during the course of the experiment. Further comment will be made in the following section.

DISCUSSION OF RESULTS

Problem 1, which consisted in the selection of the reaction mechanism on the subject's right, proved soluble for the four rats, i. e., they were able to make correct first choices in ten consecutive trials on the ten settings.

Outbred female A was successful after 170 trials and her brother D after 200. Inbred male J, of about the same age, solved the problem in 170 trials, while the younger inbred female C required 350.

In this problem the total number of doors open in the ten settings is 35. Of these 10 were of course correct. Hence the probability of a correct first choice in any trial is 10-35 and the probable ratio of correct to incorrect first choices in any series apart from experience is 1 to 2.5. The tables show that D and J started with a ratio for the first day of 1 to 9 which is much less efficient than was to be expected, while A and C were more efficient than expectation with ratios of 1 to .66. These differences were perhaps due to a tendency to go toward the right on the part of A and C, while with D the opposite tendency was manifest throughout.

After solution of the problem each animal was given 10 trials

TABLE I

Results for Rat A, Outbred Female, in Problem 1

Date	No. of trials	S. 1 1.2.3	S. 2 8.9	S. 3 3.4.5.6.7	S. 4 7.8.9	S. 5 2.3.4.5.6	S. 6 6.7.8	S. 7 5.6.7	S. 8 4.5.6.7.8	S. 9 7.8.9	S. 10 1.2.3	R	W	R	W	Ratio of R to W
July 8	1– 10	3.1	8	3	8.7	6.2	6	5	4		2.2.3.1	6	4	6	4	1:0.66
9	11– 20	3.2.1	8	4.7.3	7	5.3.6.2	7.6	6.7.5	4	7	3.3.1	4	6	13	7	1:0.54
"	21– 30	1	8	3	7	5	6	5	4	7	1	9	1	6	4	1:0.66
10	31– 40	2.3.1	8	4.7.3	7	4.6.2	6	5	4	7	3.3.3.2.1	6	4	5	5	1:1.00
12	41– 50	2.1	8	3	8.9.7	2	8.6.8.8.6	6.5	8.4	7	1	5	5	3	7	1:2.33
13	51– 60	2.1	8	6.3	9.7	6.2	6	5	6.7.4	7	3.1	5	7			
14	61– 70	1	8	5.3	8.7	2	8.6	5	4	9.7	3.1	3	4			
"	71– 80	2.3.2.1	9.8	4.3	7	2	8.6	5	4	7	3.1	6	5	11	9	1:0.81
15	81– 90	3.1	8	3	7	2	6	5	8.5.4	9.7	1	5	3			
"	91–100	1	8	5.3	8.7	2	6	6.5	5.4	7	1	7	4	13	7	1:0.54
16	101–110	1	8	3	7	5	6	5	4	7	3.2.1	6	3			
"	111–120	2.1	8	3	7	2	6	5	4	7	3.1	7	3	14	6	1:0.43
17	121–130	2.1	8	6.4.3	7	3	6	6.5	5.7.4	7	3.1	7	5	5	5	1:1.00
18	131–140	1	8	3	7	4.2	6	5	5.4	7	1	5	2	8	2	1:0.25
19	141–150	2.1	8	3	7	5.2	6	5	4	7	3.1	8	3			
"	151–160	3.1	8	7.3	9.7	2	8.6	5	4	7	1	7	4	13	7	1:0.54
20	161–170	1	8	3	7	2	6	5	4	7	1	6	0	10	0	1:0.00
		2.3.4	6.7.8.9	3.4.5	4.5.6.7.8.9	6.7.8.9	1.2.3.4.5	2.3.4.5 6.7.8	3.4.5.6.7.8	5.6.7	1.2.3.4.5 6.7.8.9					
														9	1	
20	1– 10	2	6	3	9.4	6	1	2	3	5	1	9	1			1:0.11
Retention Sept. 9		1	8	3	7	2	8.6	5	4	9.9.7	1	8	2			

TABLE II

RESULTS FOR RAT D, OUTBRED MALE, IN PROBLEM 1

Date	No. of trials	S. 1	S. 2	S. 3	S. 4	S. 5	S. 6	S. 7	S. 8	S. 9	S. 10	R	W	R	W	Ratio of R to W
		1.2.3	8.9	3.4.5.6.7	7.8.9	2.3.4.5.6	6.7.8	5.6.7	4.5.6.7.8	7.8.9	1.2.3					
July 4	1–10	3.2.1	9.8	4.6.3	9.9.8.7	6.5.3.3.2	7.7.7.6	6.5	6.5.4	7	3.2.1	1	9	1	9	1:9.00
6	11–20	1	9.9.8	4.3	9.7	5.2	6	6.5	8.7.5.4	7	2.1	3	7	3	7	1:2.33
7	21–30	3.1	9.8	6.3	7	6.5.4.3.2	7.6	7.6.5	7.5.4	7	3.2.1	2	8	2	8	1:4.00
8	31–40	3.1	8	3	8.7	2	8.6		8.7.5.4	9.7	3.2.1	3	7	3	7	1:2.33
9	41–50	3.1	9.8	7.6.5.4.3	9.7	5.3.2	7.6	5.5	7.6.4	9.7	3.2.1	1	9	1	9	1:9.00
12	51–60	3.1	9.8	7.4.3	9.8.7	6.4.2		7.5		9.7	3.1	1	9	1	9	1:9.00
13	61–70	3.1		7.4.3	7	6.4.2	6.6	5.5	4	9.7	3.1	4	6	4	6	1:1.50
14	71–80	3.1	9.8	3	9.7	5.3.2	8.6	6.5	4	8.7	3.1			4	7	1:2.33
	81–90	3.1	9.8	3	7	3.2	6	6.5	5.4	8.7	3.1	6	14	2	7	
15	91–100	3.1		3	8.7	2	6	7.5.5	5.4	7	3.1			4	6	1:1.50
	101–110	3.1	8.8	4.3	7	3.2	6	6.5	4	8.7	2.1	8	12	4	6	
16	111–120	3.2.1	8	4.3	9.7	4.2	6	7.5	4	7	3.1			3	7	1:2.33
	121–130	2.1	9.8	3	8.7	3.2	6	5.5	8.4	9.7	3.1	6	14	3	7	
17	131–140	1	8	3	8.7	2	6		4	8.7	1	6	4	6	4	1:0.66
18	141–150	1	8	3	7	2	6	6.5	8.7.6.4	7	1	8	2	8	2	1:0.25
19	151–160	1	8	3	9.8.7	2	6	5.5	4	8.7	1			8	1	1:0.17
	161–170	1	8	3	9.7	2	6	6.5	4	8.7	1	17	3	9	2	
20	171–180	1	8	4.3	8.7	2	6	5.5	4	7	3.2.1			8	4	1:0.43
	181–190	1	8	3	7	2	6	5	4	7	1	14	6	6	2	
21	191–200	1	8	3	7	2	6	5	4	7	1	10	0	10	0	1:0.00
		2.3.4	6.7.8.9	3.4.5	4.5.6.7.8.9	6.7.8.9	1.2.3.4.5	2.3.4.5 6.7.8	3.4.5.6.7.8	5.6.7	1.2.3.4.5 6.7.8.9					
21	1–10	2	6	3	4	6	1	2	6.4.3	5	1	9	1	9	1	1:0.11

TABLE III

RESULTS FOR RAT J, INBRED MALE, IN PROBLEM 1

Date	No. of trials	S. 1 1.2.3	S. 2 8.9	S. 3 3.4.5.6.7	S. 4 7.8.9	S. 5 2.3.4.5.6	S. 6 6.7.8	S. 7 5.6.7	S. 8 4.5.6.7.8	S. 9 7.8.9	S. 10 1.2.3	R	W	R	W	Ratio of R to W
Aug. 10	1– 10	3.2.1	8	7.6.5.3	8.9.8.7	6.3.2	8.6	7.5	8.6.4 ·	9.7	3.2.1	1	9	1	9	1:9.00
11	11– 20	3.2.1	8	7.6.3	8.7	6.6.2	7.8.7.6	7.5	5.4	8.7	3.1	1	9	5	15	1:3.00
"	21– 30	2.3.1	8	7.7.5.3	8.7	6.4.2	8.6	5	8.6.4	7	1	4	6	13	7	1:0.54
12	31– 40	2.3.2.1	8	3	8.7	2	7.6	5	4	7	1	7	3			
"	41– 50	2.3.2.1	8	7.4.3	7	4.3.2	8.7.6	5	4	7	2.3.2.1	6	4	13	7	1:0.54
13	51– 60	3.2.1	8	4.3	7	5.3.2	6	5	5.4	7	2.1	8	2	7	3	1:0.43
"	61– 70	2.1	8	4.3	7	4.3.2	6	6.5	6.8.4	7	3.2.1	5	5	7	3	1:0.43
14	71– 80	1	8	4.7.3	8.7	2	6	6.5	4	7	1	7	3			
16	81– 90	1	8	4.3	7	3.2	6	5	4	7	1	7	3			
17	91–100	1	8	4.3	7	4.2	7.8.6	6.5	4	7	3.2.1	7	3	13	7	1:0.54
"	101–110	2.1	8	4.3	7	4.3.2	6	5	4	7	1	6	4	5	5	1:1.00
18	111–120	3.1	8	4.3	7	3.6.2	6	6.7.5	4	7	2.1	5	5	7	3	1:0.43
19	121–130	1	8	3	7	3.2	7.6	6.5	5.4	7	1	7	3			
20	131–140	1	8	4.3	7	3.2	6	5	4	7	1	7	3			
"	141–150	2.1	8	4.3	7	2	7.6	5	4	7	1	6	4			
"	151–160	1	8	3	7		6	5	4	7	2.1	7	3			
"	161–170	1	8				6	5	4	7	1	10	0	30	10	1:0.33
		2.3.4	6.7.8.9	3.4.5	4.5.6.7.8.9	6.7.8.9	1.2.3.4.5	2.3.4.5 6.7.8	3.4.5.6.7.8	5.6.7	1.2.3.4.5 6.7.8.9	8	2	8	2	
20	1– 10	2	6	3	6.4	6	1	2	3	5	9.8.5.3.2.1	8	2	8	2	1:0.25

TABLE IV

Results for Rat C, Inbred Female, in Problem 1

Date	No. of trials	S.1 (1.2.3)	S.2 (8.9)	S.3 (3.4.5.6.7)	S.4 (7.8.9)	S.5 (2.3.4.5.6)	S.6 (6.7.8)	S.7 (5.6.7)	S.8 (4.5.6.7.8)	S.9 (7.8.9)	S.10 (1.2.3)	R	W	R	W	Ratio of R to W
June 27	1–10	3.2.1	8	3	7	4.2	6	7.5	4	7	3.1	6	4	6	4	1:0.66
28	11–20	3.3.1	8	3	7	4.4.2	6	7.5	4	7	3.1	6	4	6	4	1:0.66
29	21–30	2.1.1	8	5.3	7	6.2	6	5.5	6.8.4	9.7	3.1	4	6	10	10	1:1.00
30	31–40	2.1.1	8	3	7	5.2	8.6	7.5	4	7	3.2.1	6	4			
July 1	41–50	3.2.1	8	3	7	3.6.6.2	6	7.5	5.8.5.4	7	2.1	4	6	4	6	1:1.50
2	51–60	2.1.1	9.8	4.3	8.7	3.2	6	7.6.5	6.8.4	9.7	2.1	3	7	8	12	1:1.50
3	61–70	3.2.1	8	3	7	3.2.1	8.6	5.5	5.4	7	3.3.1	5	5	5	5	1:1.00
4	71–80	2.1.1	8	3	7	4.3.2	7.6	6.5	4	9.7	3.2.2.1	5	5	11	9	1:0.81
6	81–90	3.2.1	8	4.7.3	7	6.3.2	6	5.5	7.4	7	1	3	7	4	6	1:1.50
7	91–100	3.2.1	8	7.6.5.3	7	2.1	7.6	6.5.5	4	7	3.2.1	8	2	4	6	1:1.50
8	101–110	2.1.1	8	7.3	7	4	7.6	6.5.5	5.4	7	1	4	6	7	13	1:1.85
9	111–120	3.1	8	6.3	7	4.3.2	6	7.5	5.4	9.7	2.1	4	6	12	8	1:0.66
12	121–130	2.1.1	8	7.3	7	3.2	6	7.5	4	7	3.2.1	4	6	8	12	1:1.50
13	131–140	2.1.1	8	3	7	3.2.1	6	5.5	5.4	7	3.2.1	3	7	5	5	1:1.00
14	141–150	3.2.1	8	7.6.5.4.3	8.9.7	5.3.2	8.7.6	5.5	7.4	7	2.1.1	4	6	6	4	1:0.66
15	151–160	3.2.1	8	6.3	7	4.3.2	7.6	6.5	5.4	7	2.1.1	6	4	15	5	1:0.33
16	161–170	2.1.1	8	4.3	7	3.2	6	5.5	6.7.8.5.4	7	3.2.1	6	4	16	4	1:0.25
17	171–180	2.1	8	3	7	2	7.6	6.5	7.8.5.4	7	3.2.1	6	4	15	5	1:.033
18	181–190	2.1	8	3	7	2	7.6	6.5	4	7	2.1.1	2	8	7	3	1:.043
19	191–200	1	8	3	7	2	6	5.5	6.4	7	2.1.1	6	4	6	4	1:0.66
201–210	201–210	2.1	8	3	7	2	6	6.5.5	4	7	2.1	6	4			
20	211–220	1	8	3	7	2	7.6	6.5	4	7	1	7	3	26	4	1:0.15
221–230	221–230	1	8	3	7	6.3.2	6	6.5	4	7	2.1	8	2			
231–240	231–240	1	8	3	7	2	6	6.5	4	7	1	7	3			
241–250	241–250	2.1	8	3	7	2	6	6.5	4	7	2.1	9	1			
251–260	251–260	1	8	3	7	2	6	6.5	8.5.7.4	8.9.9.7	1	9	1			
261–270	261–270	1	8	3	7	3.2	7.6	6.5	6.4	7	1	8	2			
271–280	271–280	1	8	3	7	5.4.2	6	7.5	4	7	2.3.1	7	3	18	2	1:0.11
281–290	281–290	1	8	3	7	2	6	6.5	5.4	7	1	7	3			
291–300	291–300	1	8	3	7	2	6	7.5	4	7	1	6	4			
21	301–310	1	8	3	7		6	5.5	4	7	1	9	1	19	1	1:0.05
311–320	311–320	1	8	3	7		6	5.5	4	7	1	9	1			
321–330	321–330	1	8	3	7		6	5.5	4	7	1	8	2			
331–340	331–340	1	8	3	7		6	7.5	4	7	1	9	1			
341–350	341–350	1	8	3	7		6	5	4	7	1	10	0			
22	1–10	2.3.4	6.7.8.9	3.4.5	4.5.6.7.8	6.7.8.9	1.2.3.4.5	2.3.4.5 / 6.7.8	3.4.5.6.7.8	5.6.7	1.2.3.4.5 / 6.7.8.9	10	0	10	0	1:0.00
		2	6	3	4	6	1	2	3	5	1					

on 10 new settings to check the possibility of memorizing the particular settings rather than actually solving the problem. One of the rats did the check series perfectly, two others with only one mistake, and the other with two mistakes.   It is evident that all formed the habit of selecting the compartment at the extreme right.

A number of interesting individual tendencies were manifested in the course of the experiment.   A's method of reaction was usually as follows: passing down the right wall of the reaction-chamber to compartment No. 1, she turned leftward and followed along close to the compartments until she reached the first open door.   In many instances she turned from the right wall before reaching compartment No. 1, with the result that she entered a door too far to the left.   This factor was of course more operative with settings comprising doors at the right end.   It is evident from table I that settings 1, 3, 5 and 10 yield a larger number of incorrect first choices than do the others.   With settings farther toward the left the first approach to the doors brought the subject more often in front of a closed door and hence the first open one encountered was correct.   On Sept. 9, over seven weeks after the discontinuance of A's training, she was given 10 trials with the original settings and made 8 correct choices out of 10.   Evidently the habit was still strong.

D manifested a tendency entirely different from that of A. He ran along the left wall of the reaction-chamber and across in front of the open doors until he reached a closed one, whereupon he turned back into the last open one.   This turning back appeared to be caused by the touch of the vibrissae on the closed door rather than by the sight of it.   The turning was always in the same direction,—leftward or toward the doors.   D experienced more difficulty than the other rats with setting No. 2, i. e., doors 8 and 9.   Going down the left wall he often entered compartment No. 9, whereas he normally turned at that point. As he did poorly also on the other settings involving No. 9, it would appear that he was reacting by tactual rather than visual criteria,—habitually going along the wall until he encountered an obstacle and then turning across, etc.   The directness with which No. 9 was entered in contrast with any other door was noticeable.   A month after the training ended, although sick and able to move only slowly, he performed two trials correctly

on the first two settings, employing his customary method of reaction.

J manifested, like A, a tendency to go down the right wall of the reaction chamber to compartment No. 1 and then in front of the closed doors to the first open one. He was often, however, premature in turning to the left thus missing the first open door, and he often lost the latter part of his habit and passed several open doors without entering. As contrasted with A, he was less ready in recovery from mistakes. Both solved the problem in 170 trials, but whereas with A there were 17 trials in which more than one incorrect choice was made before the correct one, there were 31 such trials with J. It is to be remembered that J was inbred and A outbred.

C was extremely rapid in her motions, rushing toward the compartments the moment she was released from the entrance box. In her correct trials the total time from entrance-box, through the compartment and alleys to the food was frequently 5 seconds. She often ran along the back alley so rapidly that she slipped and fell at the turn into the side alley. This tendency to hasten was perhaps instrumental in her failure to solve the problem in less than 350 trials. She usually appeared to take her orientation from door No. 1, going thence leftward to the correct door. The settings comprising doors at the left proved easy by this method. The most noticeable thing about her behavior was the suddenness with which she sometimes became thus oriented. Frequently when pausing and looking in the wrong door, or smelling about in almost any part of the reaction-chamber she would suddenly dash to door No. 1 and then across into the correct one. It is possible that this is the same phenomenon mentioned by Watson,[3] where a trained rat, placed in a part of the maze other than the entrance, runs about at random and suddenly darts off correctly, having passed over a "kinaesthetic unit" which arouses a proper sequence of kinaesthetic impulses.

Problem 2, which is definable as the second mechanism from the left end of the group, proved insoluble for the two rats C and B in 800 and 900 trials respectively.

For the settings of this problem the total number of open doors is 50 with 10 of course correct. Hence the probability of

Watson, J. B. Behavior. New York, 1914, p. 218.

TABLE V

RESULTS FOR RAT C, INBRED FEMALE, IN PROBLEM 2

Date	No. of trials	S. 1 7.8.9	S. 2 1.2.3.4	S. 3 2.3.4.5.6.7	S. 4 1.2.3.4.5.6	S. 5 4.5.6.7.8	S. 6 1.2.3	S. 7 2.3.4.5	S. 8 1.2.3.4.5.6.7.8.9	S. 9 1.2.3.4	S. 10 3.4.5.6.7.8	R	W	R	W	Ratio of R to W
July 26	1– 10	7.7.7. / 9.7.8 / 7.7.7.9.7.8	3	2.2.2.7.6	3.2.1.6 / 1.4.5 / 5	4.4.4.6.7	1.1.2	2.4	4.6.7.8	3	3.3.4.5 / 3.6.7 / 3.4.5.7	2	8	2	8	1: 4.00
27	11– 20	7.8	4.3	5.2.2.4.6	5	4.6.7	1.3.1.1.3 / 3.3.3.2 / 1.2	2.4	1.3.4.5 / 6.7.8 / 5.6.7.8	1.3	6.7	1	9			
"	21– 30	7.8	1.2.3	6	6.1.3.5	6.7	3.1.3.3.2	2.3.4	4.5.6.7.8	4.1.2.4 / 2.1.3 / 4.4.1.4.3	6.7	2	8	3	17	1: 5.66
28	31– 40	7.8	1.2.3	2.3.4.5.6	6.1.3.5 / 3.2.4.1.6.3 / 1.6.2.3.4	6.4.5.6.7	1.3.3.3.2	2.5.3.5.3 / 5.2.3.5.4	4.5.6.7.8	4.3	4.5.6.7	0	10			
"	41– 50	7.8	1.2.3	2.3.4.5.6	3.2.1.6.5 / 1.3.4.5 / 6.2.3.4.5	6.7	3.2	4	5.6.7.8	4.3	3.4.5.6.7	1	9	1	19	1:19.00
29	51– 60	7.8	4.1.3	4.5.6	6.2.1.11 / 2.3.4.5	5.6.7	3.2	4			4.5.7	1	9			
"	61– 70	7.8	3	7.3.4.5.6	2.3.4.5	4.5.6.7	3.3.2	2.3.4	4.1.9.9.8	2.1.3	5.7	1	9			
"	71– 80	7.8	4.2.1.1.3	7.2.3.4.5.6	1.2.3.4.5	7	3.2	5.3.4	6.7.8	1.1.2.3	8.6.7	1	9			
"	81– 90	7.7.8	2.3	3.4.5.6	1.2.1.2 / 3.4.5	8.7	1.2	3.4	5.6.7.8	1.3	8.3.5.6.7	0	10	3	37	1:12.33
30	91–100	7.8	1.2.3	7.6	3.4.5	4.5.6.7	3.1.2	2.3.4	8	1.2.3	8.4.5.6.7	1	9			
"	101–110	8	1.2.3	7.2.4.5.6	6.1.2.3.4.5	8.7	3.2	2.3.4	7.8	1.2.3	8.4.5.6.7	1	9	2	18	1: 9.00
31	111–120	8	1.2.3	4.5.6	6.6.5	8.6.7	3.2	5.4	1.2.3.4.5.8	1.2.3	9.6.5.6.7	1	9	1	9	1: 9.00
Aug. 4	121–130	7.8	3	7.4.5.6	3.4.5	8.6.7	1.2	2.3.4	7.8	4.2.1.4 / 1.4.3 / 4.3	8.5.6.7	1	9			
"	131–140	8	3	3.4.2.3 / 4.5.6.7	6.1.2.3.4.5	8.5.6.7	3.2	5.4	7.8	2.3	3.8.4.5.6.7	2	8	3	17	1: 5.66
5	141–150	9.8	3	7.2.3.2 / 3.4.5.6	6.6.5	8.4.5.6.7	1.3.2	5.2.3.4	8	2.3	7	3	7			
"	151–160	9.7.8	4.3	2.3.4.5.6	2.3.4.5	7	1.2	4	7.8	4.3	7	3	7			
"	161–170	9.7.8	4.2.3	2.3.2.4.7 / 3.4.5.6	6.1.2.3.4.5	8.5.6.7	3.2	5.4	7.8	1.2.3	8.3.4.5.6.7	0	10			

TABLE V—*Continued*

RESULTS FOR RAT C, INBRED FEMALE, IN PROBLEM 2

Date	No. of trials	S. 1 7.8.9	S. 2 1.2.3.4	S. 3 2.3.4.5.6.7	S. 4 1.2.3.4.5.6	S. 5 4.5.6.7.8	S. 6 1.2.3	S. 7 2.3.4.5	S. 8 1.2.3.4.5 6.7.8.9	S. 9 1.2.3.4	S. 10 3.4.5.6.7.8	R	W	R	W	Ratio of R to W
Aug.																
"	171–180	8	4.2.1.2.3	7.7.6	{4.3.2.1 / 6.4.5 / 6.3.2.3.4.6 / 1.2.3.4.5	8.8.6.7	3.2	5.3.3.4	8	4.2.3	8.4.5.6.7	2	8	8	32	1: 4.00
6	181–190	7.8	1.2.3	7.4.5.6	4.5 / 6.2.3.4.5	5.6.7	3.2	4	7.8	4.3	{8.1.3.4 / 5.6.7	1	9	1	9	1:9.00
7	191–200	8	2.1.2.3	6		7	2	5.2.4	7.8	4.3	7	5	5			
"	201–210	7.8	4.3	{7.7.2.3 / 4.5.6	6.2.3.4.5	7	1.3.2	5.4	7.8	2.1.4.2.3	8.7	1	9			
"	211–220	7.8	1.2.3	7.7.4.5.6	6.2.3.4.5	8.4.5.6.7	3.1.2	3.4	8	4.1.2.3	8.7	1	9	7	23	1: 3.28
9	221–230	8	1.3	4.5.7.7.6	6.5	8.4.4.7	3.2	3.4	8	1.3	5.8.7	3	7	3	7	1: 2.33
10	231–240	7.8	4.2.3	6	6.1.2.3.4.5	7	1.3.2	5.3.5.4	8	4.3	8.7	3	7	3	7	1: 2.33
11	241–250	7.8	3	4.2.3.4.5.6	6.1.2.3.4.5	8.6.7	3.2	4	8	2.4.1.2.3	8.7	3	7	3	7	1: 2.33
12	251–260	7.8	3	3.5.6	6.5	8.4.5.6.7	3.2	5.4	8	4.3	8.3.5.6.7	2	8	2	8	1: 4.00
13	261–270	7.8	3	{4.3.2.7.5 / 4.3.2.7.6 / 7.6	6.1.3.4.5	8.4.5.6.7	3.2	5.4	8	2.1.2.3	{8.8.1.5 / 6.7	2	8	2	8	1: 4.00
14	271–280	7.8	4.3		{1.3.2.1 / 6.3.4.5	7	3.2	5.4	8	3	8.7	3	7	3	7	1: 2.33
16	281–290	7.8	3	{7.4.3.7.6 / 7.2.3.7 / 4.5.6	5	8.5.6.7	3.2	5.2.3.4	8	2.1.3	8.7	3	7	3	7	1: 2.33
17	291–300	7.8	4.3	{3.2.3.4 / 3.4.5.6 / 2.3.5.4.7.6	5	8.7	3.2	5.2.5.4	8	4.3	8.7	2	8			
"	301–310	8	4.3		6.3.2.3.4.5	8.5.4.6.7	3.1.2	5.4	8	4.3	{8.6.5.4 / 3.5.6.7 / 4.3.6.7	2	8	4	16	1: 4.00
18	311–320	7.8	4.3		{6.3.4.3 / 2.4.5	8.7	1.2	4	8	3	8.7	3	7	3	7	1: 2.33
20	321–330	7.8	2.4.1.2.3	7.5.6	6.3.4.5	8.7	3.2	3.5.4	{9.8 / 5.4.3.2.1.3 / 4.5.6.7.8	1.2.3	7	1	9	2	18	1: 9.00
"	331–340	7.8	2.3	4.5.6	6.5	8.7	3.2	4	8	1.2.3	8.7	1	9			
21	341–350	7.8	3	7.2.4.5.4.6	{6.2.3.2 / 1.4.5 / 3.2.4.3 / 2.1.5	8.7	3.2	3.4	8	2.1.4.3	7	3	7	3	7	1: 2.33
23	351–360	7.8	3	6		8.7	3.1.3.2	5.4	8	4.3	8.7	3	7			

Date	Trials													
"	361–370	7.8	3										8.7	8 2 7
"	371–380	7.8	4.3										8.7	2 2
24	381–390	7.8	4.3										7	4 6
"	391–400	7.8	3										8.7	2 8
25	401–410	8	4.3										8.7	1 9
"	411–420	8	3										8.7	2 8
"	421–430	7.8	4.3										8 6.5.4	2 8
26	431–440	7.8	4.3										8.7	0 10
"	441–450	7.8	3										8.7	3 7
27	451–460	7.8	2.1.4.3										7	4 6
"	461–470	7.8	4.3										8.7	1 9
"	471–480	7.8	3										8.7	4 6
"	481–490	8	1.4.3										7	5 5
28	491–500	8	4.3										7	4 6
30	501–510	7.8	4.3										7	3 7
"	511–520	8	4.3										6.5.4.3.6.7	4 6
31	521–530	7.8	2.4.3										8.7	1 9
"	531–540	8	4.3										3.4.5.6.8.7	3 7
"	541–550	8	3										7	4 6
Sept. 1	551–560	8	3										5.4.3.6.8.7	2 8
"	561–570	9.8	2.1.4.3										7	4 6
2	571–580	8	3										7	4 6
"	581–590	8	4.2.4.3										8.7	3 7
"	591–600	8	3										8.7	5 5
3	601–610	9.8	3										7	3 7
"	611–620	8	4.3										6.7	1 9
"	621–630	9.8	3										8.7	4 6
4	631–640	8	3											
"	641–650	8	2.4.3										7	3 7
"	651–660	9.8	3										5.8.3.7	2 9

TABLE V—*Continued*

RESULTS FOR RAT C, INBRED FEMALE, IN PROBLEM 2

Date	No. of trials	S. 1 7.8.9	S. 2 1.2.3.4	S. 3 2.3.4.5.6.7	S. 4 1.2.3.4.5.6	S. 5 4.5.6.7.8	S. 6 1.2.3	S. 7 2.3.4.5	S. 8 1.2.3.4.5.6.7.8.9	S. 9 1.2.3.4	S. 10 3.4.5.6.7.8	R	W	R	W	Ratio of R to W
Sept. 5	661–670	8	4.3	7.6	6.5	7	3.2	5.4	8	4.3	8.7	3	7			
"	671–680	7.8	4.3	7.6	1.3.2.5	7	2	4	3.1.6.7.8	4.3	7	4	6			
"	681–690	7.9.8	4.2.1.3	7.5.2.4	6.5	7	1.3.1.2	5.3.2.5.4	8	4.3	8.7	2	8	9	21	1: 2.33
7	691–700	8	3	3.7.6 7.2.4.6	5	4.7	3.2	5.4	6.8	4.3	8.4.3.7	3	7	3	7	1: 2.33
8	701–710	7.9.8	3	6	6.6.5	8.7	3.2	5.4	7.8	3	8.7	2	8			
"	711–720	7.9.8	4.3	7.6	1.2.6.5	7	3.2	4	7.6.5.4 3.2.9.8	4.3	8.7	4	6			
"	721–730	9.8	3		6.5	8.7	3.2	5.4	7.8	4.3	8.7	1	9			
9	731–740	8	3	7.6	4.3.2.4.5	8.7	2	3.2.5.4	2.5.4.3.2 5.4.3.8	2.1.4.3	8.7	3	7	10	30	1: 3.00
"	741–750	8	2.4.3	7.6	5	5.7	2	3.2.5.4	9.8	4.3	8.7	3	7			
10	751–760	8	4.3	4.3.2.5.6	6.5	8.7	3.2	5.4	8	4.4.3	7	2	8			
"	761–770	8	3	7.6	6.5	7	3.2	5.2.4	8	4.3	7	5	5	10	20	1: 2.00
"	771–780	9.7.8	4.3	7.6	6.5	8.7	3.2	5.4	8	4.2.4.3	8.7	1	9	4	16	1: 4.00
11	781–790	8.7	4.3	7.6	6.5	8.8.7	2	5.4	8	4.3.	7	3	7	2	8	1: 4.00
	791–800	8	1.4.3	7.6	1.3.6.2.6.5	8.7	3.3.2	5.4	8		8.7	2	8			

TABLE VI

RESULTS FOR RAT B, OUTBRED FEMALE, IN PROBLEM 2

Date	No. of trials	S.1 7.8.9	S.2 1.2.3.4	S.3 3.4.5.6.7	S.4 1.2.3.4.5.6	S.5 4.5.6.7.8	S.6 1.2.3	S.7 2.3.4.5	S.8 1.2.3.4.5.6.7.8.9	S.9 1.2.3.4	S.10 3.4.5.6.7.8	R	W	R	W	Ratio of R to W
June 30	1– 6	7.7.7.8	4.2.1.1.2 / 1.2.2.2.3	2.2.2.2.2 / 2.2.7* / 2.2.3.5	3.2.1.6.5	1.8.8.4*	2					1	5	1	5	1: 5.00
July 1	7– 13	8	4.3	3.6	6.2.2.1.1 / 1.4.1.3.5	4.6.4.6.8 / 4.4.8.6.7		2.2.3.3.2 / 3.2.3.3 / 2.2.5.4				1	6	1	6	1: 6.00
July 2	14– 23	7.7.9.8	4.2.1.4 / 1.4.3	2.7.2.3.2 / 7.2.3.7 / 3.3.5.6	4.2.1.3.1 / 2.3.1.6.1 / 3.1.6.5 / 6.3.2.6.2 / 1.6.1.4.3	4.8.8.4 / 4.6.8.7	3.1.1.3.2	3.2.4	2.1.3.7.1.6 / 1.4.3.4.3.9 / 2.7.1.4.8	1.4.4.1.3	8.3.3.7	0	10	0	10	0:10.00
July 6	24– 33	7.8	3	7.2.2.4.6	1.2.6.1.4 / 1.1.3.1.6 / 1.2.4.1*	8.4.8.4 / 4.4.7	3.1.2	5.4	2.5.7.8	4.1.1.4.3	5.4.3.6.7	1	9	1	9	1: 9.00
July 7	34– 43	7.7.7.9 / 7.8	4.2.1.4 / 1.3	2.4.2.4.7 / 4.3.4.5.6	4.3.2.4.6 / 1.3.1.5	8.7	1.3.1.1 / 1.2	2.2.3.5 / 3.2.3.4	3.4.5.6 / 7.8	2.1.3	5.4.5.4 / 5.6.7	0	10	0	10	0:10.00
July 8	44– 53	7.7.9.7 / 9.7.8	4.1.2.3	7.7.6	4.3.4.3.2 / 1.3.4.5	4.6.7	3.2	2.3.2.3.4	3.5.6.9.1 / 3.9.9.1.8 / 4.3.2.3.4 / 6.4.3.5.6	4.3	3.5.3.4 / 3.6.7	0	10	0	10	0:10.00
July 9	54– 63	7.8	4.4.1.4 / 2.1.3	4.6	4.3.4.5	4.6.7	2	5.4	4.5.6.3.9 / 1.4.3.6.5 / 4.1.3.7.1 / 4.8	1.3	3.3.6.8.6 / 3.4.6.7	1	9	1	9	1: 9.00
July 10	64– 73	7.7.9.7 / 7.8	3	3.5.3.2 / 5.4.5.6 / 2.3.5.6	4.5	6.7	2	2.3.2.2 / 3.4	4.5.2.3.4.6 / 2.3.4.5.2 / 1.3.6.5.8 / 7.6.5.6 / 7.8	2.3	5.3.4.7	2	8	2	8	1: 4.00
July 13	74– 83	7.7.9.7.8	2.4.2.3		3.4.6.1 / 2.4.6.5	6.4.4.7	2	3.4		4.3	5.3.4.5 / 4.6.7	1 1	9 9	1 1	9 9	1: 9.00 / :1 9.00

TABLE VI—*Continued*

Results for Rat 13, Outbred Female, Problem 2

Date	No. of trials	S.1 7.8.9	S.2 1.2.3.4	S.3 3.4.5.6.7	S.4 1.2.3.4.5.6	S.5 4.5.6.7.8	S.6 1.2.3	S.7 2.3.4.5	S.8 1.2.3.4.5 6.7.8.9	S.9 1.2.3.4	S.10 3.4.5.6.7.8	R	W	R	W	Ratio of R to W
July 14	84–93	7.8	4 4 1.2.3	4.5.6	2.3.4.5	7	3.1.2	5.4	1.2.1.3.4 / 5.6.7.8 / 3.4.5.7.5 / 6.7.5.2.4	4.2.3	7	2	8			
"	94–103	9.7.8	4.3	3.2.3.4.5 / 7.4.2.1 / 2.4.5.6	3.2.3.5	7	3.2	6.4	4.5.6.7.8 / 7.5.6.7.8 / 7.8	4.4.2.3	3.4.6.7	1	9	3	17	1: 5.66
15	104–113	7.7.8	2.3	6	3.4.5	4.5.6.7	2	5.4		4.4.1.3	8.3.4.5.6.7 / 7	2	8			
"	114–123	7.8	4.3	4.5.6	4.5	5.6.7	3.3.2	3.4		3	5.3.4.5 / 6.7	2	8			
16	124–133	7.8	2.3	6	6.6.5	5.6.7	3.1.2	5.5.5.4		4.2.3	7	1	9	4	16	1: 4.00
"	134–143	7.8	4.4.4.4 / 4.4.3 / 4.4.2.3	6	5	6.6.7	3.3.3.3.3 / 3.3.3.3.2 / 3.3.1.2	5.5.5.5 / 5.2.3.4 / 5.3.2.3.4	7.8	4.4.4.1 / 2.3 / 4.3	8.8.8.5 / 6.7	3	7	4	16	1: 4.00
17	144–153	7.8	4.2.3	7.7.7.2.3 / 2.3.4.5.6	5	8.8.5.6.7	3.3.1.2 / 3.3.1.2	5.5.2.3.4 / 5.3.4	4.5.4.9.1.2 / 3.4.5.6.7.8 / 7.8	4.2.3 / 4.2.3	8.3.4.5.6.7 / 6.7	1	9	1	9	1: 9.00
18	154–163	7.8	4.2.3	6	5	5.4.5.6.7 / 4.5.6.5	3.3.1.2	4	5.6.4.5 / 6.7.8	4.3	7	2	8			
19	164–173	7.8	3	4.5.6	6.4.2.3 / 4.5	6.7	3.3.1.2	4	6.7.8	4.4.1.2.3 / 4.3	7	1	9	2	8	1: 4.00
"	174–183	8	4.4.3	7.2.3.4.5.6	2.3.4.5	5.6.7 / 5.7	3.2	4	7.8	4.3	5.6.7	3	7			
20	184–193	8	4.4.2.3	5.6	4.5	6.7	3.2	4	4.5.6.7.8	4.4.1.3	5.6.7	3	7	4	16	1: 4.00
"	194–203	7.8	4.3	3.4.5.6	4.5	5.6.7	3.2	3.4	7.8	4.3	7	1	9			
21	204–213	7.8	4.2.3	6	4.3.4.6.4.5	8.6.7	2	2.3.4	5.6.7.8	4.3	5.6.7	1	9	4	16	1: 4.00
"	214–223	7.8+	4.3	4.5.6	5	6.7	3.2	4	4.5.8 / 3.4.6.7.9	3	7	2	8			
22	224–233	7.8	4.3	4.5.6	5	5.6.8.7	3.2	5.4	3.4.6.7.8 / 1.3.6.8 / 5.6.8	4.3	5.6.7 / 5.7	3	7	3	17	1: 5.66
"	234–243	7.8	4.4.3	4.5.7.6	4.4.4.3.5	4.5.7	3.2	2.4	4.3.2.1.3.2 / 4.3.2.1.1.4	3	4.3.4.6.5.7	1	9	4	16	1: 4.00
23	244–253	7.9.7.8	2.3	4.6	4.5	4.4.6.5.7	3.2	4	3.5.4.6.8	1.3	4.3.3.5.7	1	9	2	18	1: 9.00
"	254–263	9.7.8	3	5.7.6	4.6.5	4.6.5.4 / 4.6.5.7	3.2	4	5.4.3.2 / 4.6.8	2.4.3	6.8.7	3	7	3	7	1: 2.33
24	264–273	8														

	Trials																								Ratio
26	274–283	8	2.3	6	5	4.6.7	3.2	5.4	{ 6.7.6.5 / 9.1.8 }	4.3	{ 5.4.6.5 / 6.5.4.7 / 4.8.3.5.4.3 / 4.5.4.3.5.3 / 6.8.6.8.7 / 4.3.5.7 }	3	7	7	1: 2.33
27	284–293	9.7.9.8	4.3	{ 4.5.4.3.4 / 3.2.4.3 / 5.4.7.6 / 4.6 }	6.5	4.7	3.2	5.4	4.6.8	4.3	4.3	10	10		
"	294–303	{ 7.9.7.7 / 7.8 }	4.3		6.5	6.5.7	3.2	5.4	{ 4.3.2.1 / 7.6.8 }	2.4.3	2.4.3	10	10	0	0:10.00
28	304–313	8	4.3	6	5	4.4.6.8.7	3.2	5.4	{ 5.4.3.4 / 6.5.7.8 }	4.3	{ 3.5.6.5.4 / 3.5.8.7 / 4.3.6.5.4.3 }	7	7	3	1: 2.33
29	314–323	7.9.7.8	4.3	6	5	4.4.6.5.7	3.2	5.4	6.5.7.8	4.3	{ 6.3.5.4.3.7 / 4.6.7 }	6	7	4	
"	324–333	7.8	4.3	6	5	{ 5.4.6.5 / 4.7 }	3.2	4	5.7.8	4.3	4.6.7	7	7	3	
"	334–343		3		4.6.5	6.5.4.3.7	3.2	2.4	9.4.3.2	3	6.8	7	7	3	1: 2.00
30	344–353	8	4.3	{ 5.4.3.2 / 7.6 }	4.5	4.6.8.6	3.2	4	{ 1.7.8.6 / 5.4.3.5 / 5.4.3.2 }	3	{ 3.4.3.6.5 / 3.4.3.5 / 6.8.6.7 }	7	7	3	1: 2.33
31	354–363	8	4.3	6	5	{ 6.5.5.4 / 6.5.4.7 }	3.2	5.4	{ 1.6.8.5 / 6.1.3.5 / 7.6.8 }	4.3	7	7	7	3	1: 2.33
Aug. 4	364–373	7.8	4.3	{ 5.4.3.2.5 / 5.4.3.2.4 / 3.5.4.7.6 }	5	4.6.7	3.2	3.2.4	4.3.8	1.4.3	{ 3.6.5.4.3 / 5.4.3.6.8 / 3.5.4.3.7 }	8	9	1	1: 5.66
" 5	374–383 / 384–393	{ 7.7.9.8 / 7.9.7.7 / 7.9.7.8 }	4.3 / 4.3	3.2.4.3.2.6	3.2.1.5	4.7 / 4.7	3.2 / 3.2	{ 3.2.2.5.4 / 3.2.5.9.8 }	2.4.3	{ 4.3.2.4 / 3.2.5.4 }	8.7	8 / 7	2.3	17
"	394–403	{ 7.9.7.7 / 9.7.8 }	2.4.3	4.3.2.6	4.3.2.6.5	4.7	3.2	3.2.4	{ 5.9.1.6.8 / 2.1.8 }	4.3	3.5.4.3	9	9	1	
"	404–413	8	3	{ 5.4.3.4 / 3.6 }	5	6.5.4.7	3.2	3.2.5.4	8	3	{ 4.6.5.4 / 3.5.4.3 / 6.5.7 }	6	6	4	
"	414–423	{ 9.7.7.9.9 / 7.7.9.7.9.7 / 9.7.9.9.7 / 7.8 }	4.3	5.4.3.2.6	3.2.6.5	5.4.8.7	3.2	3.2.5.4	{ 3.2.1.6.5 / 4.3.2.8 }	4.3	4.3.8.7	10	8	0	1: 4.00

TABLE VI—Continued

RESULTS FOR RAT B, OUTBRED FEMALE, PROBLEM 2

Date	No. of trials	S.1 7.8.9	S.2 1.2.3.4	S.3 3.4.5.6.7	S.4 1.2.3.4.5.6	S.5 4.5.6.7.8	S.6 1.2.3	S.7 2.3.4.5	S.8 1.2.3.4.5 6.7.8.9	S.9 1.2.3.4	S.10 3.4.5.6.7.8	R	W	R	W	Ratio of R to W
Aug. 6	424–433	8	4.3	4.3.2.7.6	3.2.1.6.5	{4.6.5.8 / 5.4.8.7	3.2	4	4.3.2.7.6 / 5.4.3.2.6 / 7.9.1.8	4.3	{6.5.4.3 / 8.4.7	2	8	2	8	1: 4.00
7	434–443	{7.9.7.9 / 7.7.7.8 / 7.9.7.9 / 7.9.7.8 / 9.7.8	4.3	6	4.3.2.5	5.4.4.7	3.2	5.4	5.4.3.4 / 7.9.1.8 / 5.4.3.2 / 4.7.8	4.3	{6.5.4.1.6.8 / 3.6.5.7	1	9			
"	444–453	{7.9.7.9 / 7.9.7.8 / 8	3	4.3.6	6.5	4.6.8.7	3.2	3.2.5.4	3.2.4.3.2 / 4.3.2.4.3 / 3.2.4.3	4.3	6.5.7	1	9	5	25	1: 5.00
"	454–463	7.8	3	7.6	5	5.4.7	2	3.2.5.4	5.7.6.8	4.3	3.5.5.7	3	7	2	8	1: 4.00
9	464–473	8	4.3	{4.3.2.5.4.3 / 2.5.4.7.6 / 7.6	4.3.6.5	4.6.5.4.7	3.2	3.2.5.4	6.5.7.6.8	3	{3.5.3.6 / 8.7	2	8	2	8	1: 4.00
10	474–483	7.8	4.3	{3.2.5.4.6 / 4.3.2.4 / 7.6	3.2.1.4 / 3.2.5 / 4.3.6.5	4.6.5.7	2	5.4	6.5.4.3 / 5.6.8 / 2.1.5.4 / 7.6.8	{2.1.4.4 / 4.3 / 3	6.8.7	1	9	1	9	1: 9.00
11	484–493	8	4.3	7.6	6.5	4.7	3.2	3.2.5.4	3.5.7.6.8	3	3.7	2	8	2	8	1: 4.00
12	494–503	8	4.3	3.2.6	2.1.6.5	4.7	3.3.2	2.5.6.4	4.6.8	3	3.7	1	9	1	9	1: 9.00
13	504–513	8	4.3	4.3.2.4	6.5	7	3.2	5.4	8	3	{3.6.8.7 / 3.5.6.8.7 / 6.5.7	4	6	4	6	1: 1.50
14	514–523	8	4.3	3.2.6	4.5	5.4.7	3.2	3.5.4	4.3.2.5.7.8	3		2	8			
"	524–533	7.8	4.3	{4.3.2.4 / 3.2.6	5	4.7	3.2	5.4	9.8	4.3		0	10	2	18	1: 9.00
16	534–543	7.9.8	4.3	4.6	4.3.2.7.6.5	5.7	3.2	4	8	4.3	7	3	7	3	7	1: 2.33
17	544–553	7.9.8	4.3	5.4.3.7.6	4.3.2.5	8.7	3.2	4	3.2.6.5.7.6 / 5.7.6.5.8	3	7	4	6	4	6	1: 1.50
18	554–563	7.9.8	4.3	{4.3.2.7.6 / 5.4.3.2.7.6	5	7	3.2	5.4	5.4.3.2.8	3	7	3	7	3	7	1: 2.33
20	564–573	8	4.3	5.4.3.2.6	3.2.6.5	5.7	3.2	5.4	5.7.9.8	4.3	8.7	1	9			
"	574–583	8	3	5.4.3.5		4.7	3.2	5.4	4.3.6.8	4.3	6.5.7	3	7	4	16	1: 4.00
21	584–593	8	4.3	{4.7.6		4.7	3.2	4	8	4.3	{5.4.3.6 / 5.7	3	7	3	7	1: 2.33

TABLE VI—*Continued*

Results for Rat B, Outbred Female, in Problem 2

Date	No. of trials	S. 1 7.8.9	S. 2 1.2.**3.4**	S. 3 3.4.5.6.7.	S. 4 1.2.3.4.**5.6**	S. 5 4.5.6.**7.8**	S. 6 1.2.3	S. 7 2.**3.4.5**	S. 8 1.2.3.4.5 6.7.8.9	S. 9 1.2.**3.4**	S. 10 3.4.5.6.**7.8**	R	W	R	W	Ratio of R to W
Sept. "	854–863	7.9.8	4.3	7.6	2.6.5	·5 4.8.7	3.2	3.2.5.4	3.2.5.7 6.5.7.8	3	3.7	1	9	6	24	1: 4.00
8	864–873	7.9.8	2.1.4.3	4.3.6	3.2.6.5	5.4.7	3.2	4	4.3.2.7 6.5.4.8	1.4.3	8.7	1	9			
"	874–883	7.9.8	3	3.2 7.6	4.3.2.6.5	5.4.8.7	3.2	4	3.2.1.5.8 4.6.5.4	1.4.3	3.7	2	8	6	24	1: 4.00
"	884–893	7.9.8	3	6	6.5	5.4.7	3.2	5.3.2.5.4		2.4.3	7	3	7			
9	894–903	7.8	4	2.7.6	3.2.6.5	5.8.7	3.2	4	3.6.7.8 2.7.6.8	3	3.7	3	7	3	7	1: 2.33

* Refused to work; laid down.

† Ten seconds punishment introduced

a correct first choice in any trial is 1-5 and the probable ratio or correct to incorrect first choices on a given day's trials, apart from experience, is 1 to 4. With C this was exactly the ratio for the first day's trials. It was also the ratio for the last day's trials. B started with a ratio of 1 to 5 which was reduced to 1 to 2.3 at the end, but there was no constancy in the results and the reactions were so manifestly random that further training seemed useless.

Although the rats failed to solve the problem, certain important reactive tendencies were noted. C began the problem 4 days after the check series on problem 1. The old habit which was manifest at the outset disappeared gradually and was little in evidence after 100 trials. The tendency to enter the same (incorrect) door two or more times in succession also disappeared at about the same period in the training. Between trials 100 and 500 there was frequently a tendency to make several random choices and then work from right to left, entering consecutive doors successively. (cf, trials 133, 184, 338, 444). After this stage the tendency was not so manifest, for the first random choice was nearer the left. This latter fact also heightened the probability of a first correct random choice, which doubtless accounts for the higher scores in many of the later series. After trial 250 there began to appear a tendency to enter the left door and *then the second from the left*. (cf. trials 251, 254, 256, 257). This tendency was increasingly manifest throughout. In trials 721-730 and 771-780, 8 out of 10 trials showed this type of reaction. The animal did show a definite tendency to turn to the left on leaving the entrance box, and often appeared to go directly to the door at the extreme left of those that were open. Whether it was merely this habit that was operative and the second choice naturally involved the neighboring door, or whether the rat formed the habit of going into the end compartment and then the second can not be definitely stated.

B was set at problem 2 without prior training in problem 1. Consequently there was no previous habit to break. B was likewise very active. At the outset the same door would be entered repeatedly (cf. trial 3), but this was seldom the case after 150 trials. There soon appeared a tendency after an incorrect choice to enter alternate doors going rightward or to enter consecutive doors going leftward. Sometimes the one tendency was followed by the other. (cf. trials 167, 268). After trial 270 there some-

times appeared the opposite tendency,—to go leftward entering alternate or rightward entering consecutive ones.   (cf. trial 271). These two tendencies to enter consecutive or alternate doors going in either direction were somewhat manifest throughout.

At trial 224 the period of punishment for B was increased to 10 seconds and soon after that she learned to stick her nose under the door (which was raised 3-16 inch from the floor to protect the tail), and wiggle out on her side before the 10 seconds were up.   The direction in which she then turned appeared to depend much on her orientation as she came out of the compartment in this way.   On the whole, B showed less systematic attack upon the problem than C, choosing more palpably at random and getting fewer successes on the second choice.

SUMMARY

1. The first two standard multiple choice problems were presented to white rats.   These problems may be defined in terms of the constant relation of the correct mechanism to the varying group of mechanisms as: (1) the first at the right end of the series; (2) the second from the left end of the series.

2. One inbred and two outbred rats five months old solved the first problem in 200 trials or less.   Another inbred individual two months younger required 350 trials.   The indications are that visual tactual and kinaesthetic guidance sufficed for the formation of the habit.

The second problem proved insoluble for the two rats which attempted it.   Both acquired a general tendency to turn toward the left, thus more frequently making a correct random choice, but the relation of secondness from the left was evidently beyond them.

3. There were two noticeable reactive tendencies manifested by one rat.   In problem 1 she would at times become oriented very suddenly, dash to the right end and then across to the correct door.   In problem 2 she repeatedly entered the left door and then the second from the left.   Although it is tempting to ascribe these tendencies to a higher level of behavior, it would seem better to explain the first in terms of kinaesthetic units and the second by the acquisition of the habit of choosing the left door,—the following choice most naturally involving the adjacent correct door.

THE LEARNING OF A MAZE BY GOLDFISH[1]

E. P. CHURCHILL, JR.

The study of the behavior of fish when confronted by a prob-
lem such as a maze is rendered of considerable importance by
the fact that in these animals the pallium of the brain is unde-
veloped. Various investigators, while working on the problem
of color discrimination in fish, have incidentally shown that
these animals possess associative memory and can form simple
habits. Mention will, however, be made here only of litera-
ture that deals more strictly with the problem of habit formation.

Triplett[2] found that perch, after several trials, cease to try
to reach minnows on the opposite side of a glass partition.
After the removal of the partition the perch made no attempt
to pass the point where the partition had formerly been placed.

Thorndike[3] described in a general way the learning of a maze
by Fundulus. He found that this fish sought the shaded part
of the tank. To gain this he caused them to swim through
openings in partitions placed across the tank. He found that
the time required for the trials lessened from day to day.

Goldsmith,[4] working chiefly with Gobius and Gasterosteus,
showed that these fish have a well marked and enduring topo-
graphical memory. If fed at a certain point in the tank they
soon learned to come there and this habit persisted after 18
days lapse of practice. She also found that they had a memory
of direction. A simple maze was constructed by placing across
the aquarium a glass partition pierced by an opening. The
stimulus used was the nest, to which the fish endeavored to
return. On the first day the fish learned in 3.5 hours to go
directly through the opening to the nest. The number of trials
is not recorded. The next day the fish relearned the maze in

[1] From the Laboratory of Animal Behavior, Johns Hopkins University.
[2] Triplett, N. Educability of the perch. *Amer. Jour. Psych.*, 1901, **12**, 354
et seq.
[3] Thorndike, E. L. Animal intelligence. New York, 1911, Chap. IV, pp. 169-
171.
[4] Goldsmith, M. Les Réactions physiologiques et psychiques des Poissons.
Bull. de l'Institut général psychologique, Paris, 1914. **14**, 97-228.

.25 hours. The time lessened from day to day though the fish had to a certain extent to relearn the maze each day. If a partition of wire netting with openings 5 mm. square were used the fish swam at once through the passageway and to the nest. She thought the fish saw the netting and the opening through it and consequently was guided by the sense of sight. From various experiments she concluded that the illumination, distribution of light and shade, and the play of light on the walls of the container guided the fish. The objects in and about the maze were not made use of as data by the animals. The faculty of "motor memory" may be possessed by the fish but she thought it was a less important factor in solving the maze than the sense of sight. She also worked extensively on the discrimination and memory of colors and form in fish.

In view of the fact that the behavior of fish in a maze has received less emphasis than the other features of the work with this animal, it seems of interest to record an attempt at a quantitative estimate of the ability of fish to learn to run a maze of a moderate amount of difficulty.

Goldfish (*Carassius auratus*) were used because they live readily in aquaria and can subsist on the prepared food which does not diffuse through the water. As food was the stimulus used this latter point was of importance. Eight fish were used. These varied in length from individuals measuring 4.5 cm. to one of 5.5 cm. They were kept in individual numbered pens. One trial a day was given. The food was cut into squares about 4 mm. across. One such square was used for each trial and this was the only food the fish received until the next day.

A diagram of the maze used is shown in Fig. 1. It was of the same general plan as the one used by Thorndike and consisted primarily of a tank with glass sides and ends and measured 66.25 cm. in length, 37.5 cm. in width and contained water to the depth of 18 cm. The tank was divided into three compartments (1, 2, and 3, see Fig. 1) of approximately equal size by means of two partitions. In case of two groups of fish the partitions were constructed of wire netting, in the case of the other group they were of unpainted wood. In each partition was a rectangular opening 2.5 cm. square. In the case of the partition between compartments No. 1 and No. 2 the opening was situated at the surface of the water and within 5.6 cm. of

one side of the tank.   In the partition between compartments
No. 2 and No. 3 the opening was at the bottom and within
6.8 cm. of the side of the tank opposite to the opening of the
first partition.   With one group of fish the openings were bor-
dered by a black pasteboard band 2.5 cm. in width attached
by wire clips to the partition on the side nearer the end of the
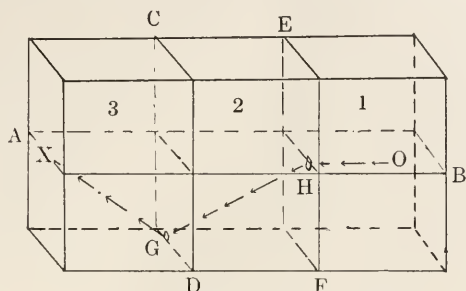
FIGURE 1.   Diagram of the maze with the compartments 1, 2 and 3.   AB, sur-
face of the water.   CD and EF, the partitions.   G and H, the openings for
the passage of the fish.   The food was placed at X and the fish at O.   The
line of arrows represents the shortest possible route through the maze.

tank where the food was placed.   The light was furnished by
a 40-watt Mazda lamp suspended over the center of the tank
at a distance of one meter above the surface of the water.   The
food was placed in compartment No. 3, on the surface of the
water, midway of the glass forming the end of the tank and
touching the glass where it would remain until found by the
fish.   The observer sat either near the end of the tank where
the food was placed or at a point entirely removed from the
range of vision of the fish.
    The fish were given preliminary trials with no partitions in
the maze.   At the expiration of about a week the fish would
come fairly regularly and take the food which they found by
the sense of sight.   The partitions were then put in and daily
trials started.   The procedure was as follows: Sunlight was
excluded from the room and the light turned on.   About fifteen
minutes were allowed to elapse in order to give an opportunity
for the fish to become adapted to the light.   A square of food
was placed in the position described above.   Then fish No. 1,
e.g., was lifted from its pen by means of a small net and placed
gently in the center of compartment No. 1.   The time was
noted at that instant.   The fish was watched until it had swum

through the maze and the time noted the instant it touched the food. The fish was allowed about five minutes in which to eat the food and was then removed from the maze.

Group I consisted of four fish which were used with the wire partitions with no visual signs about the openings. The curve representing the averages of the length of time of their trials is shown in Fig. 2. Three of these fish were given 60 trials, the fourth 46. In Fig. 2 the part of the curve enclosed in parentheses represents the averages for three fish only. It will be seen that the average time fell from 105 minutes for the first trial to 3 or 4 for the last trials. After the thirty-sixth trial the time never exceeded 5 minutes. The elevation at the point marked "x" is partly due to the exceedingly poor record of two individuals after the group had undergone a cessation
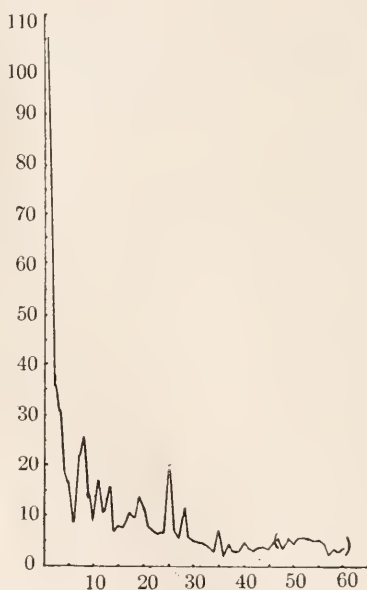
FIGURE 2. Curve for Group I representing the average time of the daily trials. The elevation at x was caused by the poor record of two fish after a cessation of practice of two weeks. The portion enclosed in parentheses represents the time for three fish only. The abscissae indicate trials, the ordinates, time in minutes.

of practice of two weeks duration. Individual variations were quite noticeable. Fish No. 1 consumed 240 minutes during its first trial, while No. 2 required only 17, but went as high as 80

on its eighth trial.   Fish No. 3 was the best of the group.   Its last five trials, the forty-second to forty-sixth inclusive, never exceeded one minute in length while the last three were of a duration of thirty seconds each.   The average physiological limit of the group seemed to have been reached at about the thirty-sixth trial, though the habit bore up well for the remaining trials.

The members of this group apparently used the sense of sight very little in running the maze.   They would repeatedly swim directly past the opening without passing through.   The interstices of the wire netting were fairly large, three to every 2.5 cm., and it is doubtful if the fish discriminated by the sense of sight between these and the openings intended for their passage.   As far as could be observed they found the passageway by playing about the netting and thrusting the head into the interstices until the opening was hit upon, this being large enough to allow their passage.   They gradually learned to explore more and more closely about the opening and thus the time was reduced.   Toward the last they swam fairly accurately to the opening and passed through with very little nosing about.   This was especially true when they were passing through the second partition.   The passage from compartment No. 1 to No. 2 usually required more time than that from No. 2 to No. 3.   This was no doubt due to the fact that the fish had to orient itself after being placed in compartment No. 1.   The fish of this group very seldom went back into the compartment from which they had just come.

In Group II two fish were used with the wire partitions provided with the black bands about the openings.   The curve for this group is shown in Fig. 3.   Forty trials were given in this case.   The curve is very abrupt in its initial part.   Neither fish succeeded in running the maze the first day.   The number, 405, toward which the arrow points in Fig. 3, represents the average time the fish were left in the maze during the unsuccessful attempts.   On the next day one fish ran the maze in 7 minutes and never consumed more than 15 minutes at any later trial. As far as could be seen the failure of the first trial was due to fear on the part of the fish.   They avoided the region of the openings during the first trial.   However, after the first few trials the improvement was more rapid and the final achievement
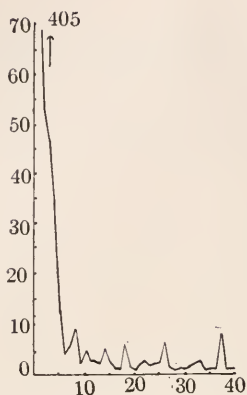
FIGURE 3. Curve for Group II, the position of the beginning of the curve being indicated by the arrow. The abscissae represent trials, the ordinates, time in minutes.

greater than was true of Group I. It will be seen that the curve descends more rapidly and farther and remains lower than does that of Group I. The fish went back to a previously occupied compartment more frequently than did the members of Group I.

Group III was made up of two fish which were used with the wooden partitions. Their initial trials, although successful, required considerable time (Fig. 4). This seemed to be due to
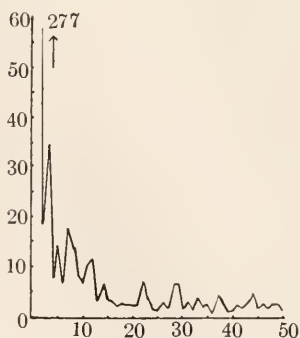
FIGURE 4. Curve for Group III. The abscissae represent trials, the ordinates time in minutes.

the fact that the fish did not play about the dark wooden partitions to any extent. When they did reach a point an inch or two directly before the opening they usually went through. The reverse passage of the openings was made much more

frequently than in either of the previous groups. The record of this group is better than that of Group I, but not as good as that of Group II (Fig. 5). The chief difference was that their improvement was not quite as rapid, their final attainment being as great as that of Group II. Fig. 5 shows the three curves plotted together, the trials being grouped in fives. The openings in the wooden partitions were not as conspicuous from
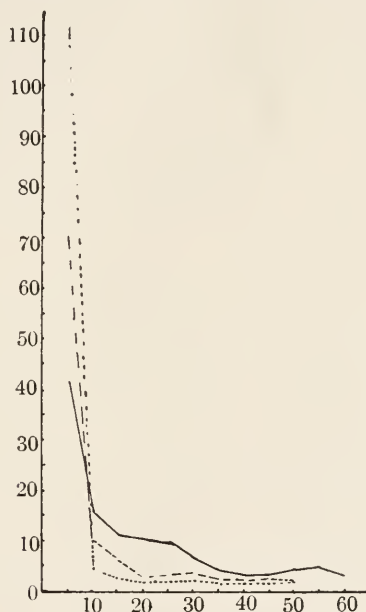
FIGURE 5. Curves for the three groups plotted together for purposes of comparison, the trials being grouped in fives. Continuous line represents Group I, dotted line Group II, broken line Group III. The abscissae represent trials, the ordinates, time in minutes.

a distance, unless the fish were directly in front of them, as were the black-banded openings. This may account for the fact that the record of Group III was not as good as that of Group II.

Retention tests were tried with two fish. In Group I practice with one individual was allowed to cease for thirteen days after the forty-sixth trial. The record for the last three trials was 30 seconds each. After the interim the first trial required 7.5 minutes. The time dropped to one minute on the fifth trial. One individual of Group II was given a retention test

of thirteen days after the fortieth trial. The time rose from one minute to 3.5, but fell at the third trial to one minute.

Some tests were made with the positions of the openings in the partitions reversed so that the fish had to swim down to one side when leaving compartment No. 1 and up to the other side when leaving No. 2. One individual from Group I, which had been running the maze in from one to two minutes required 12.5 minutes to run it when thus reversed. The fish tried first the regions where the openings had formerly been situated. An individual from Group II was given a trial in the reversed maze. It tried once at the point where the opening had formerly been but turned then and swam directly to the black-banded opening and passed through. A fish from Group III, when the wooden partitions were reversed, tried quite persistently at the points where the openings has been previously situated before finding them in their new positions.

The fact that in Groups II and III, where the openings were more apparent to the eye, the improvement was more rapid and the final achievement greater than in Group I leads to the conclusion that the sense of sight was a factor in the running of the maze, especially in the earlier trials. However, the fact that the members of Group I learned the maze only a little less rapidly and thoroughly than did those of the other two groups shows that kinesthetic factors were involved in the process. They probably came to function more and more exclusively as the practice went on. That kinesthesia was an important factor is further proved by the behavior when the positions of the openings were reversed and the fish proceeded to the region where they had formerly found the passage-way. The sense of touch also aided, especially in the case where a visual sign was not used and the fish nosed about the netting. As perfection of the habit was more nearly approached the use of the senses of sight and touch fell more and more into the background and when the physiological limit was reached kinesthesia was largely the factor employed.

SUMMARY

Goldfish, although lacking a pallium, are capable of forming a definite habit of a moderate degree of complication and of retaining this habit for some time.

The physiological limit for the running of the maze when daily trials were given was, for Group I, 2 minutes reached on the thirty-sixth trial; for Group II, one minute on the twentieth trial; for Group III, one minute on the thirty-sixth trial. The habit was fairly well retained after 13 days lapse of practice.

The senses of sight and touch were instrumental in the initial steps of the habit formation but later were superseded to a great extent by kinesthesia.

TWO METHODS OF SUBJECTIVE LEARNING IN THE MONKEY *MACACUS RHESUS*

EDWARD J. KEMPF, M. D.

Clinical Psychiatrist to the Government Hospital for the Insane,
Washington, D. C.

The studies of the learning processes of monkeys have led to some disagreement as to whether or not monkeys learn by the imitation method or through perseverance of trial and error or by both methods. The researches of Kinnaman, Shepard, Watson, Thorndike, and Haggerty show that the monkey learns principally by the perseverance method, but also, if the problem with which he is confronted is not too complex and contains only such elements or steps to be associated together for success as he has already mastered, by imitation.

A review of the researches of the above observers shows that practically all the studies of the monkey's learning processes have been through the problem method, requiring the monkey to *manipulate in a certain manner or sequence* objects of a general type for which all monkeys have a great natural fondness and interest.

One factor that has made some of the studies of learning not altogether convincing has been the unnaturalness of some of the movements required of the ape and other animals to solve the problem or to imitate another animal's movements. The animal often simply does not have the reactions or reflex systems in its repertory and lacks neurologically the capacity to acquire the necessary movements or associations of movements, or associations of sensations and sensory images, to solve the problem. Also the factor of internal, emotional distractibility has been underestimated. The uneasiness of the subject caused by the nearness of the human is so persistent and reflex in type that it always causes more or less distractibility, presenting a proportionate degree of incoördination, like the pupil who fears his teacher and cannot learn from him, or the uneasiness produced in a speaker by the mere presence of a crowd. For example:

Shepard says that he placed the glass tube and stick in the cage with the animal " to see if he could push out the food in the tube *after his attention had been attracted and he had been shown by the experimenter how the stick was to be manipulated* for obtaining the banana or peanut." Monkeys are not only afraid of a man but are ready to flee when a stick appears in one's hands. Although the monkeys saw the experimentator use the stick from 72 to 228 times, none of them showed any signs of imitation. If, as is most probable, the monkeys were the hosts of even slight fear reactions from the hand or stick, imitation, above everything else, could not be expected. Kinnaman similarly spoke of making *suggestive movements* with a key (an object in the hand) to indicate its necessity in procuring the food. The monkeys did not imitate.

Otherwise this work has so thoroughly covered this phase of the monkey's learning methods that perhaps further contributions are not needed. However, quite by accident the monkeys themselves revealed that they had other problems to master besides the *objective ones* of manipulating objects in proper sequence or manner; problems of a more *subjective* nature, such as when they knew perfectly well what they wanted to do, and in a way, how to do it, and saw how other monkeys performed an act, but to acquire the same results they had to learn how to control and manipulate their own muscles, of the body, arms and hands, in a certain manner.

Since this seems to be an important condition of the learning process of the monkey it is thought to be worth reporting.

The following observations were made from six *Macacus rhesus* monkeys. Three of them, A, B, and C, are immature, well formed and presumably half grown. A and B are males. C is a female. They differ markedly in disposition but a study of their personalities need not be given here, except to state that A is very timid and gives way to the demands of all the others. He is forced to adapt himself to their demands in any other way than by using force.

B is a very active, aggressive monkey and frankly competes for food with any of the others. He rarely fights back at D, E, or F, and I only observed once that he tried to take food from one of the larger monkeys. B dominates A and C. C is very much like B in disposition and used to dominate him,

but ever since F punished C when B, C and F were caged to-
gether, B punishes her and she submits to his aggressions.

D, E and F are about matured males. E is the largest and
most powerful and dominates the band. D is next in strength
and dominates all but E. That is, he punishes all but E. F is
not liked by the other monkeys, and they all have preferences
for some other monkey than F. F dominates A, B and C.

The studies were conducted in a basement where they live
in three cages. Besides one or two boxes, a barrel and a chair,
there is no other furniture in the room. My presence during
the studies could have had very little influence since they all
are used to me. They are more or less timid toward me, but
pay practically no attention to me when I am quiet and remain
at a distance.

The problem studied was accidentally suggested. The cages
are all raised 18-19 cm. from the floor by blocks, one under
each corner. There is an aperture about 4 cm. wide and 80
cm. long between the flooring of the cages and the lower hori-
zontal wooden bar to which the screen is attached. This aper-
ture is closed by a movable wooden bar to keep the sawdust
in the cage and is easily removed for cleaning the cage and
watering. A small wooden box, 25x30x16 cm. happened to be
at hand. One evening I noticed some of the monkeys trying
to reach to the floor for some peanut shells. It occurred to me
to drop a few peanuts into this box and push it up to the cage
and see the monkeys reach for the nuts.

A, B and C were in this cage. They promptly reached through
the wires into the box but the distance was too great to reach
the peanuts. The bar was then removed and A, B and C im-
mediately returned to grab peanuts. B and C returned first
and, true to their habits, overlooked the new opening and utilized
as before, the nearest wire screen area above the box. They
repeatedly reached through the spaces but could not quite
touch the nuts. A tried to reach from this place also but was
pushed away by B and C, whereupon he tried it lower down
and pushed his hand through the horizontal aperture between
the floor and the crossbar and then extended his hand into the
box containing the nuts. He chuckled his delight as he drew
out the nut. Immediately B and C tried this aperture and
succeeded in reaching the nuts. (Objective learning through

imitation.) After that they all promptly used the lower space and abandoned the wires for reaching food from this box. They seem to be equally quick at it, often requiring only about one-half a second to make the movement.

The food box was then presented to D, E and F, who were caged together. D, E and F saw A, B and C feed from the box and F may have imitated them, but since he had often reached to the floor before, this is not likely to have been the case. He immediately placed himself in the proper position and reached the food. D and E could not reach the food, although they extended their hands through the proper aperture.

Before relating D and E's methods of finally acquiring the food from the box it is necessary to make clear the type of movement required to reach the food. The extreme simplicity and naturalness of the position necessary to acquire the food should be given the most consideration.

To take a nut from the box the movement of A, B, C and F was simply that of crouching close to the floor on all fours with the body parallel to and near the aperture, then extending the forearm of the arm nearest to the bar through this aperture, pronating the hand so that the palm faces the food and simultaneously pushing the arm through the aperture up to the shoulder. A, B, C and F did this within a few seconds from the beginning and quickly became so expert that they could perform the movement in less than a second. All monkeys learn this crouch in infancy, as do most four-footed animals. It is one of their most natural and frequent positions. To crouch on the perch in this manner and reach over the edge with one hand to scratch another monkey below is a very frequent movement for all of them to make. So in this movement probably no new motor coördinations were required or sensory stimuli given, and on the other hand one of their most frequent positions and movements was necessary to reach the food. One thing must be added, however. When the monkey's head remained above the cross bar and near the wire netting he could see the food while he reached for it; and when he crouched close to the floor and extended his arm through the aperture beneath the cross bar, his face would be beneath the cross bar, and he would be unable to see the food or his hand when he reached. He would have to depend upon touch to orient himself. On

the other hand every monkey is fond of sticking his fingers into places where he cannot see what he touches.

For three months, in which time the problem was placed before the monkey from about a quarter of an hour to an hour at a time on an average of three times a week, D and E were unable to get any.hing out of this box. Although they had innumerable opportunities to watch and did watch very closely while in the presence of A, B, C, or F, or several, or all of them, or when by themselves. They also tried to solve the problem when alone. It is perhaps needless to add that they were urged to do so by the odor and sight of many tempting fruits, nuts and vegetables, during states of great, little, or no hunger and they were unable to learn. Their efforts to reach into the box at times were perfectly ridiculous and grotesque. They would twist themselves into the most awkward positions, even for a monkey, stand on their hands, pushing their faces into the aperture and hold to the wires with their hind feet, almost standing on their heads, or climb up the wires backwards, turn their backs to the food and try to reach it, twist themselves around and around in a circle, call for the food, get angry, punish the other monkeys and what not.

They were helpless and would probably have starved if their struggles for food had been the sole means of living.

They learned to snatch food from the other monkeys and when this failed, at times they would sit by the box and shake it back and forth or drive the other monkeys away. D and E would often sit by the aperture and watch another monkey reach for the food and then snatch it as he drew it through the aperture. F then adjusted to this by pressing his face into the aperture and pushed the nuts into his mouth without raising his head. When he had several in his pouch he would then dash away.

B would frequently grab food out of the box and dash to the top of the cage and eat it. E would cautiously climb up to get near enough to grab him. As soon as E would be far enough from the box B would dodge him, dash to the box, grab food and be away before E would get back to the box. Occasionally B would make an enticing chuckling sound to E which was very similar to the sound made when wishing sexual play. This

would usually induce E to come away from the box and give B an opportunity to dash by him.

In the beginning the study was not intended for publication, so a count of the distinct attempts to reach into the box was not made. It is safe, however, to estimate that D and E each made more than two hundred, probably twice that number of attempts to reach the food and neither seemed to make any progress. They repeated over and over again about the same futile movements. D and E would both often crouch at right angles to the box, look over the bar into the box and thrust their arms through the aperture up to the elbow. Although they would pronate the forearm they could not bend the elbow to lower the hand into the box, being anatomically impossible in the narrow aperture with the body at right angles to the opening and the head above the bar. They would then usually shake the box back and forth or try to lift it or turn it around.

The observations of two periods are given here to make clear what happened. The period of April 8 is typical of all the periods previous to it. During the period of April 19 D succeeded for the first time in his efforts to obtain food.

OBSERVATIONS

April 8.—D and F are in the cage together. Several prunes were dropped into the problem box. D reached through the aperture to the elbow. F pushed his way to the aperture, crouched and extended his arms through the aperture and helped himself to the prunes. *D crouched right beside F, watching him intently, especially F's hand reaching for food, and he moved his forearm through the aperture the way F did but did not turn his body properly. He clearly tried to imitate F's method of reaching.* (Subjective learning through imitation.) *F grabbed all the prunes.* A few minutes later F grabbed all the nuts and bread without exception. This is about what occurred each time the problem was tried throughout twelve weeks.

April 19.—D and F in a cage together. One dried peach was dropped into the box. F grabbed it. D pursued F to take it from him. Piece of dried bread dropped into the box. F grabbed it. Bread again dropped into the box before F finished eating. D turned the box around and pulled it back and forth;

placed himself in many awkward positions. Extended his hind legs and body in a vertical position, holding to the wire netting with his hind feet. He turned around, finally standing upside down in a vertical position with his head near the aperture. He succeeded in scratching the bottom of the box but could not reach the food. Then he seemed to lose his balance and fall over on his side. This accidental position was correct for reaching the food. He pulled out the piece of bread. He ate the bread. A peach was lying in the box. He tried repeatedly to reach it but could not and did not assume the proper position again. F grabbed the peach. Handful of peanuts were dropped into the box. F grabbed most of them.

Now D tried all types of movements, squirming into one position after another in a most useless and fruitless manner. Twice his body happened to get into the proper position to easily reach the food but each time he changed his reaching hand from the one beside the aperture to the one on the opposite side of his body. He continued to try, raised his body and hind legs into the upside-down vertical position, holding on to the screen with his hind feet; then reached into the aperture with the off side hand and pressed his face into the aperture. His hand touched the nuts and he extracted four despite the awkward position of his hand. He then left the box to eat. Then he returned to get more nuts and seemed to be unable to reach them or resume his old position. He shook the box fruitlessly.

The next day the observations were repeated and D seemed to learn all over again. He went through a series of trials and errors and finally. more quickly than the day before, assumed his unique, awkward method. This method he developed until he became fairly dexterous.

He places his right hand on the wires just above the cross bar to steady himself and raises his body and hind legs above his head and shoulders, placing himself in a more or less vertical position. The abdomen and chest are pressed against the wires. He extends the left hand, which is on the opposite side of the body, through the aperture, this allows the arm to remain nearly straight, and *scrapes the back of the fingers* over the box floor until he happens to touch a nut. He required 5, 3, 3, 4, 10, 10 and 156 seconds for each trial to extract a nut.

The presence of F bothered D somewhat instead of assisting him to learn. But D was often tried alone and rarely did more than to pull the box around or twist himself into awkward positions.

E seemed to have even more difficulty in learning than D, although he had the longest arms of the six monkeys. Like D, he was given the opportunity to watch B, C and F take food from the box. He seemed to watch very closely but he never showed so clearly efforts to *imitate* as D tried to imitate F. That is he never sat beside B, C or F and moved his arm forward automatically as the other monkey's arm passed into the box.

Most of E's trials were made in company with B or alone. He would usually drive B away and shake the box back and forth or extend the arm to the elbow through the aperture. B probably interfered with E's learning process because of his quick dashes to the box and disconcerting eating when E was hungry. E preferred to take food from the others rather than try to procure his own. Despite this he made a great many trials with no result. Like D he seemed to bungle about the wires, twisting himself around in the most awkward positions, until he fairly fell into a crouch near the aperture. Then his hand easily reached the food. That it was an accidental association of movements was evident because after he seized the second nut he was unable to repeat his method. It happened as follows:

April 24.—E and B were in the cage together. B was isolated in the rear compartment. E tried a variety of futile movements in order to reach the food. He extended his arm up to the elbow into the box and tried repeatedly. Finally he supinated the forearm and raised the posterior part of the body above his head, similar to D's method. This failed and with his arm still through the aperture, seemingly fatigued, he lowered his body to a crouch and rested. He looked at me as he crouched there; then he gradually extended his arm further. His position happened to be correct and his arm easily passed through to the shoulder. The hand reached the bottom of the box and he easily extracted food. He repeated this arm movement a second time and then changed his position to eat. After eating he tried to obtain more food and seemed unable to repeat his method. He pushed the box back and forth. After some time he resumed D's method and extracted an onion. Then B was readmitted.

B immediately dashed to the box and obtained food. E took it from him after a chase. A handful of nuts were dropped into the box. E tried awkwardly to reach them. Finally he reached in with the back of the hand towards the food—D's method— and extracted a nut. After this E learned rapidly. He gradually modified the position of his body until he no longer uses the wires to raise himself but forces his head tightly against the bar or floor and is able to reach the food with either hand. D also abandoned the vertical screen position but still keeps the posterior half of his body elevated. Both D and E now place their bodies nearly parallel to the aperture. The tendency is still to use the arm on the off side with the back of the hand facing towards the food in the box unless the hand is extremely extended, when the thumb also reaches the food—the most awkward position of the hand for grasping.

E and D are good specimens of the *Macacus rhesus*, well developed young adults. That spontaneous subjective learning should be so slow and laborious a process, even in an organism so highly developed as this species of monkey, when trying to adapt well developed movements to a new situation is surprising upon first estimation.

CONCLUSIONS

The observations seemed to show repeatedly that the following phenomenon occurred: D was the host of a motive— to acquire food. This motive discharged itself through a manifold of more or less incoördinated movements to acquire the food. A novel, accidental association of movements permitted complete expression of the motive. Hence there was a tendency to repeat similarly associated movements, eliminate the unnecessary and finally *reach a maximum of efficiency whereby the hunger motive could express itself with a minimum of effort.* In other words, the motive was the force, the box, etc., the mold, and the repertory of movements the material to be molded. A novel or accidental association of movements finally made the molding possible.

That is to say, D did not strictly try one movement and then another as a process of elimination of the useless movements but more aimlessly seemed to be the host of a stream of force that caused a continuous pressure for expression and ac-

cidentally the proper series of sensorimotor neurones became connected up and the motive flowed out through the series of effectors that acquired the food and placed it in the mouth.

In the cases of B and C watching A, and of D watching F, B and C imitated A in that they saw where A reached and did the same thing. D saw where and to an extent how F reached and reached from there also, but could only imitate the first one of F's movements even though he had probably made very similar movements under other circumstances.

The utilization of the fit and the elimination of the unfit, *whereby a maximum of the desired result is developed for a minimum of expenditure of energy*, is the great fundamental principle of force underlying all evolution, progress and efficiency.

Imitation seems possible only when similar movements under similar circumstances have already been previously acquired by the organism. Imitation seems to permit of a very limited margin for new modifications of the old repertory of movements. Trial and error gives much more extensive possibilities for learning; requires more time, energy and perseverance. ·

Subjective learning, in the sense of learning to manipulate the body, is a very important element in the development of the individual. It occurs through imitation and through the perseverance method of trial and error.

Subjective learning depends largely upon perfect freedom, the absence of fear and the urge of a motive.

BIBLIOGRAPHY

HAGGERTY, M. E. Imitation in Monkeys. *Journal of Comparative Neurology and Psychology*, **19**, 337-455. 1909.

KINNAMAN, A. J. Mental Life of Two Macacus Rhesus Monkeys in Captivity. *American Journal of Psychology*, **13**, 98-148; 173-218. 1902.

SHEPHERD, WILLIAM T. Some Mental Processes of the Rhesus Monkey. *Psychological Monographs*, **12**. 1910.

THORNDIKE, E. L. The Mental Life of the Monkeys. *Psychological Monographs*, **3**. 1901.

WATSON, J. B. Behavior. Chapter VIII, p. 227.

NOTE

TITLES OF BEHAVIOR PAPERS

WALTER S. HUNTER

Professor Yerkes has suggested that I embody in a note certain views concerning the titles of behavior papers. All students who read widely and at the same time selectively are handicapped by the very frequent inability to determine the contents of a paper from a perusal of its title. Problem and animal bibliographies are difficult to compile for the same reason. If this is true now, when the science is but well begun, how much more true will it be ten or twenty years hence, unless some change is instituted? The suggestion is, therefore, made that titles of behavior papers include the names of all animals tested as well as a specific characterization of the nature of the problem. Popular names, e.g., raccoon, dove or pig are preferable for vertebrates at least. Technical names, e.g., *Procyon lotor* and *Sus scrofa*, may be added when deemed necessary. The title " Maze habits in the white rat and the dog " is thus preferable to "A study in habit formation." " The delayed reaction in rats, dogs, raccoons and children " would be preferable to " The delayed reaction in animals and children."

Titles constructed on the basis here suggested will possibly be longer than is usual at present. What we desire, however, is clearness and efficiency and not aesthetic satisfaction.

COMPARISON OF THE BEHAVIOR OF STOCK AND INBRED ALBINO RATS

ADA W. YERKES

The Psychological Laboratory of Harvard University

For a number of years the Wistar Institute of Anatomy and Biology has been carrying on experiments in inbreeding the albino rat, *Mus Norvegicus albinus*, for the purpose of studying the anatomical effects of such procedure. In October, 1911, some of the rats, which had then been inbred to the sixth generation, were sent to the Johns Hopkins University and were used by Doctor Basset[1] for comparative studies in habit formation.

In April, 1913, while Basset's experiments were still in progress, the suggestion of similar coöperation in the study of the effects of inbreeding on the formation of habits was made by the Wistar Institute to the Harvard Psychological Laboratory and gladly accepted. It was then so late in the collegiate year that only a few preliminary experiments were made at that time by Professor Yerkes and two students, using the method of brightness discrimination. The following October the writer undertook, at Professor Yerkes' suggestion,[2] a study of certain

---

[1] Basset, G. C. Habit formation in a strain of albino rats of less than normal brain weight. *Behavior Monographs*, 1914, vol. 2, no. 4.

[2] In suggesting to Mrs. Yerkes a comparative study of stock and inbred rats, I expressed especial interest in the attempt to analyze "the temperament" of the animals, for certain previous observations in comparison with those reported by Basset had convinced me that crude measurements of modifiability, if directly compared, might lead to seriously misleading conclusions because of differences in timidity, savageness, aggressiveness, sensibility, etc., in the two groups of organisms under observation.

Mrs. Yerkes' work, unfortunately, was seriously interfered with by unexpected difficulties in the breeding of rats in the new Harvard Laboratory of Animal Psychology. From the statistical standpoint, her results are unsatisfactory because of this difficulty.

forms of behavior of these rats, which had then reached the twelfth generation of inbreeding. The scope of the work was more limited than that of Doctor Basset because of lack of time, and the number of animals tested was smaller. My thanks are due Doctor Donaldson of the Wistar Institute for supplying us with our original stock of rats, and to Doctor Hatai for the examinations which supplied the anatomical data. I wish, also, to express my thanks to Mr. Pedrick and Mr. Dine for assistance with some of the experiments.

The inbred rats which were sent to us in October, 1913, were of the thirteenth generation. In January some belonging to the twelfth and also to the fourteenth generation were obtained. Our normal control rats were secured partly from the Wistar Institute and partly from Miss Lathrop, Granby, Massachusetts. They were kept in a special room in the laboratory on the fourth floor of Emerson Hall, in clean wire cages, with sawdust on the floor and shredded tissue paper for nests. They were fed bread soaked in milk, cracked corn, oats, and occasionally green stuff, such as lettuce and celery tops. For some reason still unknown to us, although they appeared for the most part to be in excellent physical condition, they bred very slowly, and the work was occasionally delayed for lack of material of the right age. The rats with which the later experiments were made were also considerably underweight for their age, as shown in the anatomical data of table 11 (p. 293). It was found impracticable to forward to Philadelphia for examination the rats used in the earlier tests, so that the relative brain weights are given for only the last lot of seven rats.

Two methods were employed in the comparative study of the behavior of stock and inbred animals: the maze and the brightness discrimination methods. Time, distance, and error data were obtained for the maze experiments; and time and error data for the discrimination experiments.

1. MAZE EXPERIMENTS

The type of maze used in these experiments was the circular one devised by Watson.[3] The method of recording the path

---

[3] Watson, J. B. A circular maze with camera lucida attachment. *Jour. An. Behavior*, 1914, **4**, 56-59.

was that described by Yerkes and Kellogg.[4] A similar method has also been used by Miss Hubbert.[5]

In our work the path through the maze was somewhat modified from that used by Miss Hubbert, as indicated in the accompanying figure 1. Instead of turning alternately to the right and then to the left as in the Johns Hopkins maze, in our maze a rat must turn R, L, R, R, L, L, R in order to traverse the maze correctly. This may have increased the difficultness.
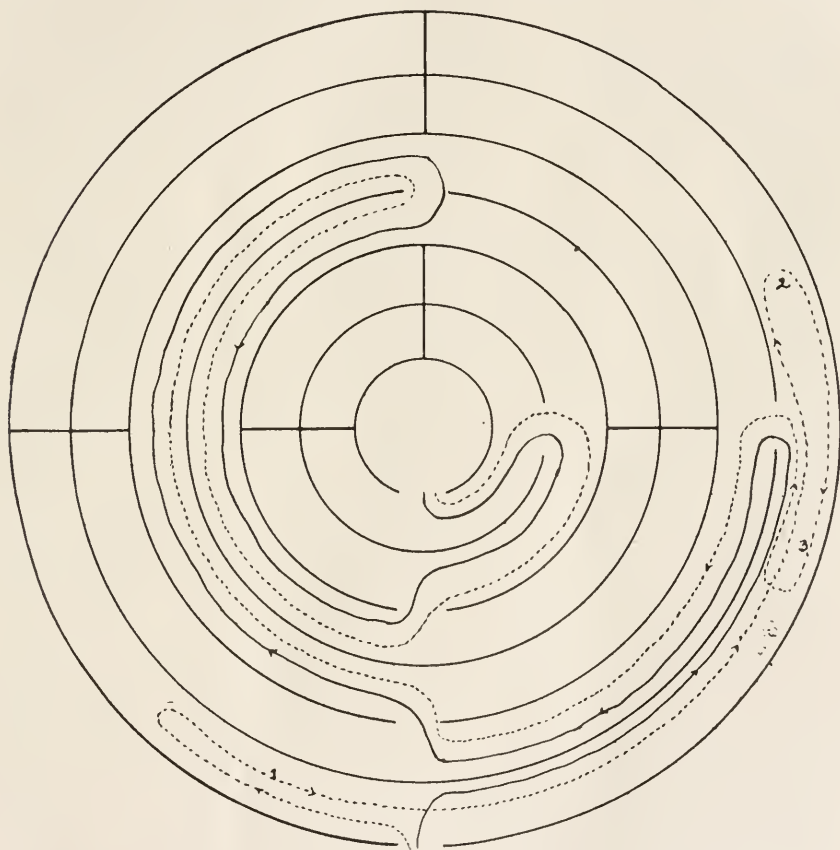
FIGURE 1.—Maze. ———— Direct path; . . . . . . Path with three errors.

[4] Yerkes, R. M. and Kellogg, C. E. A graphic method of recording maze-reactions. *Jour. An. Behavior*, 1914, **4**, 50-55.

[5] Hubbert, H. B. Time versus distance in learning. *Jour. An. Behavior*, 1914, **4**, 60-69.

The correct path is shown by the solid line in the figure. There are eleven blind alleys which may be entered either by going straight ahead past an opening or by turning in the wrong direction after passing through an opening. Entering any one of these alleys was counted an error; also turning back so that the animal was running in the wrong direction in any section of the maze, i.e., between successive openings, was counted an error for each section of the maze through which it ran. The dotted line in figure 1 shows a path in which three such errors occur. This definition of an error is in accordance with Mrs. Hicks' two propositions, namely, that errors shall include all total and partial returns, and that a runway, the distance between two corners, or its equivalent in the circular maze, the distance between two openings, shall be taken as the unit of error.[6]

After a number of animals had been tested in this form of maze, it was decided to simplify the maze and shorten the path to the centre by cutting out the outer circles. The inner wall of the outer circle was shifted so that the opening faced the entrance to the maze. Blocks were then placed on either side of the opening so that a straight passageway was formed from the entrance through to the third circle. The correct turns were then L, R, L, L, R. This form is hereafter referred to as the short maze. That this change made the problem much easier is shown by the fewer trials required to learn it correctly, as indicated in table 1, where the stock rats (average age about 66 days) in the long maze required an average of 55.25 trials; the inbred, 65 trials; in the short maze (age 35 days), stock, 19.2 trials; inbred, 23.75.

The attachment for recording the maze path consists, briefly, of a mirror attached to the ceiling; this mirror reflects the image. of the maze through a lens to a drawing board, enveloped in a hood of black cloth, and holding a pad of paper on each sheet of which had been printed a diagram of the maze. This diagram exactly fitted the image of the maze received from the lens. The sheets of paper could be easily and quickly removed with practically no interruption of the tracing and thus the course of a rat in its devious wanderings could be readily fol-

[6] Hicks, V. C.   The relative values of different curves of learning.   *Jour. An. Behavior*, 1911, 1, 138-156.

lowed with a pencil on successive sheets. In early tests of a rat frequently seven or eight sheets would be used for one record. The record thus obtained was traced with a Keuffel and Esser chartometer, and the result was a record of the distance, in centimeters, of the path as projected on the paper. The ratio of the size of the image to that of the maze was as 1 to 6.75. The number of centimeters as recorded by the chartometer was therefore multiplied by 6.75 to obtain the actual distance covered by the rat. The distance is given in centimeters in the accompanying tables.

In preliminary experiments, in order to remove possible error due to fear of the strange environment, all blocks shutting off the blind alleys were removed and the animals allowed to roam at will throughout the maze, finding their way to the food in the center if possible. One such trial a day was given for three, or five, days prior to the regular experiments. Later, the better expedient was adopted of feeding the animals in the food box in the centre of the maze for twenty minutes each day for three to five days. When the regular experiments were begun with the long form of maze the rats were allowed to feed in the centre for five minutes after completing the circuit and were then given additional food in the cage. In the short form of maze the animals were fed only in the food-box for twenty minutes at the close of the day's work. By the latter method it was possible to regulate better the amount of hunger which served as an incitement to activity in traversing the maze, but it is possible that with only one such trial a day the animals were underfed. This may account for their small size, as noted later.

The habit was considered perfect when a rat made three correct runs in succession, i.e., runs in which there were no errors. The distance for the shortest path in the long maze was 556.88 centimeters; in the short maze, 357.75 centimeters.

In the preliminary experiments a rat was allowed thirty minutes in which to find the way into the centre. Later this was reduced to fifteen minutes, since it was discovered that almost invariably, if the rat had not succeeded within the first fifteen minutes, it spent the remainder of the time sitting still in a corner or doorway. The figures followed by a + in the time columns of the tables indicate that a rat was given the full allowance of time and then removed for the day. When

TABLE 1

Stock	Inbred	Gen.	Age	P. T.	Maze	No. of Tr.	Av. No. of Tr.	M. No. of Tr.	Abs. Ret.
23♂	.....	.....	70d.	Open M.	Long	67	Stock	29	60″
47	.....	.....	51	Fed	"	35	.....	6	87.1
22♀	.....	.....	?	Open	"	98	55.25	6+	67
50	.....	.....	71	"	"	41	.....	9+	58
.....	1♂	13B	69	"	"	80	Inbred	32	83.3
.....	2♀	13B	74	"	"	68	65.00	12+	79.3
.....	62	13A	55	"	"	47	.....	.....	.....
81♂	.....	.....	36	Fed	Short	18	Stock	.....	.....
83	.....	.....	35	"	"	32	.....	.....	.....
85	.....	.....	41	"	"	12	19.2	.....	.....
80♀	.....	.....	35	"	"	16	.....	.....	.....
82	.....	.....	36	"	"	18	.....	.....	.....
.....	87♂	13A	37	"	"	23	Inbred	.....	.....
.....	89	13A	37	"	"	20	23.75	.....	.....
.....	84♀	13A	37	"	"	26	.....	.....	.....
.....	86	13A	37	"	"	26	.....	.....	.....

the tendency merely to sit still without effort to solve the problem was very marked, the animal was given a chance on at least three successive days, and showing no improvement, was discarded. Fifteen rats, seven stock and eight inbred, were discarded on this basis. Sixteen rats completed the training, nine stock and seven inbred, and a seventeenth (stock) whose timidity and wildness had made her exceptional throughout the experiments, was discarded after the one hundred and tenth trial, as she showed little sign of improvement.

The rats with which the first tests were made were eight to ten weeks old. The later ones were younger, for the effort was made to start them at seven weeks (later at five weeks). The nine rats used in the short maze were all born on the same day and were thirty-five days old when the experiments were begun. Not all were started on the same day.

In table 1 is presented a list of the rats used in the maze experiments, their sex, strain, generation, age, preliminary training, number of trials required for learning the maze and for re-learning after an interval of twenty-eight days, and the

TABLE 2
Data for Stock Rats in Long Maze

	Females				Males		
No.	Time*	Error	Dist.	No.	Time	Error	Dist.
1	1118.5	31.0	3584.3	1	1313.7	32.5	5158.7
6	142.2	11.0	1576.1	6	199.6	13.5	2386.1
11	65.1	4.5	968.6	11	663.0	10.0	1476.6
16	38.3	3.0	528.2	16	74.2	4.5	985.5
21	64.3	6.0	894.5	21	144.0	7.0	1623.4
26	47.0	3.5	1161.0	26	103.7	5.5	1201.6
31	37.5	3.5	666.5	31	86.4	2.0	865.7
36	68.2	9.0	1216.7	36	27.0	2.0	877.5
41	34.6	3.0	793.1	41	12.2	0.0	580.5
46	23.0	2.0	644.6	46	58.2	6.0	1485.0
51	27.0	4.0	1134.0	51	31.0	5.0	1377.0
56	31.4	1.0	681.8	56	55.5	9.0	2217.4
61	35.2	2.0	880.9	61	13.5	1.0	648.0
66	64.7	3.0	756.0	66	12.8	0.0	556.9
71	16.0	1.0	658.1	67	7.3	0.0	540.0
76	22.0	1.0	658.1	68	12.0	0.0	536.6
81	116.4	12.0	2322.0				
86	53.6	2.0	796.5				
91	35.0	1.0	742.5				
96	20.2	0.0	543.4				
97	15.0	0.0	553.5				
98	29.4	0.0	550.1				

* Time in seconds.
Distance in millimeters.

TABLE 3
Data for Inbred Rats in Long Maze

	Females				Males		
No.	Time	Error	Dist.	No.	Time	Error	Dist.
1	991.6	12.0	2246.1	1	135.8	5.0	1269.0
6	281.6	8.5	1954.2	6	86.5	5.0	1285.9
11	150.3	5.0	1270.7	11	127.2	12.0	2062.1
16	352.0	10.0	2543.1	16	29.0	2.0	887.6
21	146.0	6.5	1550.8	21	52.0	9.0	1687.5
26	314.3	7.0	1706.0	26	92.0	8.0	1431.0
31	129.6	3.0	943.3	31	87.2	2.0	897.8
36	73.1	3.0	1017.5	36	61.2	2.0	624.4
41	61.6	2.0	799.9	41	160.3	6.0	1552.5
46	26.0	0.0	577.1	46	166.0	5.0	1531.0
51	92.8	4.0	1312.9	51	53.0	2.0	803.3
56	157.0	1.0	708.8	56	63.6	2.0	891.0
61	70.6	1.0	661.5	61	55.2	3.0	705.4
66	12.5	0.0	560.3	66	61.6	2.0	830.3
67	10.5	0.0	550.1	71	126.1	5.0	1296.0
68	11.0	0.0	556.9	76	16.0	0.0	594.0
				80	9.4	0.0	563.6

TABLE 4

Data for Stock and Inbred Rats in Short Maze

5 Stock				4 Inbred			
No.	Time	Error	Dist.	No.	Time	Error	Dist.
1	373.4	16.0	1998.8	1	900.0+	10.0	664.9
2	125.7	9.4	1128.6	2	765.0	18.5	1515.4
3	149.5	8.0	1208.2	3	639.3	17.2	1532.2
4	61.7	6.8	905.8	4	416.5	11.5	1292.6
5	61.9	7.4	1200.8	5	313.2	6.0	836.1
6	35.5	5.0	913.3	6	70.4	5.7	799.8
7	41.1	7.0	988.9	7	50.4	5.0	744.2
8	24.3	3.4	719.5	8	63.7	8.5	1354.2
9	24.6	3.4	724.3	9	27.5	4.7	816.7
10	15.5	2.2	587.9	10	29.4	5.5	958.5
11	9.0	0.8	428.6	11	33.7	5.5	1151.7
12	7.9	0.6	422.5	12	44.8	7.0	1178.7
13	10.4	1.2	540.8	13	42.6	6.2	1326.4
14	10.2	1.0	471.6	14	27.2	4.0	897.7
15	8.7	1.2	475.0	15	43.6	7.5	1180.0
16	10.6	1.5	552.6	16	29.2	4.0	798.2
17	8.1	0.6	462.4	17	15.9	5.7	1106.1
18	11.9	1.6	578.2	18	15.6	2.7	615.1
				19	21.3	2.5	800.7
19	25.9	3.0	749.3	20	20.8	1.2	551.8
20	4.9	0.0	357.8	21	37.4	3.0	803.2
21	14.1	1.0	681.8	22	22.1	1.6	535.5
22	15.0	0.0	367.9	23	11.0	0.6	486.0
23	17.1	0.0	378.0	24	10.1	0.0	383.1
24	12.3	2.0	587.3	25	7.2	0.0	379.7
25	23.2	2.0	756.0	26	7.6	0.0	376.3
26	17.2	0.0	398.3				
27	8.0	0.0	381.4				
28	16.2	2.0	735.8				
29	27.2	2.0	779.6				
30	8.4	0.0	378.0				
31	12.0	0.0	381.4				
32	19.2	0.0	374.6				

" absolute retention," i.e., the length of time required for the first trial after that interval.

In table 2 are given the averages of records of time, errors, and distance for four stock rats, two males and two females, trained in the long maze; in table 3 are the records for three inbred rats, also in the long maze;[7] in table 4 the records for five stock rats (three males and two females) and four inbred rats (two males and two females) trained in the short maze.

[7] In tables 2 and 3 only the records for every fifth trial are here given in order to save space. The records given in table 4 are complete, however, and the curves plotted from these records only are shown.

Figures 2, 3 and 4 give, respectively, time, distance, and error records for males and females averaged together, in the short maze.

Consulting the tables for the males in the long maze, we find that during the first thirty trials, time, distance, and error records of the stock rats were higher than for the inbred; that there were more high records for the stock than for the inbred rats in all three items, especially time; and further, that the stock rats acquired the habit sooner than the inbred (table 1), the former requiring an average of fifty-one trials, the latter, eighty. In other words, the male stock rats in the long maze traveled greater distances, took a longer time for most of the trials, especially the first twenty, and made on the whole more errors, but acquired a perfect habit sooner than the inbred.

The same thing does not appear to be true of the females. Here the course of the inbred females is much more erratic than that of the stock. The stock rats, because of persistent activity,
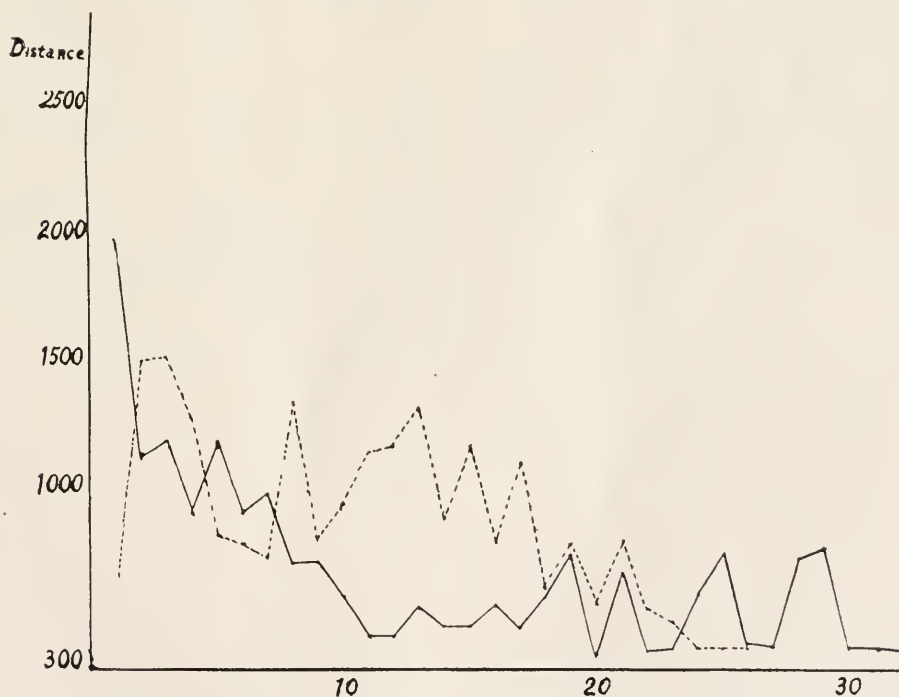
FIGURE 2.—Short maze. Distance in mm. Stock, ———— ; inbred........
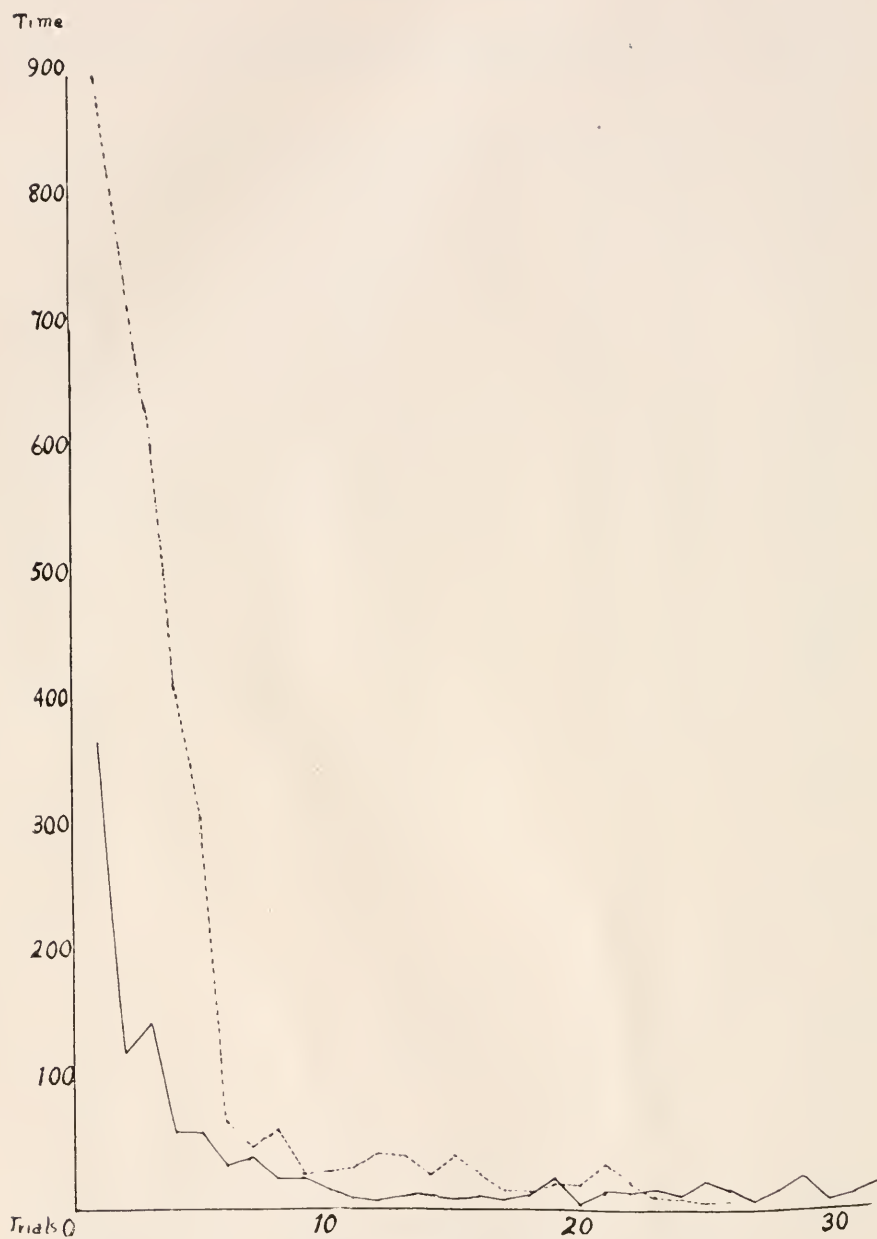
FIGURE 3.—Short maze.   Time in seconds.   Stock, ———— ; inbred, ...
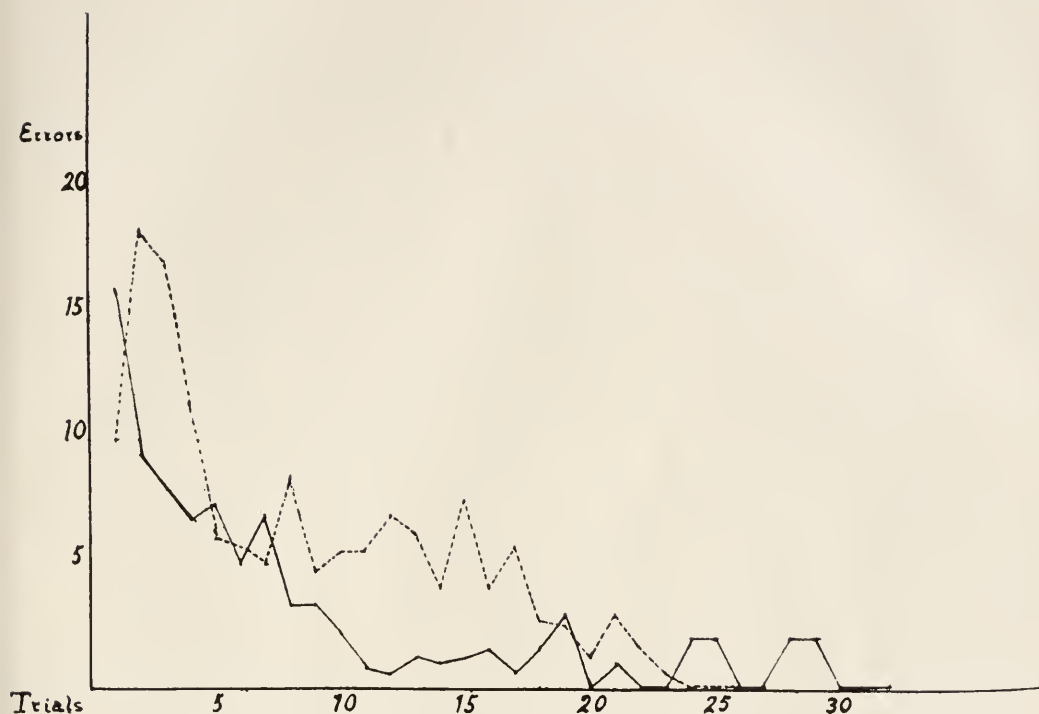
FIGURE 4.—Short maze. Errors. Stock, ———— ; inbred, ...

required more than the allotted limit of fifteen minutes in order
to complete the first trial.   The time, however, immediately and
rapidly decreased and remained low and fairly regular.   The
inbred rats, on the other hand, spent the full time allowed in
the first two trials sitting in corners, and did not reach the
centre at all.   The distance and error records were therefore
very low at the beginning, but increased as activity increased.
The amount of time correspondingly increased, but in much
greater degree and with great irregularity.   The curves which
were plotted for these records but are not reproduced show for
the inbred rats sharp variations from day to day in time re-
quired for each trial between the tenth and thirtieth trials and
high records obtained.   After the thirtieth trial the time was
only a little greater, while distance and error records for the
inbred rats were on the whole lower than those for the stock
rats.   The inbred females also acquired a perfect habit sooner,

with an average of 57.5 trials as against 69.5 trials for the stock females.

Consulting the time, distance and error curves for the short maze (figures 2-4) we find the time records very high for the inbred rats during the first five trials. In the first trial, in fact, none of them finished the trip in the time allowed (900″) and one did not even in the third trial. Evidently because of timidity they sat still most of the time allowed, making a low distance record for those trials. As they became accustomed to the maze the time rapidly diminished, though remaining a little higher than the stock records until the last few trials. The distance, and correspondingly the error records, on the other hand, increased after the first and are considerably higher than for the stock rats. The inbred rats, therefore, apparently traveled at a higher rate of speed when their timidity was once overcome. The distance and error records for the inbred rats also show greater irregularity from day to day.

In both long and short mazes, the distance and error curves for each set of rats are very similar, almost identical. Where differences occur they may be due to the place where the error occurs, i.e., in the long outer runways or the inner and shorter ones. It will be noticed, however, that the disparity between time and distance curves is very great, especially in the early trials.

In a discussion of the relative values of the different curves of learning, Mrs. Hicks[8] refers to the distance curve as a nearly ideal one but impracticable because of the difficulties of recording the distance exactly. These difficulties have since been overcome. Miss Hubbert[9] in her comparisons of time and distance curves found them so similar in character "when normal animals are tested that it is impossible to state which is the better criterion of learning." In the present comparison of behavior of stock and inbred rats, the time and distance curves are not similar. If either time or distance were taken alone, a true picture of the learning process would not be obtained. The records of distance alone would make the inbred rats appear the quicker, at first, in learning the correct path,

[8] Hicks, V. C. The relative values of the different curves in learning. *Jour. An. Behavior*, 1911, **1**, 138-156.

[9] Hubbert, H. B. Time versus distance in learning. *Jour. An. Behavior*, 1914, **4**, 60-69.

which the time records show was not the case.   A combination
of time and error or time and distance curves apparently gives
the most adequate representation of the facts obtained from
these stock and inbred rats.

2. DISCRIMINATION METHOD

When the inbred rats were first received from the Wistar
Institute, a few preliminary experiments were made by Pro-
fessor Yerkes and two students, using the brightness discrimi-
nation method and twelve animals, six stock and six inbred,
three males and three females each.   The results of these ex-
periments are given separately from the writer's, which were
conducted a year later at the Franklin field-station.   The former
animals are designated Group 1, the latter, Group 2.   The
apparatus was exactly the same for all.   Artificial light was used
for the earlier, and daylight for the later experiments.   The
animals of the first group·were from 46-55 days old when the
experiments were begun; those of the second group were eight
of the nine young rats which had recently been tested in the
short maze.   As soon as the maze experiments were finished
the rats were sent from Cambridge to Franklin and experi-
ments were begun June 17.   The rats were at this time 75
days old.   One of the stock rats met with an accident soon
after the beginning of the experiments so that the results are
given for four stock and four inbred rats, two males and two
females each.

The apparatus used was in essentials the Yerkes discrimi-
nation box.[10]   It consisted of a box 52 cm. long by 40 cm. wide
by 18.5 cm. deep.   Attached to this at one end was a smaller
food·box 16 cm. by 14 cm. by 18.5 cm., having a hinged wooden
cover, with a small hole in the centre.   An animal to be tested
was allowed to enter from the food box, by means of a sliding
door, a narrow passage.   This led through a door of wire mesh,
swinging inward from the top, to a chamber 15.4 cm. by 18 cm.
From this led two pathways or discrimination boxes, 20 cm. by
8.5 cm., differentiated only by the amount of light entering
them.   These communicated by openings in the side walls at
the rear with passageways by means of which return was effected
to rooms adjoining the entrance passage from which the animal

---

[10] Yerkes, R. M.   The dancing mouse.   New York, 1908, p. 92.

could reënter the food box. The floor of the discrimination boxes was covered with a series of copper wires connected with a No. 6 Columbia dry cell and a Porter inductorium set at 5.75 on the scale. Used in daylight the experiment box was placed facing a window so that when uncovered the two boxes received the same amount of light.

The first degree of difference in amount of light was made when a piece of black cardboard, black side down, was placed on top of one box and the other was left open. These were designated, then, the dark, D, and the light, L, boxes. The rats were required to choose the light box; if they chose the dark one, they received a slight electric shock from the wires on the floor of the box and were not allowed to pass through. The dark side was changed from left to right irregularly but according to a definite schedule printed on blanks on which the records were kept. The time from entrance through the swing-ing wire door into the chamber facing the dark and light boxes until the choice was made was taken by means of a stop watch. It was called a choice when an animal placed both forefeet far enough across the wires to receive the shock, if the choice were wrong. This discrimination time varied from four-tenths seconds to more than thirty minutes when the animals were timid or discrimination was difficult. The total time required for the regular daily series of five or ten trials was also noted.

In order to teach the method of procedure and also to test possible preference for dark or light, two preliminary series, A and B, of ten trials each were given without shock and with the dark box open for free passage through. Each regular series thereafter consisted of five trials, and one series was given a day, at the same hour of the morning. One rat was in the apparatus at a time. They were not hurried but were gently and firmly directed through the entrance doors, allowed to choose, guided back, if necessary, to the food box, and allowed to eat for 15-30″ before the next trial. The readiness with which the rats learned of their own initiative to pass through the swinging wire doors was used as a measure of their degree of initiative. This is discussed in the next section. Bread crumbs soaked in milk and mixed grains were the food used in the food box. After the series for the day was completed the animals were allowed to feed for half an hour in another cage before being returned to their own cage.

TABLE 5. DISCRIMINATION EXPERIMENT. GROUP 1. MALES

No.	Stock No. 14♂ Con.	R.	W.	Av. T.	Stock No. 19♂ Con.	R.	W.	Av. T.	Stock No. 25♂ Con.	R.	W.	Av. T.	Inbred No. 30♂ Con.	R.	W.	Av. T.	Inbred No. 1♂ Con.	R.	W.	Av. T.	Inbred No. 10♂ Con.	R.	W.	Av. T.
A	P	4	6		P	1	2	3.0	P	5	5	1.5	P	2	8		P	6	4	2.0	P	6	4	1.4
B	P	4	6		P	6	4	1.0	P	5	5	16.8	P	1	9		P	5	5	.9	P	5	5	1.1
1	1	2	3	6.6	1	3	2	0	1	3	2	24.8	1	4	1	30.6	1	2	3	3.8	1	3	3	13.4
2		1	0	8.8		2	3	2		1	0	13.6		5	0	38.8		3	2	6.2		2	2	4.6
3		5	0	14.8		3	3	1		5	2	18.6		5	0	17.8		3	1	15.6		2	3	2.2
4		3	2	13.6		2	2	233.0		3	0	33.0		4	1	21.4		3	1	314.8		3	2	1.0
5		4	1	5.4		3	3	191.0		5	0	11.8		5	0	7.4		4	0	29.2		2	2	0
6		5	0	13.2		Sa va ge.				5	0	20.2		5	0	19.4		5	1	18.6		2	3	4.4
7		4	1	4.2		2	2	123.8		5	0	14.0		5	0	12.4		4	0	30.8		3	2	1.4
8		5	0	4.8		5	0	194.0						5	0	8.2		5	0	8.8		3	3	1.2
9		5	0	6.2		5	0	302.0						5	0			5	0	10.4		2	3	1.0
10		5	0	8.8		5	0	73.0										5	1	4.2		2	3	2.1
11		5	0	10		10	0	38.0										9	0	12.7		2	1	6.7
12																	10	0	14.1		1	4	5.1
13																	9	1	14.2		1	1	10.4
14																	10	0	19.1		4	2	5.4
15																			9.7		2	0	4.7
16																					1	0	3.7
17																					0	0	3.4
18	2	4	1	24.6	2	5	0	150.6	2	4	1	17.8	2	5	0	11.6	2	5	0	22.0	2	5	0	16.4
19		5	0	8.8		4	1	194.0		4	1	23.2		5	0	5.2		4	1	32.0		4	1	8.0
20		8	2	5.3						8	1	25.7		10	0	4.4						9	1	6.5
21		9	1	5.8						8	2	96.7		10	1	13.7						10	1	8.1
22		9.	0	2.0						4	1	106.0		9	0	11.7						6	0	10.6
23		10	0	19.						4	1	46.2		10	0							9	1	9.8
24	2	5	0		3	10	0	128.6	3				3	5	2	6.0	3	10	0	32.0	3	2	1	23.4
25	3	5	0			10	0	105.5						5	2			8	2	76.6		4	1	15.6
26	4	5	5	2.6						3	9.	1	27.4	4	6	2					
27	6	5	5	28.0						4	6	2	16.1	6	5	2					
28	5	5	2	30.6						5	6	4	55.4	5							
29	4	10	0	17.1						4	6	4	27.9	4							

TABLE 6. DISCRIMINATION EXPERIMENT. GROUP 1. FEMALES

No.	Stock No. 13♀				Stock No. 21♀				Stock No. 24♀				Inbred No. 80♀				Inbred No. 90♀				Inbred No. 20♀			
	Con.	R.	W.	Av. T.	Con.	R.	W.	Av. T.	Con.	R.	W.	Av. T.	Con.	R.	W.	Av. T.	Con.	R.	W.	Av. T.	Con.	R.	W.	Av. T.
A	P	4	6		P	5	5	2.4	P	6	4	1.2	P	5	5		P	2	8	5.2	P	5	5	3.7
B	P	4	6		P	5	5	1.8	P	5	5	1.3	P	7	3		P	4	5	.9	P	4	6	2.4
1	1	2	3	49.4	1	2	3	14.2	1	2	2	10.6	1	5	0	16.6	1	2	3	3.2	1	3	3	13.6
2		5	0	54.2		2	3	2.1		2	2	19.2		5	0	11.6		3	2	2.2		2	2	11.2
3		5	0	65.0		2	3	4.6		3	3	21.1		5	0	9.4		5	0	8.1		1	3	5.5
4		5	0	22.2		2	3	8.0		5	0	17.8		5	0	14.8		4	1	4.0		2	4	12.5
5		5	0	19.2		3	3	0.0		3	2	8.0		5	0			5	0	8.0		1	5	5.8
6						4	1	4.0		1	0	13.2						4	1	6.0		5	3	8.9
7						4	1	4.6		5	0	5.5						5	0	2.2		3	3	8.0
8						5	1	2.0		3	0	5.5						5	0	0.0		3	4	9.0
9						5	0	6.0		5	0	3.6						5	0			4	4	20.0
10						5	0	6.3		5	0							5	0	1.2		4	4	8.0
11										5	0											5	5	11.6
12										5	0											5	3	6.3
13										5	0													
14										5	0	4.2												1.7
15										5	0	3.5		9	1									3.4
16														10	0									
17														10	0									
18	2	5	0	33.6	2	4	1	13.4	2	0	0	10.2	2	3	2	229.0	2	0	2	67.	2	1	3	13.0
19		5	0	9.2		3	2	2.1		3	3	12.6		4	1	145.4		2	0	19.		2	2	9.5
20		0	1	22.7						2	2	6.0		0	0	29.3						1	2	5.5
21		1	0	11.7						7	7	8.4		1	1	76.7						0	1	9.7
22		0	1	17.8						3	3	13.2		0	0	47.3						1	0	7.7
23										0	0	24.3										1	1	7.8
24	3	4	0	4.0	3	7	3	1.5	3	2	3	28.0	3	5	0	31.6	3	8	2	7.2	3	4	1	16.4
25						5	5	38.		3	2	32.4						9	1	9.0		5	0	19.2
26	4	5	0	12.0									4	4	1	25.6								
27	6	6	4	7.1									6	4	1	116.0								
28	5	0	5	8.2									5	4	1	60.8								
29	4	5	5	4.7									4	1	1	260.0								

TABLE 7

Group	No.	Stock No. 81♂			Stock No. 83♂			Inbred No. 87♂			Inbred No. 89♂		
		R.	W.	Av. T.	R.	W.	Av. T.	R.	W.	Av. T.	R.	W.	Av. T.
1	A	3	7	2.7	6	4	4.9	1	9	3.1	4	6	.7
	B	6	4	1.1	6	4	12.2	4	6	.7	5	5	.6
	1	2	3	9.2	3	2	146.8	1	4	17.5	2	3	388.6
	2	4	1	199.5	5	0	65 5	4	1	70.2	4	1	143.8
	3	3	2	73.7	5	0	23.8	4	1	68.9	5	0	82 0
	4	5	0	26.2	5	0	28.7	5	0	68.8	5	0	21.2
	5	5	0	2.2	5	0	9.3	5	0	20.7	5	0	2 3
	6	5	0	1.0	4	1	21.5	5	0	4.1	5	0	2.3
2	7	5	0	3.0	5	0	108.7	5	0	14.2	5	0	97.0
	8	5	0	5.0	5	0	33.5	5	0	7.1	4	1	13.3
	9	5	0	3.1	5	0	23.8	4	1	44.8	5	0	30.5
	10	5	0	3 1	5	0	11.8	5	0	3.9	5	0	34 7
3	11	5	0	1.7	5	0	14.2	5	0	1.3	5	0	16.3
	12	3	2	11.5	5	0	16.3	5	0	3.6	5	0	2.0
	13	4	1	1.9	5	0	26 3	5	0	.8	5	0	3.4
	14	4	1	1.4	5	0	11.6	5	0	1.3	5	0	3 7
	15	5	0	2.2	5	0	7.9	5	0	2.6	5	0	6.0
	16	5	0	1.0	5	0	5.4	5	0	1.8	5	0	1.4
	17	5	0	.8	5	0	2.8	5	0	1.7	5	0	6.1
4	18	5	0	2.3	5	0	2.2	5	0	1.7	5	0	1.8
	19	5	0	2.7	5	0	6.2	5	0	1.0	5	0	5.9
	20	4	1	40.4	5	0	3 1	5	0	13.3	5	0	1.4
	21	5	0	4.2	5	0	2.3	5	0	1.8	5	0	1 3
	22	5	0	3.2	5	0	21.3	4	1	33.1	5	0	5.3
	23	5	0	7.0	5	0	17.2	5	0	31.3	4	1	303.4
5	24	5	0	2.9	3	2	181.0	5	0	6.2	5	0	69.9
	25	5	0	1.6				5	0	41.5	5	0	11.4
	26	5	0	4.8				5	0	10.1	5	0	6.7
	27	4	1	1.1				5	0	10.0	5	0	11.6
	28	5	0	4.2				4	1	7.7	4	1	20.3
6	29	5	0	1.7				5	0	14.5	5	0	92.4
	30	5	0	1.2				5	0	6.6	5	0	15.7
	31	3	2	9.2				4	1	8.0	5	0	.5
	32	3	2	7.3				4	1	12.6	5	0	11.9
	33	4	1	9.0				4	1	10.4	4	1	10.4
9	34	5	0	14.7				3	2	19.4	5	0	14.6
	35	4	1	6.9				4	1	91.1	4	1	60.4
10	36	4	1	59.4				5	0	76.5	5	0	3.6
11	37	5	0	47 0				5	0	52.1	5	0	22.9
	38	5	0	6.4	5	0	273.6	5	0	25.6	5	0	4.4
12	39	5	0	20.0	5	0	145.7	5	0	14.2	5	0	8.6
	1	5	0	77.1	5	0	258.7	5	0	63.3	5	0	21 9
	2	5	0	4.9	5	0	110.0	5	0	38.6	5	0	2 2

TABLE 8

	No.	Stock No. 80 ♀			Stock No. 82 ♀			Inbred No. 84 ♀			Inbred No. 86 ♀		
		R.	W.	Av. T.	R.	W.	Av. T.	R.	W.	Av. T.	R.	W.	Av. T.
1	A	4	6	.75	3	7	1.4	4	6	3.9	5	5	1.3
	B	4	6	66	4	6	4.3	4	6	2.4	3	7	1.6
2	1	3	2	176.4	3	2	112.4	3	2	.6	4	1	1.5
	2	4	1	38.8	4	1	28.2	4	1	49.2	2	3	44.2
	3	5	0	12.3	3	2	11.4	4	1	50.2	5	0	109.6
	4	5	0	16.6	5	0	14.5	5	0	48.5	5	0	127.4
	5	5	0	4 7	5	0	7.4	5	0	37.6	5	0	11.9
	6	5	0	1.5	5	0	2.7	5	0	53 3	5	0	1.9
	7	5	0	23.7	5	0	3.6	5	0	64.7	5	0	21.3
3	8	5	0	6.5	5	0	1 7	5	0	5.6	5	0	8.5
	9	5	0	6.2	3	2	7.6	3	2	70.0	4	1	21.4
	10	5	0	5.8	3	2	67.1	5	0	31 6	5	0	18.2
	11	5	0	6.9	5	0	108.2	5	0	18.8	5	0	1.4
	12	5	0	7.2	5	0	94.2	5	0	10.8	5	0	18.8
	13	5	0	3.5	5	0	78.2	5	0	7.3	5	0	7.9
4	14	5	0	4.6	5	0	20.3	5	0	3 3	5	0	4.9
	15	5	0	19.5	5	0	16.7	5	0	6.1	5	0	4.1
	16	5	0	9.6	5	0	31.7	5	0	2.8	5	0	3.1
	17	5	0	4.2	5	0	36 5	5	0	3.3	5	0	1.0
5	18	5	0	3.7	5	0	21.4	5	0	5.3	5	0	1.0
	19	5	0	7.9	4	1	23.6	5	0	4.6	5	0	12.6
	20	5	0	40.4	5	0	18.2	5	0	3.1	5	0	2.2
	21	5	0	7.2	5	0	32.8	5	0	10.3	4	1	140.4
6	22	5	0	7.1	5	0	31.1	4	1	3.5	5	0	32.1
	23	5	0	5.6	5	0	20.9	4	1	36 0	5	0	39.3
7	24	4	1	18.1	4	1	11.8	5	0	6 3	5	0	5.8
	25	3	2	66.4	5	0	94 6	5	0	8.7	5	0	1.2
8	26				5	0	16.2	5	0	8.9	5	0	19.6
	27				5	0	14.7	4	1	11.1	4	1	1.9
	28				4	1	30.6	3	2	31.8	5	0	10.0
	29				5	0	38.9	5	0	56.8	5	0	13.5
	30				5	0	39.3	5	0	27.1	5	0	3.3
	31				5	0	99.2	5	0	23.8	5	0	11.0
	32				4	1	25.6	5	0	57.1	5	0	6.8
	33				4	1	81.5	5	0	28.1	5	0	10.2
	34				4	1	104.8	3	2	72.3	5	0	53.0
	35				4	1	105.1				4	1	12.0
	36				5	0	91.9	4	1	10.6	4	1	10.2
	37				5	0	26.1	5	0	36.2	5	0	17.2
9	38	5	0	47.1	5	0	8.1	5	0	34.3	5	0	4.7
	39	5	0	16 9	5	0	13.2	5	0	36.7	5	0	5.5
	1	5	0	15.9	5	0	39.0				5	0	41.7
	2	5	0	1 9	5	0	15.9				5	0	62.4

After the rats had learned to discriminate between the open box and the box covered with black cardboard, a sheet of milk glass was laid over the open box. To increase the difficultness of discrimination thereafter sheets of ordinary typewriter paper were added one by one to the milk glass, cutting off, increasingly, the amount of light entering the light box. The various conditions of discrimination are given thus:

A, B, PREFERENCE SERIES, NO SHOCK

Condition 1. Black cardboard versus open box.
"   2. Black cardboard versus milk glass.
"   3. Black cardboard versus milk glass and 1 paper.
"   4. Black cardboard versus milk glass and 2 papers.
"   5. Black cardboard versus milk glass and 3 papers.
"   6. Black cardboard versus milk glass and 4 papers.
"   7. Black cardboard versus milk glass and 5 papers.
"   8. Black cardboard versus milk glass and 6 papers.
"   9. Black cardboard versus milk glass and 4 papers.   Review.
"   10. Black cardboard and paper under, versus milk glass + 4 papers. Review.
"   11. Black cardboard and paper under, versus milk glass.   Review.
"   12. Black cardboard and paper under, versus milk glass.   Memory.

Table 5 presents the records of the six male rats (stock and inbred); table 6, the six female rats, tested by the earlier workers; tables 7 and 8, similarly, give the records of those tested by the present writer.

In the tables each horizontal black line indicates a change in condition. For conditions 1-5 the rats were required to present perfect records (5 right, 0 wrong) for four successive series of five trials each. Later, when discrimination became more difficult, this was reduced to three, and then to two. When any rat, after making perfect records under the previous easier conditions, began to make one or more mistakes each day, the discrimination was deemed too difficult and the experiment was terminated. When all had reached the limit of their discriminating ability a review series was given to all with only four papers added to the milk glass; then a series of five trials in which a sheet of white paper was laid under the black cardboard to determine whether the rats, by any chance, were choosing because of the difference in the black and white covers rather than by the difference in lightness and darkness.

Finally, after twenty-eight days, two series were given on successive days, as a memory test, under the same conditions as the latest previous test, but with no punishment for failure.

One of the inbred females had died just before these tests were
given, but of the seven remaining everyone gave evidence of
perfect memory of the habit.

It will be noticed that in the tables for group 1 the records
are somewhat irregular owing to the variety of experimenters
and to lack of time. It seems worth while to present them,
however, as far as they go. The tests under condition 1 were
carried out to twenty perfect trials in succession and then in
some cases review series were given. The latter are not in-
cluded in the figures given in table 9. Discrimination under
condition 2 with these rats was in no case carried out to the
same limit, but it will be.noted that even where fifty trials
were given, the animals had not succeeded in attaining this
standard. It is possible that under these easy conditions of
discrimination further training might have ended in perfect
discrimination. Observation showed, however, that punish-
ment following repeated errors made the rats both timid and
reckless, and the increasing difficulty of working with animals
who were frightened, sulky, and careless made it inadvisable to
carry discrimination further than condition 3 except in a few
trial cases.

The results in these tables present the following facts. (1)
There was shown a decided preference by all the rats for the
dark box.

PREFERENCE SERIES

	Light	Dark
Group 1....... Stock..............	54	59
Inbred............. .	52	67
Total............	106	126
Group 2....... Stock..............	36	44
Inbred..............	30	50
Total............	66	94

This preference was more marked in the inbred than in the
stock rats for the latter of both groups chose the dark 103 times,
the former chose it 117 times.

(2) Of the twelve rats of Group 1 only one succeeded in
making a perfect record (20 correct trials) under condition 3.
Of the four rats which were tested further than this two showed
evidence of discrimination under condition 4 but they were not
allowed to carry the experiment far enough to secure a perfect

record.   All eight of the rats in group 2 (tables 7 and 8) on the other hand, were capable of carrying discrimination as far as condition 6, i.e., cardboard versus milk glass and 4 papers. One stock rat stopped there.   The other three stock animals went as far as condition 7, where also one inbred male halted, while the other three were able to discriminate until condition 8 (milk glass and six papers) was reached.   The inbred rats therefore were able to discriminate under more difficult conditions than the stock rats.

(3) Two of the stock rats of group 2 after experiencing the electric shock several times under condition 1 made their choices so carefully that only one further error occurred before they reached the limit of their discriminating ability.   At that point they were so disturbed by the shocks received that it was impossible to work further with them.   Even when the others were ready for the review series they still refused to attempt to discriminate at all.   These two rats finished in 24 and 25 series of trials as against 34 and 35 for the others.   The average number of trials required to discriminate perfectly under condition 1, condition 2, and the total number of trials (exclusive of review series) given in the discrimination apparatus are shown in table 9.

TABLE 9

AVERAGE NUMBER OF TRIALS IN DISCRIMINATION APPARATUS

	Stock females	Inbred females	Stock males	Inbred males	
Condition 1...............	41.6	51.6	43.3	76.6	Group 1
	32.5	32.5	30.0	32.5	Group 2
Condition 2...............	33.3	33.3	30.0	33.3	Group 1
	27.5	32.5	22.5	30.0	Group 2
Totals of all conditions .	96.6	102.3	91.6	133.3	Group 1
	150.0	172.5	150.0	175.0	Group 2

From this table it appears that the inbred rats, especially those of group 1, required a larger number of trials under conditions 1 and 2 in order to acquire the habit of discriminating perfectly than did the stock rats.   The stock females.of group 1 averaged lowest, stock males next, then inbred females and inbred males.   Of group 2, the stock males required fewer trials, then the stock females, inbred females and inbred males. Since the inbred continued the experiments under more diffi-

cult conditions than the stock rats, it is to be expected that the total number of trials would be greater, but the comparison of figures under conditions 1 and 2 shows that a large part of the total difference is due to differences under the earlier conditions. After the rats had learned to discriminate under the simpler conditions, very few mistakes were made until discrimination became difficult.

The time records (average of 5 trials) of series 1 indicate marked individual differences in the effects of punishment on the different individuals. The two inbred females of group 2 (table 8) made choices very quickly in spite of mistakes and shocks. Their choices were made more slowly on the days following those on which mistakes were made, though never as slowly as were the choices made by some of the other rats. Three of the stock rats and one inbred male were very much delayed in making their decisions by being punished for mistakes. The fourth inbred rat was rendered so excited that after resisting vigorously reentering the apparatus, he dashed wildly in and chose at random, making quick choices and many errors. These facts will be discussed further in the following section.

3. GENERAL BEHAVIOR

In both the maze and the discrimination experiments certain of the differences in behavior of the stock and inbred rats have been indicated in the preceding sections. Notes made each day concerning the general behavior of individuals throw additional light on the differences and help us to interpret them more correctly. To anyone who is accustomed to working with animals nothing is more striking than the fact that no two animals are alike in behavior. Even among white rats the individual peculiarities are so great that the animals can readily be distinguished from one another by behavior alone, by one familiar with their habits.

We will consider first those animals which were tested in both the short maze and the discrimination apparatus, since they form a homogeneous and readily comparable group. From the beginning of the experiments these young rats showed a marked difference in timidity between stock and inbred rats. When the cage door was opened for the stock rats to be removed to the experiment box they would crowd up to the opening, climb-

ing over one another to get out first, running along the edge of the cage and showing no fear of being caught. The inbred rats, on the other hand, after running forward at first, would retreat to the rear corner of the cage and huddle there, trying to escape capture. None of these animals gave any evidence of savageness or wildness.

During the experiments the stock rats paid no attention to occasional noises in the room. The inbred rats, especially in the early experiments, were startled by slight noises and would jump and crouch in a corner.

The stock rats, in the maze experiments, usually ran steadily and rather fast at first, making complex tangles in the outer circles but finding their way to the centre fairly quickly, well within the time limits. They showed much curiosity, poking into blind alleys, stretching to the top of the walls, smelling at the doorways, etc. When acquainted with the maze their speed increased greatly, though here there was considerable variation in method. No. 80, stock female, for instance, ran very fast from the sixth trial on but made very few errors aside from the one of turning in the wrong direction on first entering the maze. No. 82, stock female, on the other hand, ran very fast but in a confused, scatterbrained sort of way, racing back and forth many times in the same alley. Two of the male stock rats ran back and forth repeatedly in the outer circles at first but soon learned merely to look into the blind alleys instead of entering and then ran very fast and quite directly. Only one showed any reluctance to enter the maze and none hesitated to enter the food box.

All the inbred rats, on the contrary, were reluctant to enter the maze; in the first three trials all four ran very little but crouched near the entrance until removed at the end of the time limit. In the fourth and fifth trials they gradually found their way into the centre after lingering near the entrance and wandering in the outer circle. After getting in once each one ran faster, more directly, and soon cut down errors to entering blind alleys once. They showed apparently, therefore, not less ability to form the maze habit than the stock rats but simply a greater timidity in unfamiliar situations, which hindered their forming the habit as quickly. This is borne out by the results of the discrimination experiments where the inbred rats

were capable of carrying discrimination further than the stock rats, although they required more time and made more errors in doing so.

An attempt has been made in table 10 to grade these rats in respect to certain characteristics. Since all the animals, when they became accustomed to the surroundings and procedure, would run through the experiments without showing evidences of the timidity and inactivity characteristic of their earlier behavior, the figures given represent the behavior when confronted by new conditions. The characteristics measured are timidity, initiative, sensitiveness, and activity, and the grading is on a scale of 0-5.

TABLE 10

No., Stock	Timid- ity	Initia- tive	Sensitivity to shock	Activ- ity	Maze	Discrimination
81♂	1	5	1–2	5	Many errors..........	Hasty choice. Many errors.
83♂	0–1	4	4	4	Steady, few errors....	Careful choice. Few errors.
85♂	0	5	. . .	5	Fast, steady..........	
80 ♀	0–1	4	1	5	Fast, few errors.......	Careful choice. Few errors.
82 ♀	0	5	1	5	Fast, reckless.........	Careful, but much running. Excited.
Inbred						
87♂	5	1	3	0	Quiet 2 days.........	Hard to start. Quick, excited.
89♂	5	3	3	0	Quiet 3 days.........	Easily excited. When easy, slow, cautious, sure.
84 ♀	4	4	3	0	Fast...............	Businesslike.
86 ♀	5	2	4	0	Quiet 2 days.........	Careful choice.

On a scale of 0-5, for example, the stock rats showed little or no timidity and great activity; the inbred, on the other hand, just the reverse. Initiative was measured by the readiness with which the rats entered the maze, passed through doorways, or opened by themselves the swing doors of the discrimination box. Sensitiveness was more difficult to measure because of its close

relation to timidity. It could not be measured at all in the maze experiments but in the discrimination records those rats were judged not particularly sensitive which rushed back into the dark box immediately after receiving a shock.

In activity, as shown in the discrimination experiments, the rats varied greatly. Some made their choices carefully, with due caution, and with strict attention to business. Others would investigate the box thoroughly, try to climb out, stretch heads into the discrimination chambers, stop to eat, etc After a shock several, especially the inbred rats, would become greatly excited, trying repeatedly to climb over the walls.

In regard to the time taken for each choice the timidity of the animals expressed itself in various ways. The quickest time in which the discrimination could be made was .4″. No. 89, inbred male, made an average for ten trials in preference series A of .7″, and B of .6″. After making two mistakes in training series 1, he was apparently panic-stricken, resisted being urged to enter again, crouched in the alley, darting back to the food box several times. When finally he entered the discrimination chamber he crouched by the door of the dark box, gazing into it without moving for over half an hour. Repeatedly after being shocked he would try frantically to jump out over the edge of the passage. He was large, quick, strong, and active, and when discrimination was easy, made quick trips and quick but careful choices.

The other inbred male (No. 87) showed his timidity in excessive resistance to entering the discrimination box. He would crouch in the passageway in front of the swing doors, and it required much ingenuity and some force to persuade him to enter without getting hurt in the process. Once inside, however, in early experiments, he would dash to one of the boxes, halt abruptly to make a quick comparison with the other, dash in and around to the food box as fast as he could go. All of his choices even .when discrimination became difficult, were made quickly but always after careful comparison of the two chambers.

Three of the four inbred rats, even in the preference series where there was no shock to frighten them, were at first too timid to eat when they returned to the food box. One of the females invariably tried to climb out of the small hole in the cover of

the food box, a trick none of the others attempted. All four of the stock rats ate readily on returning to the food box, even after having been punished.

In the discrimination experiments one peculiarity was early noticed. Five of the eight rats developed the habit, on entering the space in front of the discrimination chambers, of running immediately to one side or the other, right or left, but always the same for each rat. When discrimination was easy, if that chanced to be the side on which was the light box they would enter at once or stop for a brief comparison of the two boxes. Four of the five always went to the right, one to the left. A sixth one showed a tendency to go first to that side on which the light box had been in the previous trial.

4. ANATOMICAL DATA

Under the conditions of these experiments it was found impossible to have a large number of rats finish at the same time and anatomical data were obtained, therefore, for only the seven rats which survived at the close of the memory tests given after the discrimination experiment. These data are given in table 11.

The section of the table marked W. I. R T. (Wistar Institure Reference Tables) gives data compiled at the Institute, from many rats having the same body length, and serves as a standard for comparison. If we examine the first horizontal line we find that No. 80, stock female, had a body length of 179 mm.; tail length, 144 mm.; body weight 133.5 grms.; brain weight 1.6805 grms.; spinal cord weight .4578 grms.; we'ght of water in the brain 1.3212; in cord .3296; per cent of water in brain 78.619; in cord, 71.997. Comparing this with the Wistar average of rats having the same body length, we find that in No. 80 the tail length is low, body weight low, brain and cord weights low, and the per cents of water in the brain and cord are high. This is uniformly the case with all seven animals, but it is noticeable that especially in the inbred rats is the per cent of water high. For their age all the rats were under weight, as the Wistar average for males of that age was over 200 grams., and for females nearly 200 grams. It is probable that in feeding the animals only once a day, at the close of the experiments, they did not get enough food for normal growth, although they did keep in good physical condition.

TABLE 11

W. I. R. T.*

No.	Sex Age	Body Tail length mm.	Body weight grms.	Brain Cord weight grms.	Weight of water	Per cent of water	Body Tail length mm.	Body weight grms.	Brain Cord weight grms.	Per cent of water	Stock
80	♀ 173	179	133.5	1.6805	1.3212	78.619		144.4	1.754	78.1	b. Apr. 3, 1914 –
		144		.4578	.3296	71.997	155.7		.508	70.0	d. Sept. 23, 1914
81	♂ 173	191	170.2	1.7391	1.3713	78.851		166.2	1.818	78.1	
		151		.5213	.3776	72.434	160.7		.529	70.0	
82	♀ 173	176	136.7	1.5427	1.2178	78.939		136.8	1.740	78.1	
		150		.4632	.3355	72.431	152.7		.496	70.0	
83	♂ 173	195	176.8	1.7563	1.3843	78.819		178.1	1.836	78.1	
		151		.5528	.3996	72.287	164.5		.545	70.0	
86	♀ 173	177	131.1	1.6283	1.2893	79.181		139.3	1.745	78.1	Inbred
		153		.4437	.3229	72.775	153.7		.500	70.0	
87	♂ 173	193	172.0	1.7247	1.3673	79.278		172	1.827	78.1	
		162		.5088	.3713	72.976	162.6		.537	70.0	
89	♂ 173	192	167.0	1.7297	1.3689	79.141		169.1	1.822	78.1	
		160		.5313	.3890	73.217	161.7		.533	70.0	

* Wistar Institute Reference Tables.

In order to compare these data with those obtained by Basset[11] in his work on habit formation in albino rats, the averages for these seven rats are given in table 12. Like Basset's rats, these inbred animals have a somewhat greater body length and body weight than the stock rats, and have a larger per cent of water in the brain and cord. Unlike his rats the brain weight of the inbred rats is greater, not less, so that the relations of brain weight to body length and to body weight are very nearly alike for stock and inbred rats, and very close to Basset's averages for normal animals, a little less in the former case, a bit greater in the latter.

TABLE 12

	Body length in mms.	Body weight in grms.	Brain weight in grms.	Cord weight in grms.	Per cent water in brain
Stock...............	185.25	154.3	1.67965	.4987	78.807
Inbred..............	187.33	156.7	1.69423	.4946	79.200

	Per cent water in cord	Per cent brain weight in relation to body weight	Per cent brain weight in relation to body weight	Age
Stock................	72.287	.90669	1.08856	173
Inbred...............	72.989	.90441	1.08247	173

The data of these experiments differ, therefore, from Basset's in that these rats inbred for thirteen generations did not show a brain weight much less than that of normal rats of an entirely different strain. The results of Basset's experiments showed that his inbred rats of the seventh and eighth generation, having a less than normal brain weight, showed a less than normal ability to form habits, less retention of the habit when formed, and took a longer time to relearn than the normal rats. In the experiments whose results are presented in this paper, a smaller number of animals were tested. Of the rats for which anatomical data were obtained, the inbred learned a trifle more slowly than the stock rats, both in the maze and in the discrimination experiments, but they carried discrimination of lightness and darkness further, and showed the most pronounced difference only in their greater timidity and instability of behavior.

[11] Bassett, G. C. Habit formation in a strain of albino rats of less than normal brain weight. *Behavior Monographs*, 1914, vol. 2, no. 4, p. 11.

SUMMARY

1. Almost an equal number of stock and inbred rats, because of excessive inactivity, could not be used in the experiments.

2. In the long maze, the male stock rats traveled greater distances, took longer times for the trials, and made more errors, but acquired a perfect habit sooner than the inbred males.

3. In the long maze, the female inbred rats traveled greater distances, took longer times for the trials, and acquired the habit sooner than the stock females. The irregularity in the records is greater. The time records are very high in comparison to distance and errors.

4. When males and females are averaged together, the stock rats show a smaller number of trials required to form a perfect habit than the inbred (55.25 as against 65.00).

5. In the short maze the stock rats acquired the habit sooner than the inbred rats (19.2 as against 23.75).

6. In the short maze the time records are relatively high for the inbred rats, especially during the first few trials.

7. There is greater irregularity in distance and error records for the inbred rats.

8. In the discrimination apparatus all the rats showed a greater preference for the dark than for the light box.

9. The inbred rats showed this preference more markedly than did the stock rats.

10. All the rats learned to discriminate the lighted from the dark box when the difference in illumination was great, and to choose the lighted one in opposition to their preference for the dark one.

11. The inbred rats required a larger number of trials than did the stock rats in order to perfect the habit of choosing the light box.

12. The inbred rats continued to be able to discriminate under more difficult conditions than did the stock rats.

13. The inbred rats showed a brain weight in relation to body length very slightly less than that of the normal rats, and the same is true of the relation of brain weight to body weight.

14. The inbred rats had a larger proportion of water in the brain and cord than did the stock rats.

15. The inbred rats showed an ability to form the same habits as the stock rats but they did it slowly and with greater irregularities from day to day.

16. This slowness seems chiefly to have been due to a greater timidity and a greater susceptibility to environmental conditions.

NOTES ON THE REACTIONS OF BIVALVE MOLLUSKS TO CHANGES IN LIGHT INTENSITY: IMAGE FORMATION IN PECTEN

D. H. WENRICH

I.   INTRODUCTION

During the summer of 1913, while enjoying the privileges of the Bermuda Biological Station for Research, the writer became interested in the reactions of bivalve mollusks to changes in light intensity.   Little more was done, however, than to observe the constancy with which the various species tested responded to shadows, that is, to decreases in the intensity of the light. Further observations were made in the Harvard Zoölogical Laboratory during the first half of the 1913-14 school year, when a few hours each week were devoted to a study of the reactions to changes in light intensity of one of the common fresh-water

mussels, Anodonta fluviatilis.[1]   I am indebted to Professor G. H. Parker for advice and assistance during this part of the work.   Observations on marine forms were renewed the following summer while the writer was occupying a table at the U. S. Fisheries Laboratory at Woods Hole.   Here special attention was given to the reactions of Pecten to moving objects.

II.   RESULTS WITH ANODONTA

A.   Methods

In the experiments on this fresh-water mussel, the following arrangements were made use of for the control of the lights and for making the observations.   The vessel in which the animals were placed for experimental study was a rectangular museum jar of a capacity of about 6 liters.   Coarse sand was placed in the bottom to a depth of about 5 centimeters, and enough water was added to make a depth of from 10 to 15 centimeters above the sand.   The mussels were always placed near one end of the jar with their siphons toward that end, and with their long axes parallel to the longer horizontal axis of the jar. A wooden box was painted black inside and provided with a black cover through which a small observation hole was made. In one end of the box another hole, 5 centimeters in diameter, was bored about 7 centimeters from the bottom, so that its height would correspond to that of the siphons of the mussels when the jar containing them was placed in the box.

Electric lights (incandescent bulbs) were employed as sources of illumination.   Two sources were placed on opposite sides of a line which coincided with the long axis of the mussels in the jar and the center of the hole in the end of the box.   The lights were so placed that their rays made equal angles with this line. A screen was arranged so that the light from one of the bulbs could be suddenly cut off without interfering with the rays from the other bulb.   The screen was not allowed to set up vibrations by touching the floor.   Further precautions against vibrations, to which the animals are very sensitive, were taken by supporting the experimentation-box by another box on the cement floor of a basement room, and then placing wads of

---

[1] I am indebted to Mr. W. F. Clapp for advice in the determination of the species mentioned in this paper.

paper under the lower box, between the two boxes, and under the jar containing the animals. All other light than that used in experimentation was, of course, excluded from the room.

In order to have an expression indicating the intensities of the different lights and their relationships the following formula was employed: Let A equal the intensity of the light—expressed in candle-meters—cut off to produce the decrease; let B equal the intensity of the uninterrupted light—expressed in candle-meters. Then A + B would equal the total intensity before decrease, and $\frac{A}{A + B}$ would be the ratio of the amount of decrease to the total or maximum intensity. For a criterion of equal effects with different intensities, the " inhibition point " was determined; in other words, that value of $\frac{A}{A + B}$ for which A was the lowest intensity at which a response could be obtained when it was cut off. At a slightly lower value for A, B would be great enough, with respect to A, to inhibit a reaction when A was cut off. For the determination of this inhibition point, either A or B could be kept constant and the intensity of the other varied. The value of $\frac{A}{A + B}$ at the inhibition point was used as an index of the degree of sensitivity of an animal.

One source of possible error was the use of the commercial values for the candle-power of the light bulbs employed. The actual intensity of the light falling on the siphons was of course less than this because it had to pass through the glass of the jar and about 2 or 3 centimeters of water. No claim to complete accuracy can be made, therefore, but since the conditions were similar for all the experiments, it is believed that the results are accurate enough to be of value.

B. Results

The points determined in this investigation on Anodonta were, briefly: (1) The degree and kind of sensitivity; (2) the variations in sensitivity among individuals and in the same individual; (3) the recognition of a normal condition of sensitivity, during which could be obtained measurements useful in making comparisons.

1.   Kind and Degree of Sensitivity

As a general rule the animals reacted by closing one or both siphons, seldom by closing the valves. The use of greater intensities of light might have resulted in greater muscular contraction in the reactions. The exhalant siphon was far more sensitive than the inhalant siphon and frequently was the only part that reacted to the stimuli. In all the experiments not a single instance was found in which a typical reaction was given in response to an increase in light intensity. On the other hand, decreases so slight as not to be detected by the eye of the experimenter gave rise to unquestionable and typical reactions.

2.   Variations in Sensitivity

a.   Variations in a Single Individual

The differences in the sensitivity of an animal at different times may be said to be due to differences in the "physiological states" of the animal. In attempting to account for these differences the following factors need to be considered: (1) The previous adaptation to light or darkness; (2) the previous condition with respect to stimulation or non-stimulation; (3) the previous condition with respect to a natural or unnatural position of the body of the animal; (4) the condition of the mantle chamber with respect to the presence or absence of a quantity of foreign material; and (5), probably, the presence or absence of eggs or embryos in the gills of the females.

(1) Only one experiment was carried out to test the differences in sensitivity due to the previous adaptation to light or darkness. In experiment No. 41, mussel No. 203 was left in the experimental box in the dark from 8:15 a. m. until 1:30 p. m., when a series of trials was made in rapid succession to determine the inhibition point. With the light B remaining constantly at a value of 2 candle-meters, the intensity of light A, which was a 10 candle-power bulb, was gradually increased by moving it closer to the animal until it reached the value of 2.5 candle-meters, when a slight but definite reaction was obtained. In this case the value of $\dfrac{A}{A + B}$ at a point very near to the inhibition point was 0.444. The animal was then left in quiet for half an hour with the lights remaining as above,

that is, A equaling 2.5, and B equaling 2 candle-meters. After this adaptation to a small amount of light, the animal was again tested and barely gave a response when A had the value of 0.5 candle-meters, light B remaining constantly at a value of 2 candle-meters. Under these conditions the value of $\frac{A}{A + B}$ was 0.20. In other words, the sensitivity had increased. This result is just the opposite of that obtained by C. Hess ('10) with Psammobia. He found the ' dark adapted" animals much more sensitive to changes in the intensity of the light than the "light adapted" ones. But in the case of Psammobia the animals were sensitive to increases in light intensity instead of to decreases. In the case of both Psammobia and Anodonta, therefore, the animals became more sensitive after exposure to that condition of their surroundings which tended to be non-stimulating.

(2) During experiments involving successive stimulations with intervals of from one to several minutes, if not carried far enough to cause fatigue, the sensitivity of the animals seems to increase. This was shown in numerous instances, of which the following is a good example. In experiment No. 43, mussel No. 203 was left for 4 hours under a constant light intensity of 10 candle-meters. A few tests showed the value of $\frac{A}{A + B}$ at the inhibition point to be about 0.14, when B had the value of 2 candle-meters. (It is to be noted that the sensitivity in this case is greater than that of the same animal in experiment No. 41, described above, and that the greater sensitivity is correlated with an adaptation to a higher intensity of light.) At the end of 2 hours, during which time half-hour periods of experimentation were alternated with half-hour periods of rest, the sensitivity had risen to such an extent that the value of $\frac{A}{A + B}$ at the inhibition point was 0.04, when B had the value of 2 candle-meters. In view of the 4-hour exposure to a light intensity of 10 candle meters previous to the tests made, it seems most probable that the increase in sensitivity was due to conditions resulting from the stimulations in the subsequent period of 2 hours,

rather than to the possible effect of the two hours additional exposure to light.

The increase in sensitivity in this experiment was of considerable proportions, and its absolute value indicates a rather high degree of sensitivity in these supposedly sluggish animals, for only 4 per cent of the total light intensity needed to be cut off to produce a reaction.

The increase in sensitivity as a result of repeated stimulations is indicated in another way. When an animal is left undisturbed it will spontaneously (i.e., without any observed stimulation) close its siphons from time to time. After a period of stimulation, however, the frequency of the spontaneous contractions of the siphons becomes greatly increased, which increase, it seems reasonable to conclude, is an indication of increased irritability to whatever causes operate to induce such closure when the animals are undisturbed as far as the conditions of the light are concerned.

(3) Occasionally individuals refused to respond in a typical manner, or perhaps refused to respond at all, although at other times the same individuals reacted in a normal way. Since it was noticed that of the various animals taken from the aquarium for experimentation, some were found lying on their sides and others in a natural position, the idea suggested itself that perhaps an unnatural position of the body tended to interfere with normal physiological activities. Such a result would not be unexpected in view of the presence of equilibration organs, in the form of the so-called otoliths. A series of pairs of animals were tested, one member of each pair having been in a natural position, while the other had been lying on its side or on its dorsum for a period of several days. The animal which had been in a natural position reacted in nearly every case more normally than the one which had been in an unnatural position. In a few cases the differences between the members of a pair were not very great, so that some other causes must have been involved in interfering with normal behavior.

(4) At other times, during the course of an experiment, an animal would cease to give consistent reactions. In some of these cases the cause seemed to be the accumulation of foreign material in the mantle cavity. For after a period—usually short—of non-responsiveness, a sudden contraction of muscles

would cause the valves to close partially, and at the same time eject a stream of water from the exhalant siphon carrying with it a greater or less amount of debris from the mantle cavity. Such activities would recur at short intervals until the mantle chamber was apparently free from the foreign material. Then the responses would become normal again. The presence of the foreign material in the mantle chamber seemed to act as a counter irritant, inhibiting for the time being the reactions toward decreases in light intensity.

(5) Some of the largest animals proved to be responsive very slightly or not at all, to decreases in light intensity. They would keep their siphons open wide, with vigorous currents passing in and out of the openings, and fail to close them when the light intensity was reduced. These were gravid females, and their non-responsiveness may have been due to the physiological necessity of maintaining a constant flow of water along the embryo-filled gills.

b. Variations Among Different Animals

The differences in sensitivity among different individuals is perhaps largely to be explained likewise by differences in physiological states induced by the same factors that were found to be effective in single individuals. Doubtless other unrecognized factors are involved in both cases, and individual peculiarities among the clams are also to be expected. A single example will indicate some of the differences to be met with. Mussel No. 203, normally, after stimulation at one-minute intervals for 15 or 20 minutes, begins to show irregularities in the responses, doubtless due to fatigue, and these irregularities increase if the stimulation is continued. In one experiment mussels Nos. 203 and 205 were placed side by side and subjected to the same conditions. No. 203 failed to open its siphons at all on this occasion, while No. 205, on the other hand, reacted to decreases in light intensity promptly and without any irregularities every minute for 50 minutes, at the end of which time the experiment was discontinued.

3.   Comparative Measurements of Sensitivity

A sufficient number of experiments were performed on mussel No. 203 to make it possible to recognize a normal type of behavior

for this individual. When it was responding normally, values of $\frac{A}{A + B}$ could be obtained which were comparable. This line of experimentation was not pursued very far, but some examples of the results obtained will be given. In one series of experiments (Nos. 42-46) conducted on different days, a number of tests were made in the course of each experiment. When the value of light B was allowed to remain constantly at 2 candle-meters, and the value of A varied till the inhibition point was reached, the values of $\frac{A}{A + B}$ were successively, for the different experiments, 0.14, 0.14, 0.10, 0.14, and 0.125, which show a fairly close degree of correspondence. In experiments Nos. 44-46, further tests were made with higher intensities of light. In these additional tests, the value of light A remained constantly at 22.2 candle-meters and the value of B was varied till the inhibition point was found. In these cases the value of $\frac{A}{A + B}$ at the inhibition point were successively 0.078, 0.08, 0.08, which series also shows close agreement. But the sensitivity in the latter case is seen to be very much greater than in the former. This increase may have been due to an increase in sensitivity accompanying the use of higher intensities of light, as was indicated on page 301, or to an increase in sensitivity due to previous stimulation (for the values for the higher intensities were obtained after those of the lower intensities) or to both causes. This line of experimentation, if pursued further, would permit the testing out the applicability of the Weber-Fechner law to the behavior of these animals.

The results obtained from these few experiments on the fresh-water mussel, while incomplete and fragmentary, nevertheless may indicate some lines of experimentation which might profitably be pursued further.

III. RESULTS WITH MARINE SPECIES

The experiments and results at Woods Hole may be grouped under two heads: (A) qualitative tests with different species, and (B) results with Pecten.

A. Qualitative Tests with Different Species

1. Classification Based on Sensitivity

Nagel ('94) has called the sense by which animals distinguish changes in light intensity "der photoskioptischen Sinn," or light-shadow sense, and speaks of animals as being "photoptic" or "skioptic," when they are sensitive respectively to increases or to decreases in light intensity. He gives a list of over 20 species of bivalves that he has tested and divides them into 6 classes, grading from purely skioptic through photoskioptic to purely photoptic. I find it more convenient to group the species tested at Woods Hole into 3 classes, viz.:

a. Sensitive both to increases and decreases.	*b.* Sensitive to decrease only.	*c.* Sensitive neither to increases nor decreases
1. Mya arenaria	1. Pecten gibbus (var. borealis)	1. Cumingia tellinoides
2. Ensis directus	2. Ostrea virginiana	2. Yoldia limatula
3. Venus mercenaria	3. Modiola demissus (var. plicatula)	3. Solenomya velum
4. Petricola dactylus	4. Modiola modiolus	4. Tellina tenera
5. Spisula solidissima	5. Mytilus edulis	5. Nucula proxima (?)
6. Callocardia morrhuma	6. Liocardium mortoni	
	7. Anomia simplex (?)	

A question mark is placed after Nucula because the animal is so small and the siphons so short that slight movements may have been overlooked. So far as could be observed, however, there were no reactions. Since Nagel ('94) puts Tellina complanata and T. nitida rather high in the photoskioptic class, it may be that my failure to get responses from T. tenera was due to unfavorable physiological states of the animals experimented with. There is also some question about the position of Anomia simplex, for, although the animals tested reacted only to decreases, it is probable that the change from a depth of 8 to 10 meters—the level at which they were collected—to the surface caused a very great decrease in physiological tone. Such a loss in physiological tone was especially noticeable in Pecten and Arca collected from similar depths. In fact, Arca failed to give any consistent responses. I failed to find any species which reacted to increases only. Some of those in class *a* reacted more strongly to increases than to decreases, e.g., Venus, but all except those in class *c* reacted to decreases.

2.   Relation of Sensitivity to Presence or Absence of Pigment

It is worthy of note that all the species named in classes *a* and *b* had more or less pigment deposited on the ends of the siphons, or along the edge of the mantle, as in Pecten and Ostrea; and these pigmented areas seemed in every case to be the parts sensitive to changes in the intensity of the light.   In class *c* there was a total lack of pigment so far as I could discover by examining the living specimens.   The correlation of the presence of pigment with the sensitive areas of these animals is in accordance with a general rule throughout the animal kingdom. That pigment is not necessary to such sensitivity has been well established by Beer ('01), R. Hesse ('02), and others.   Nagel ('96) finds that Psammobia has no pigment on the siphons, yet it is very sensitive to increases in light intensity.   On the other hand, I have found that Cummingia, which has relatively very long, non-pigmented, separate siphons, that move about actively, gave no sign of sensitivity to either increase or decrease in intensity in any of the two or three dozen animals that I tested. While the correlation between the presence of pigment and sensitivity is apparently perfect as far as my investigations go, this is not proof but that species may be found on our eastern coast for which this correlation fails to hold.

3.   Differences in Reactions to Increase and Decrease of Light Intensity

Another point may be noted with respect to some members of class *a*, namely, that in certain cases, and especially in that of Mya, a different set of muscles is involved in the reaction to increase from that involved in the reaction to decrease of light intensity.   Time after time specimens of Mya were tested and the reactions followed the same general rule, viz., for decreases in intensity, the movement was that of the muscles involved in closing the siphonal openings, while in responses to increases, the siphon tubes were withdrawn.   In the latter case the withdrawal of the siphon tubes was sometimes accompanied by closure of the openings, especially if the reaction was a vigorous one, but as a general rule, when the movement of the siphon tube was not great, no closure of the openings resulted.   Just why one set of muscles should be used for the reaction to in-

creases and another set for reactions to decreases, is difficult to understand. Since Mya usually inhabits stretches of the shore which are exposed at low tide, it might be thought to be an adaptation to the conditions of its habitat for the siphons to be withdrawn as the tide goes out, accompanied as it would be with gradual increases in light intensity. But under the conditions of the experiments the reaction was to a sudden increase in the intensity of the light rather than to a slow or gradual increase. Another possibility is that the reaction is due to an increase in heat rather than to an increase in light. Experiments were not undertaken to determine this point. On the other hand, it is equally difficult to understand why decreases in intensity, which might accompany the approach of an enemy, were responded to by a mere closure of the siphonal openings, without a withdrawal of the siphon tube. A similar difference in reaction was noticed in Petricola and Spisula.

B. Results with Pecten

1. Sensitivity to Increase and Decrease

It will be noticed that Pecten is placed in class b, that is, among those which react to decrease only. Nagel ('94) classes Pecten and Arca among those which are "photoskioptic," but Dakin ('09) and Bauer ('12) say that Pecten does not react to increases in intensity. It is not strictly correct to say that Pecten does not react to increases, for at times sudden increases, especially when the light is very strong, will cause the animals to close their valves. But such reactions are very irregular and occur only after a latent period of several seconds (Nagel mentions the long atent period for reactions to increases). On the other hand, the reaction to decreases is nearly always immediate and regular. With respect to immediate and regular responses, therefore, it is proper to place Pecten gibbus (var. borealis) in class b. This property of Pecten seemed to offer an oppotunity to test the image-forming powers of its eyes by employing a moving object in such a way that it would be accompanied by an increase instead of a decrease in the intensity of the light.

a. Methods

For these experiments the following methods were employed. In a wooden box, about 45 x 30 x 30 centimeters, a hole about

4 centimeters in diameter was bored at one end near enough to the bottom to correspond to the height of the animals when they were placed in a dish containing sand and the dish was set in the box. On the outside of the box a circular disk of bristol board, blackened with India ink, was fastened at its center so that it could be rotated. Openings of various sizes were made in the disk near its periphery in such positions that they would coincide with the hole in the box when the disk was rotated. In a rough way, therefore, the amount of light falling on a given area of an animal could be controlled. For cutting off the light a separate black card was passed between the box and the light source (usually the window) close to the box but not touching it. Further precautions were taken to prevent vibrat'ons, 'to which many species are very sensitive, by supporting the box and the dishes containing the animals on wads of cotton.

b. Results

Under the above conditions it was found that Pecten was very sensitive to decreases in light intensity, but reacted seldom to increases, and then only after a relatively long latent period. There was therefore little danger of confusing the two types of reactions. It was further observed that Pecten reacted more readily to decreases when the illumination was low, than when it was very bright. Low intensity corresponds more nearly to the conditions of their natural habitat than does high intensity, and it may be that their greater sensitivity at the lower intensities is an adaptation to their normal surroundings. Pecten differs in this respect from Anodonta, which lives in much shallower water.

Rawitz ('88) stated that a considerable number of eyes must be affected by a shadow in order to produce a response. Some attempts were therefore made to limit illumination to a small area of the mantle margin. By means of narrow slits or small round openings in the disk, it was possible to restrict the area subjected to bright illumination. In these cases direct sunlight was reflected from a mirror. In one instance only two eyes were thus illuminated, yet definite reactions followed the cutting off of the light. In several instances of this kind, where only a small area of the mantle edge of one side was illuminated, the response to a cutting off of the light was a very local mus-

cular contraction involving little more than the illuminated area. These results are certainly quite different from those reported by Rawitz. Dakin ('10a) also states that a considerable number of eyes must be affected by a shadow in order to produce a reaction. Rawitz and Dakin, however, used small objects to produce local shadows instead of the local illumination method just described. The difference in method may account for the different results. The local responses obtained as a result of localised stimuli indicate their reflex character.

2.   Reactions Toward a Moving Object

a.   Experiments

For testing the image-forming powers of the eye in Pecten, the following methods were employed. A piece of bristol-board about 25 x 15 centimeters was blackened with India ink and pasted to a piece of heavy cardboard to give it rigidity. This was used as a background for the moving object, which was a white card 7.5 centimeters square. The animals were placed in the end of the box bearing the hole and the revolving disk, and the black bristol-board was stood up in the opposite end, that farthest from the window. To the white card a black thread was attached and passed vertically over a convenient gas jet—in lieu of a pulley—so that the card could be raised and lowered without the corresponding movement of the hand being visible to the animals.

First the animals were tested for increases and decreases in the usual way. Additional tests for increases were frequently made by flashing on to the animals a reflection of the light from the window by means of a mirror held in the hand. If the animals were found to be reacting normally, they were then tested with the moving card. Since the white card was receiving the light from the window, it will readily be understood that as the card moved upward from the bottom of the box, it would receive more and more light, and therefore would reflect more and more light on to the Pectens in the other end of the box. Each upward movement of the card would therefore be accompanied by an increase in the intensity of the light to which the animals were subjected. Any reaction they might give, therefore, could not be attributed to a decrease in the

intensity of the light. Nevertheless, whenever the card was moved upward the animals gave immediate and vigorous responses by closing the valves or by contraction movements of the vela and tentacles. The reactions followed alike when the movement of the card was slow—i.e., about 5 centimeters per second—or when the card was suddenly jerked upward. Similar reactions were also obtained when the card was moved downward, or from side to side at a constant level. When a black card was substituted for a white one, reactions sometimes resulted, sometimes not. I cannot be certain whether there was enough contrast in the amount of light reflected from the background, compared to that from the card, to allow the animals to form an image of the moving black card, or whether some slight movement of the arm or body of the observer in connection with the pull'ng of the thread may not have been the source of the stimulus. That the eyes were concerned in the reception of the stimuli from the moving cards is indicated by the results of the following experiment. In all the previous experiments the animals were always placed with the open, or ventral, side toward the moving card. Now they were turned around 180 degrees so that their dorsal, or hinge, side was toward the card. In this position light from the card could not fall on the eyes and the animals gave no responses to the movement. Next they were turned back 90 degrees, so that either the anterior or posterior margins with their eyes were turned toward the card. In this position they gave fully as vigorous responses as when the ventral side was toward the card.

In one series of experiments the size of the white card was successively reduced to determine the lower limit of size to which the animals would respond. The smallest card, the movement of which produced a definite reaction, was 1.5 centimeters square and its d'stance from the animal about 35 centimeters. No attempt was made to determine a larger limit, nor any distance limits.

It is believed by the writer that these experiments with the upward moving white card on a black background, since any possibility of the movement being accompanied by a diminution of the intensity of the light was excluded, and since definite and vigorous responses were obtained, constitute a demonstration of the ability of the Pecten eye to form an image. Perhaps

absolute proof could only be obtained by removing all the eyes and then subjecting the animals to the same tests. Such a method might also demonstrate whether the eyes alone, or other parts of the mantle-border as well, are sensitive to the changes in light intensity. But the operation involved would undoubtedly be a great shock to the animals and their subsequent behavior might not be typical.

b. Discussion

The complex and highly organized structure of the eyes of Pecten has attracted the attention of histologists for many years. Those who have undertaken a careful study of the structure have usually found many difficulties to overcome, and unsatisfactory results were often obtained on account of imperfect technique. The most recent, and perhaps the most reliable, detailed study of the Pecten eye is that of Dakin ('10b), to which the reader is referred.

Many of those who have studied the histology of these eyes have assumed that the animals could "see" with them. The following quotation from Garner ('37) indicates the typical attitude among some of the earlier investigators: Garner says (p. 488): " In Pecten, Spondylus, and Ostrea we find small, brilliant, emerald-like ocelli, which, from their structure, having each a minute nerve, a pupil, a pigmentum, a striated body, and a lens, and from their situation at the edge of the mantle, where alone such organs could be useful, and also placed, as in Gasteropoda, with the tentacles, must be organs of vision." Similarly, on anatomical grounds, Grube ('40), Rawitz ('88), Schreiner ('97), R. Hesse ('00), and others conclude that these eyes are organs of vision. But very few of the histologists have performed crucial experiments to determine whether or not Pecten really could form an image. And some of them have indulged in various speculations as to some function other than vision.

As an example of such speculations I may quote Hickson ('80). He says (p. 454): " Little is known and little can be said concerning the function of the eyes of Pecten. The presence of such a well-formed tapetum makes it probable that they are capable of appreciating very diffused light. The close approximation of the lens to the retina makes it exceedingly improb-

able that any image is formed upon the latter. A few experiments have been made on the extent of their visual power, which make it very doubtful whether they are of much value to the animal in avoiding its enemies. The most reasonable theory of their function seems to be that, when on the ebbing tide a probability arises that they will be left high and dry on the shore, they can appreciate the fact by the growing intensity of the light, and by the peculiar flapping motion of their valves the Pectens are so remarkable for, move away into deeper water."

Sharp ('87) criticises this idea of Hickson, calling attention to the well-formed eyes of the species found in the Mediterranean, where scarcely any tide exists. Earlier ('84), he had said (p. 458): " Now, I am inclined to believe, as has been suggested by Hensen ('65), that the pigmented epithelial cells that cover this organ and the stalk on which it is situated, and the only place where we find a marked deposit of pigment, is the seat of vision for these animals and that the so-called eye may be an organ of some other sense. . . . If the organ in question is so highly developed, we must necessarily conclude that vision, if that be the sense, is also highly developed, which does not appear to be the case. . . ." But in 1886 he offers the suggestion that they are phosphorescent organs, saying (p. 61): " It is not unreasonable to suppose that organs for emission of light would be constructed on the same principles as those for the admission of light." Dakin ('10b) tested out this phosphorescent theory and obtained only negative results.

Patten ('86) regarded the eyes of Pecten and Arca as organs for the absorption of energy from the sun, and termed them "heliophags." This idea has received no support from later investigators.

Attention should be called to the fact that Pectens, as well as other bivalves, fail to give consistent responses unless they are in good physiological condition. I found this to be true of all the different species experimented with, and in the case of Pecten I was able to get consistent responses only from those collected in very shallow water. Animals collected from a depth of 10 to 12 meters gave irregular responses and usually died at the end of two to four days in the laboratory aquaria.

As already stated, Rawitz ('88) claimed that no reactions were

obtained from Pecten unless the shadow furnishing the stimulus affected several eyes, i.e., a considerable length of mantle edge. The shadow of a small object, such as a needle, brought no responses unless the shadow was made to fall on a series of eyes in quick succession, in which case the stimulation was the same as if a larger object had been used. From these results, and from the study of the structure of the eye, he concluded that the animals possessed a mosaic type of vision, saying (p. 548):

" Wird somit in jedem Auge nur ein kleiner Teil desjenigen Objectes abgebildet, welches sich gerade im Gesichtsfelde befindet, und sind zur deutlichen Wahrnehmung immer eine grossere Zahl von Augen notwendig (wie viel, weiss ich nicht; doch ist die Zahl der notwendigen Augen für diese Batrachtung nebensächlich), so heisst das· das Gesamtbild, welches eine Muschel wharnimmt, setzt sich aus einer bald grosseren, bald geringeren Zahl von Einzelbildchen zusammen, die linear aneinandergereiht sind. Wir haben es hier also mit einer Art musivischen Sehens, und zwar linearen musivischen Sehens zu thun." Rawitz made use of shadows in his experiments, thereby failing to make a distinction between reactions to decreases in the intensity of the light and reactions to the movement of an object. It would have been possible to have attributed the reactions he obtained to decreases in light intensity alone. As previously stated, I obtained responses with decreases when only two eyes were illuminated. Unfortunately, I did not attempt to determine the reaction of a single eye to the moving card in my experiments.

Nagel ('94) distinguishes between the sensitivity to changes of light intensity, which he called the "photoskioptic sense," and the sensitivity to the movement of an object. He says (p. 387): " Im Gegensatz dazu (photoskioptic animals) würden die ikonoptischen Tiere solche sein, bei welchen zu den photoskioptischen Wahrnehmungen der einzelnen sensiblen Elemente die Perception eines durch einen lichtbrechenden Apparat erzeugten Bildes hinzukommt." He regarded Pecten as "ikonoptic" and says ('96, p. 64): " Die verscheidenen Arten von Pecten, welche bekanntlich Augen in erheblichen Zahl am Mantelrande tragen, schliessen ihre Schalen schon, wenn man nur in the Nähe kommt, ohne dass ein Schatten auf sie gefallen wäre." While this latter statement is probably correct, these

reactions might have been the result of very slight decreases in illumination due to the approach of the observer, or his passage between the animal and some of the windows of the room. I have obtained similar results under similar circumstances but regarded the observations as far less conclusive than those made in connection with the experiments with the moving card.

Greater conservatism is shown by some of the investigators, who have not jumped to unproved conclusions. Drew ('06, p. 50) says: "It is difficult to determine how well a scallop sees. . . . Quick motions outside of an aquarium made so the illumination is not materially affected and so the aquarium is not jarred, frequently seem to cause responses, but the results are so frequently negative that apparent responses may be accidental. Experiments to test the power of vision have not been devised." Differences in physiological states may account for the inconsistent results obtained by Drew.

Dakin ('10b) experimented on various kinds of Pecten and states (p. 102): "The eyes show no evidence of being phosphorescent organs, though I have observed and stimulated them at night and in the dark. A shadow thrown on to the eyes of an open Pecten causes a closure of the valves, and this reaction usually takes place very rapidly, though very often the perception of light stimuli does not appear to be any better than by Arca with very simple eyes or others with pigment spots." Dakin further states that no evidence of accommodation could be obtained experimentally. In regard to pigment spots it may be worth while to mention that the Pectens used in my experiments possessed, in addition to the eyes, pigment spots along the mantle edge similar to those found on the mantles of eyeless forms, and these pigment spots may be sensitive to changes in light intensity. However, the only method of testing the matter seems to be that of eliminating all the eyes and then subjecting the animals to changes of light intensity.

Only a few investigators have carried out careful experiments to determine the extent of the powers of vision in Pecten, and usually no adequate discrimination has been made between reactions to decreases in light intensity and the possible reactions to the movement of an object. Bauer and von Uexküll have performed the most critical experiments on Pecten. Bauer ('12, p. 134) says: "Es muss dagegen betont werden dass bei Pecten

nicht die Harebsetzung der Lichtintensität den auslösenden Reiz darstellt, sondern dass das Tier die Bewegung des Schattens 'sieht'." In support of this conclusion he points out that when an opaque object is passed between the animal and the light source, there may be obtained an upper and a lower limit of rapidity with which the object can be moved and still produce a reaction. But in this experiment no distinction is made between the effect of the movement and that of a diminution of the light intensity. However, he relates that in preparing his camera for photographing the animals in the aquarium, the movement of his arm before the dark background of the black-cloth camera-cover was sufficient stimulus to cause a reaction. There was no shadow in this case, according to his statement. He also performed a series of experiments to determine the rôle of the eyes in the righting reflex (" Umkehrreflex") and con-cludes that they are vitally concerned in, and necessary for, the carrying out of this reflex.

Von Uexküll ('12) got the usual results with a shadow, i.e., closing of the shell. When, however, he placed a starfish—a natural enemy—on the glass side of an aquarium adjacent to the one in which the Pectens were confined, there was not the response that was to have been expected if the Pecten "saw" its enemy. The starfish was then made to move and the Pecten responded by extending its tentacles in the direction of the starfish. Dakin ('10a) showed that when fluid drawn from a chopped-up starfish was pipetted on to the tentacles of a Pecten it would close its shell or swim away. Von Uexküll argues, therefore, that a series of reactions is involved in the closure of the shell following a stimulation of the eyes by a moving object. The perception of the movement causes a positive reaction of the tentacles which extend toward the moving object. If the tentacles then receive a stimulation by some chemical substance, the shell is closed by the adductor muscles. In my experiments with the moving card there was no intermediate reaction of the tentacles, the reactions to the movement of the card being in nearly every case an immediate closure or partial closure of the valves. In the case of Von Uexkull's experiment, however, there seems to be no reason to doubt that the animals did react to the movement of the starfish, thus indicating the ability to form an image.

Thus while some experimental evidence has been produced indicating an image-forming capacity for the eyes of Pecten, many of the experiments have been uncritical in that they have not been conducted so as to distinguish between reactions to decreases in light intensity and reactions to the movement of an object. The experiments and observations of Nagel, Bauer, and Von Uexküll, however, seem to be fairly conclusive. It is believed that the experiments described in the present paper were so conducted as to avoid any confusion of the two kinds of stimulation, and therefore, to establish that Pecten gibbus (var. borealis) responds to the movement of an object and consequently may be thought to form an image in its highly organized eyes.

IV. SUMMARY

A. Results on Anodonta: 1. Anodonta is sensitive to decreases in light intensity but not to increases. Responses were obtained to decreases so slight as not to be detected by the eye of the observer

2. Sensitivity is influenced by the physiological states of the animals in at least the following ways: (a) Animals kept in the dark a few hours are less sensitive than when kept in the light, even when the light is very weak (e.g., 4 or 5 candlemeters). (b) Animals are more sensitive after periods during which successive experimental stimulations were given than after periods of quiet. (c) Unnatural positions of repose for the animals seem to interfere with normal sensitivity. (d) The presence of foreign material in the mantle chamber may temporarily inhibit reactions to stimulation by decreases in light intensity. (e) The presence of eggs or embryos in the gills of gravid females appears to inhibit responses to decreases in the intensity of the light. (f) Inherent differences in sensitivity between individuals probably exists.

3. By letting A equal the amount of light (expressed in candlemeters) cut off to produce a decrease, and B equal the amount of uninterrupted light (expressed in candle-meters), the degree of sensitivity may be measured by the value of the fraction $\dfrac{A}{A + B}$ when A has the lowest value for which a response is given.

B. Results on marine species: 1. Three classes were distinguishable as follows: (a) Those sensitive to both increase

and decrease in light intensity (e.g., Mya); (b) those sensitive to decrease only (e.g., Pecten); and (c) those sensitive neither to decreases nor to increases (e.g., Cumingia).

2. A perfect correlation was found for the animals studied, between sensitivity and the presence of pigment in the epithelium of the sensitive areas.

3. In the case of Mya arenaria, and some others, reaction to increases resulted in a withdrawal of the siphon tubes, while reaction to decreases resulted in a closure of siphonal openings, often unaccompanied by any withdrawal of the tube.

4. Experiments on Pecten, which is sensitive only to decreases (with exceptions noted in the text), demonstrated that: (a) vigorous reactions by closing the valves may be obtained when a white card is moved over a black background, even when the movement involves an increase in the intensity of the light falling on the animals. This is believed to show that the Pecten eye may form an image. (b) The smallest white card the movement of which produced a response at a distance of 35 centimeters was 15 millimeters square. (c) When bright illumination was employed reactions occurred on decrease in intensity even if only two eyes were affected. Response in this case was local.

V. LIST OF PAPERS CITED

BAUER, V.   Zur Kenntnis der Lebensweise von *Pecten jacobaeus* L. in beson-
    1912.   deren über die Funktion der Augen. *Zool. Jahrb., Abt. f. allg. Zool.*,
        Bd. 33, pp. 127-149.

BEER, T.   Ueber primitive Sehorgane. *Wiener klin. Wochenschr.*, Jahrg. 14,
    1901.   pp. 255-261, 285-293, 314-324, 30 Textfig.

DAKIN, W. J.   Pecten. *Liverpool Marine Biol. Com., Mem.*, XVII, pp. viii+136,
    1909.   9 pl., 4 text fig.
    1910*a*.   The Visceral Ganglion of Pecten, with some Notes on the Physiology
        of the Nervous System, etc. *Mitteil. Zool. Sta. Neapel*, Bd. 20,
        pp. 1-40, pl. 1-2, 1 text fig.
    1910*b*.   The Eye of Pecten. *Quart. Jour. Micr. Sci.*, Vol. 55, pp. 49-112, pl.
        6-7, 2 text fig.

DREW, G. A.   The Habits, Anatomy and Embryology of the Giant Scallop, *Pecten*
    1906.   *tenuicostatus* Mighels. *Univ. of Maine Studies*, No. 6, pp. 1-71,
        pl. 1-17.

GARNER, R.   On the Nervous System of Molluscous Animals. *Trans. Linn.*
    1837.   *Soc.*, Vol. 17, pp. 485-501, tab. 24-27.

GRUBE, A. E.   Ueber Augen bei Muscheln. *Arch. f. Anat., Physiol., und wiss.*
    1840.   *Med.*, pp. 24-35.

HENSEN, V.   Ueber das Auge einiger Cephalopoden. *Zeitschr. f. wiss. Zool.*, Bd.
    1865.   15, pp. 155-242, Taf. 12-21.

HESS, C.   Neue Untersuchungen uber den Lichtsinn bei wirbellosen Tieren. *Arch.*
    1910.   *ges. Physiol.*, Bd. 136, pp. 282-367, 6 Taf.

HESSE, R.   Untersuchungen über die Organe der Lichtempfindung bei niederen
1900.   Thieren. VI. Die Augen einiger Mollusken. *Zeitschr. f. wiss. Zool.*,
             Bd. 68, pp. 379-477, Taf. 25-32, 1 Textfig.
1902.   Untersuchungen über die Organe der Lichtempfindung bei niederen
         Thieren. VIII. *Zeitschr. f. wiss. Zool.*, Bd. 72, pp. 565-656.

HICKSON, S. J.   The Eye of Pecten. *Quart. Jour. Micr. Sci.*, Vol. 20, pp. 443-455,
1880.   pl. 34-35.

NAGEL, W. A.   Beobachtungen uber den Lichtsinn augenloser Muscheln. *Biol.*
1894.   *Centralbl.*, Bd. 14, pp. 385-390.
1896.   Der Lichtsinn augenloser Tiere. Jena, 8vo., 120 pp., 3 Textfig.

PATTEN, W.   Eyes of Molluscs and Arthropods. *Mitteil. Zool. Sta. Neapel*, Bd.
1886.   6, pp. 544-756, pl. 28-32.

RAWITZ, B.   Der Mantelrand der Acephalen. Erster Teil. Ostreacea. *Jena.*
1888.   *Zeit. f. Naturw.*, Bd. 22, pp. 415-556, Taf. 13-18, 1 Text fig.

SCHREINER, K. E.   Die Augen bei Pecten und Lima. *Bergens Museums Aarbog*
1897.   for 1896, No. 1, pp. 1-51, 4 pl.

SHARP, B.   On the Visual Organs in Lamellibranchiata. *Mitteil. Zool. Sta. Neapel*,
1884.   Bd. 5, pp. 447-470, pl. 26.
1887.   On the Eye of Pecten. *Proc. Acad, Nat. Sci.*, Philadelphia, 1886,
         pp. 61-62.

UEXKÜLL, J. v.   Studien über den Tonus. VI. Die Pilgermuschel. *Zeitschr. f.*
1912.   *Biol.*, Bd. 58, pp. 305-332, 6 Textfig.

NOTES

NOTE ON THE BEHAVIOR OF CAPONS WHEN BROODING CHICKS

H. D. GOODALE

Massachusetts Agricultural Experiment Station

References to the brooding of chicks by capons are often found in the literature but descriptions of their behavior do not seem to be on record. During the past season five tests with capons have been made. Two of the capons used were Rhode Island Reds, a race in which the females are very much inclined to broodiness and make excellent mothers, while three were Brown Leghorns, a race the females of which rarely become broody. The chicks used have all been Rhode Island Reds. They readily accept the capon as a foster-parent. Much of the success of the experiments is due to the excellent care given the birds by the foreman of the poultry yards, Mr. John Sayer.

First instance.—This capon was a Rhode Island Red hatched in April, 1913, and caponized in late July in the usual commercial manner by an expert caponizer. He had all the usual characteristics of his kind. The chicks were four in number, hen-hatched and also brooded by the hen for the first two or three days of their lives. The capon was placed in a coop on the night of May 20, 1914, and two of the chicks placed beneath him. He accepted them without trouble and hovered them from the start. The remainder of the chicks were given to him the next morning. During the day he was taken a little distance from the coop, leaving the chicks behind. On being released, he returned at once to his charges. The capon and his flock were then removed from the coop and given the run of a large yard. The chicks followed the capon about, who clucked to them occasionally in an *imperfect* way as though he did not quite know how to do it, and found bits of food for them. Although somewhat disturbed when approached, he did not ruffle up his feathers and spread his wings as a hen would do, but

simply retreated. Neither did he cluck as often nor as regu-
larly as a hen.

By this time it was evident that the chicks would be cared for
by the capon and the brood accordingly was removed to an
out-door yard. The capon showed no disposition to leave his
charges, though adult birds, including his recent companions,
were in neighboring yards. In a few days the cluck of the capon
became more like that of a hen, the bird giving voice to it fre-
quently as he walked about the yard. He continuously hunted
food for the chicks and on finding a morsel called the chicks to it
as a hen would do, but less vociferously. He also attacked anyone
who attempted to interfere with the chicks but did not give a call
like the warning call of the hen as far as observed. When these
chicks were about three weeks old, another lot of chicks a week
younger was added to the flock. The capon accepted these
without trouble, though confined in a relatively large yard,
18 x 50 feet. Hens do not as a rule accept chicks much younger
than their own. The new chicks, however, were somewhat slow
to follow their foster-parent, partly because they were weaker.
It was necessary on this account to round up the flock once or
twice the first day. The next few days were uneventful, but
before the new chicks were a week old a hen in an adjoining
yard came off with two ducklings. About one-half the younger
chicks promptly deserted the capon and adopted the hen.

Thus far the behavior of the capon, as far as caring for the
chicks is concerned, has been essentially like a hen. There are,
however, two points in which he differed decidedly from hens.
First, the capon began caring for the chicks without becoming
broody or without previous training. The chicks were simply
placed beneath him and he began to care for them. The hen
becomes first broody, i.e., stops laying, remains continuously
on the nest, clucks and ruffles her feathers when disturbed, and
sometimes, at least, will not take chicks until she has been broody
for some time. The second point was wholly unexpected and
adds to the general anomaly of the capon's behavior.

This point of behavior may be described as follows: At one
moment the capon is moving sedately about. Suddenly he
seizes one of the chicks by the nape of the neck and dangling
it in the air squats and goes through sidewise shaking move-
ments of the posterior part of the body, as a cock does when

treading a hen.   The orgasm is soon over; the struggling chick is released and the capon resumes his rôle of caretaker.   Sometimes, though not often, the act is repeated two or three times with the same or different chicks within a short time—ten or fifteen minutes.   On one or two such occasions, I have seen him employ a trick used by the cock in getting a hen indifferent to his attentions within reach.   This trick consists in uttering the food call, at the same time standing with head down, repeatedly pretending to pick up and drop an imaginary bit of food, but at the same time with an eye on the hen.   When she comes within reach, he attempts to seize her.   A hen with chicks calls them to the food but in a different way.   The capon's behavior toward the chicks leaves little room for doubt that he is attempting to tread them.   Though hens have since been kept in the same pen, this capon has not been observed treading them.   This capon reared all the chicks given him.

In the second instance the capon was a Brown Leghorn, hatched June 29, 1913, and caponized by the writer August 8, 1913.   The same procedure was adopted with the Brown Leghorn as with the Rhode Island Red.   The hen-hatched chicks were accepted just as readily as before.   However, he was extremely wild, so that whenever anyone approached he promptly attempted to escape from the coop or yard in which he was confined.   He made no attempt to fight off an intruder but promptly deserted his charges for the far corner of the pen.   As soon, however, as the intruder withdrew he returned to the chicks.   This bird clucked very little, even when he had a tidbit to offer.   His movements were very quick.   After a little he learned to fly out of the pen, and as the meshes of the wire were coarse, the chicks were able to follow him. . Only two of the four originally given him survived beyond the first few days.   The trio kept together all summer until the capon moulted.   Soon after his new feathers were about two-thirds grown he was observed at several different times on top of a post, crowing.   In appearance he is as typical a capon as any other.

The third instance was a Rhode Island Red capon of similar history to the first.   The chicks used were incubator-hatched. The bird was shut up in the evening of July 12 and two chicks placed beneath him.   He took them readily.   The following night the rest of the hatch, some twenty-five in number, was placed

beneath him. The entire flock was accepted and cared for. This bird from the start clucked more like a hen than the first capon used. The chicks and capon were kept in a loft for a few days, and then placed in a large "A" coop out-of-doors, the chicks being allowed to run out between the slats. This capon took most excellent care of the chicks. He was never observed making any attempt to tread them.

The fourth capon was a Brown Leghorn of similar history to the others. He was given incubator-hatched chicks in early September. They were poor chicks and died after a few days. This capon was fairly quiet and as far as could be seen gave the chicks good care while they lived, which was less than a week. Before the bird's band number was taken, a heavy wind blew open the door of the coop, permitting his escape. He returned of his own accord to the pen which contained the flock of capons, so that it is uncertain whether this or another Leghorn was used in the fifth trial.

Much the same procedure was employed in the fifth trial as with number four. The capon, a Brown Leghorn, was placed in a coop in a loft and given five chicks, three of which soon died. A few days later he was removed out-of-doors into a large "A" coop. This bird, while somewhat wild at first, soon quieted down and paid little attention to people who came near the coop. He wandered up and down the coop very much like a hen, with an eye on the chicks which ran at large. His cluck, made at intervals, sounded much like that of a hen. The chicks spent most of the time racing about outside the coop. As far as observed he did not attempt to tread the chicks. If released from his coop he led the chicks about like a hen, scratched for them and called them to him. If one picked up a chick, the bird spread himself like a hen and advanced to the attack.

The general behavior of capons is anomalous. In many respects quieter than normal males, they do not as a rule give evidence of sexuality. Usually, they impress one as being essentially neutral in sexual behavior, very much like any immature bird. Darwin states that they are said to incubate eggs as well as care for the chicks. We have not yet tested this report. Their behavior with chicks, in the main, is very much like that of the hen, such differences, with the exception of the actions of the first capon in treading the chicks, being of a

minor character and difficult to distinguish clearly from those of a broody hen.   On the other hand they sometimes crow and may give attention to the hens, their behavior at such times being as complex as that of the cock.

It is remarkable that the Leghorn capons should receive the chicks quite as readily as the Rhode Island Reds.   S nce the females rarely become broody (only two or three per cent) one would not expect to find such strong evidences of the broody instinct in capons of this race.   The differences in the races with regard to broodiness is well marked.   Of the Reds, only about two per cent *fail* to become broody at least once during the first year, while many individuals become broody eight or ten times within a year from the time they begin to lay.   We have no statistics of our own on the Leghorns, but a breeder of white Leghorns reports that his records show that of nearly three hundred pullets only twelve became broody (most of them only once) but one became broody five times and one three times.   My own experience with Brown Leghorns is of the same general character.   As a rule, Leghorns that show signs of broodiness rarely make good mothers, for the exhibitions of broodiness are very transitory.

Although the tests are not extensive enough to warrant definite conclusions, it would appear possible that the brooding instincts of the capon are after all not necessarily a female character.   Many male birds, e.g., pigeons, assist in brooding and rearing the young.   The domestic cock sometimes assists the hen in finding a nest.   An instance of a broody cock which hatched a clutch of eggs was recently published in " Fur and Feathers."   Darwin states in "Animals and Plants," as follows: " The capon takes to sitting on eggs, and will bring up chickens. . . . Reaumur asserts that a cock, by being long confined in solitude and darkness, can be taught to take charge of young chickens; he then utters a peculiar cry, and retains during his whole life this newly acquired maternal instinct."

Tests of non-broody hens, castrated hens, normal males and chicks of various ages from various races will have to be made in order to throw more light on the question of the capon's behavior.   Older chicks are sometimes used as leaders in teaching very young chicks the way in and out of a brooder.   A single test that was made of a normal male gave negative results.

Obviously, until more studies have been made of the behavior of fowls, the brooding instinct of the capon cannot be cited as proof of the assumption of a female secondary sexual character by a castrated male.

NOTE.—In a recent paper in this journal Pearl makes the following statement: "It appears to be the case that in the domestic fowl the brooding instinct has to a large degree disappeared along with the fact of domestication." He points out that at the Maine Station they have found great difficulty in finding hens that would incubate eggs through the full period of twenty-one days. My own experience with several varieties of poultry, extending over several years, does not coincide at all with Pearl's. Instances in which the birds fail to complete the full period have not been frequent. At various times, by providing a fresh lot of eggs, hens have been made to incubate eggs for six weeks or longer. In the Little Compton district, a noted poultry center, hens are depended upon almost entirely for hatching and rearing chicks. The natural method is also used extensively by farmers and poultrymen in general. The interesting results reported by Pearl would seem to apply only to *some* flocks of birds belonging to the so-called broody races (Rocks, Wyandottes, Orpingtons, etc.), but can hardly be considered of general applicability to such races. Quite the reverse, however, would be true of the Leghorns and similar non-broody races where, as stated above, only a small per cent show any traces of the broody instinct.

THE HABITS IN OVIPOSITION OF THE BEETLE *BRUCHUS*

J. ARTHUR HARRIS

Station for Experimental Evolution, Cold Spring Harbor, N. Y.

Beetles belonging to the genus *Bruchus* may either deposit their eggs upon the outside of the young pods of large-seeded legumes (*Phascolus, Pisum, Vigna, Vicia* and others) through which the young larvae penetrate to the developing seed, or upon the surface of the dry, stored seed.

If the behavior[1] of the insect in oviposition be dependent in any degree upon the characteristics of the young pod, such modification of behavior as may take place because of the varying characteristics of the developing ovary may (although it will not necessarily) be recorded in the differences in the incidence of parasites as determined from samples of matured seeds drawn from pods of known matured characteristics. One cannot assert upon failure to find a relationship between the characteristics of matured pods and the incidence of parasites that some such relationship does not exist in the case of the young pods. On the other hand, a relationship actually demonstrated on the basis of matured pods only should be interpreted with caution. These statements are true for the reason that the degree of agreement between the characteristics of mature and developing pods is not fully enough known. It is here that direct observations upon behavior seem almost indispensable.

The analysis of the data[2] for two experiments, involving

---

[1] These dates were secured in connection with some physiological work on seed weight in beans in which it became necessary to consider the question of the incidence of *Bruchus o-tectus* in experimental cultures of *Phaseolus* made several years ago. They are presented in full in the *Journal of the New York Entomological Society*, December, 1915. The purpose of this note is to call the attention of students of animal behavior to an addition to the list of instances in which records made by the organism itself may greatly facilitate the study of behavior, and to the need for direct observations upon behavior supplementing the data here given.

[2] The seeds studied were parasitized almost exclusively by insects developing from eggs on the pods in the field. I cannot assert that *none* were parasitized in storage, but if an appreciable number were so injured it makes the results here given even more significant, since any random injury would tend to obscure differential parasitization.

quite dissimilar horticultural varieties and comprising 6,233 and 8,018 pods maturing 18,575 and 21,231 seeds respectively, leads to the following conclusions for *Phascolus*:

1. No relationship between the position which a seed occupies in the pod and its liability to parasitization has as yet been demonstrated.

2. The relative number of seeds which are parasitized[3] increases from pods with the lower to pods with the higher numbers of ovules. That is to say, the percentage frequency of seeds which are injured by parasites is higher in pods with the larger numbers of ovules. Of course this percentage is based upon the total number of seeds matured, not upon the total number of ovules[4] originally laid down.

3. The same relationship holds for the number of seeds matured per pod and the incidence of the parasites. The seeds are relatively more extensively infested in pods maturing larger numbers of seeds.

4. It is difficult to differentiate and to measure the independent influence[5] of these two characters of the ovary upon the incidence of the insects. Apparently the number of seeds matured has some influence independent of that of the number of ovules per pod with which it is correlated. Since this relationship seems to be slight, it is probable that the number of ovules laid down is the primary factor.

The simplest hypothesis in explanation of the observed relationships would seem to be that in the young pods size is correlated with the number of ovules formed and the number of seeds which are beginning to develop, just as they are known to be in matured pods of other forms,[6] and that in consequence the maintenance of a foothold and oviposition are easier in the larger ovaries. This is, however, merely a suggested hypothesis which must be confirmed or disproved by actual behavior studies.

[3] In any future studies of this kind the seeds should be so preserved that the number of insects, if more than one, which emerge from each seed may be determined.

[4] The number of ovules per pod includes the number of seeds actually matured and the number of abortive seeds.

[5] Since number of seeds matured and number of ovules formed per pod are positively correlated (Harris, J. Arthur, *Arch. f. Entwicklungsmech. d. Organism.* **35,** 500-522, 1912) a relationship between either of these characters and the incidence of weevils would necessarily result in some relationship between the other character and frequency of parasitization, even though there were no direct causal relationship between them.

[6] Harris, J. Arthur, *Bot. Gaz.,* **50,** 117-127, 1910; *loc. cit.,* **53,** 204-218, 396-414, 1912.

TONE AND NOISE PERCEPTION IN THE WHITE RAT

JOSEPH PETERSON

The University of Minnesota

In the field of human psychology, studies in audition seem gradually to be accumulating evidence in favor of a resonance theory of perception. In a previous paper I have pointed out briefly some of this evidence.[1] It has been shown by Ewald that a thin rubber membrane nearly as small in its dimensions as the human basilar membrane can be made to take up sympathetically the vibrations of a tone. In this experiment the membrane was suspended in a liquid as is the basilar membrane. It seems highly probable at present that either the basilar membrane or some other structure in the cochlea can serve as a resonator of a low degree of elasticity, and can respond sympathetically to periodic vibrations and to vibrations that do not depart far from periodicity. That different parts of this resonating structure respond to tones of different frequencies is an hypothesis that gets support directly and indirectly from various kinds of facts, some of which have been suggested in the paper mentioned above. Resonators in the ear, however, do not necessarily imply specific energy of the nerve elements in the cochlea, and *vice versa*.

Evidence for or against the specific energy theory of hearing has frequently been derived from experiments upon animals, coupled with the destruction of certain parts of their cochleas. In the paper to which reference has been made I pointed out the fact that Kalisher's results, now well known, were not to be relied upon. The experiments of Johnson[2] have completely disproved the validity of Kalisher's conclusions. Johnson's experiments, as well as those by Hunter,[3] make the evidence both for and against the specific energy theory, obtained by destruction of sections of the cochlea, practically worthless, even

---

[1] The place of stimulation in the cochlea versus frequency as a direct determiner of pitch, *Psychol. Rev.*, XX, 1913, 312ff. Cf. Hardesty, *Am. Jr. Anat.*, **18**, 471ff.

[2] Audition and habit formation in the dog, *Behavior Monographs*, **2**, no. 3, 1912.

[3] The auditory sensitivity of the white rat, *Jour. An. Behavior*, **4**, 1914, 215-222. and **5**, 1915, 312-329.

to those who had overlooked the obvious imperfections of such experiments as they had been carried out. With improvement in methods of determining reactions to specific sounds, however, the problem may be attacked with some degree of success; but there still remain grave difficulties in connection with the operative technique.

Yerkes found that the dancing mouse is deaf to all sounds, except for a few days early in life.[4] The examinations of the cochlea of this animal by such investigators as Rawitz, Cyon, Alexander and Kreidl, and Kishi are not very satisfactory from a number of standpoints. For example, the fitness of structures in the cochlea for resonance of tones, a difficult matter to determine, is a question that is not answered. The recent experiments of Hunter, checked by various controls, seem to indicate that the rat is deaf to tones in the lower end of the scale—possibly to all tones—while it hears noises of the same predominant pitches. Hunter suggests that if after all " there is a sensitivity to tonal stimuli as here tested, then, for the rat, tones and noises are very different classes of stimuli."[5] Miss Barber, working under Hunter's supervision, has found similar evidence for the rat's deafness to tones,[6] and has suggested[7] that her own and Hunter's results, indicating a sensitivity to noises and an insensitivity to tones, " may point to separate bases for the perception of noise and tone." What may be the nature of these bases is not conjectured. It is on this point that I wish to make a suggestion.

If Hunter's results prove to be correct, the white rat should furnish us valuable data toward settling the question as to how the ear analyzes the complex vibrations of the air waves; for there can be little doubt that tone perception by the ear follows the same principle in the higher animals as in man. Why the rat fails to hear tones and yet hears noises should be discoverable somehow, and the answer will likely require careful anatomical as well as experimental work.

Personally I do not believe that in animals just above the rat in hearing—animals hearing both ·noises and tones—separate structures are involved in noise and in tone perception. To

[4] The dancing mouse, 1907, 52-92.
[5] *Op. cit.*, vol. V, 327.
[6] The localization of sound in the white rat, *Jour. An. Behavior*, 5, 1915, 292-311.
[7] *Ibid.*, 311.

explain Hunter's results, in case they prove to be correct, we
need only posit a lack in the rat's ear of suitable structures for
resonance, thus making possible only forced, or highly inelastic,
movement of cells in the cochlea.   The basilar membrane may
consist of tissue, for instance, too loose and flabby for resonance;
or there may be ossification under the basilar membrane, as has
been found by Shambaugh to be the case under the narrower
end of the basilar membrane of the pig's ear.   Various other
conditions may be responsible for the lack of sympathetic reso-
nance in the white rat's cochlea, but it is useless to speculate on
them further.   It is sufficient, in our present ignorance of the
real nature of the rat's cochlea, merely to set the hypothesis
so as to direct the attention of anatomists to matters which are
crucial and which have not infrequently been overlooked in
anatomical investigations.

If there are no structures in the white rat's ear suitable to
serve as resonators periodic vibrations will have very slight
stimulating effect.   Noises coming with richer and more irregular
pulsations would therefore be audible even though tones are
inaudible.   It would be interesting to try periodic vibrations of
very low frequencies, near man's lower limit.   The intensity of
all tones should be as great as possible.   Miss Barber used as
a control an interrupted organ pipe without, I believe, giving
the period of interruption.   Further experiments along this line
with various frequencies, both of the interrupted tones and of
the interruptions themselves, might give significant results   The
periods of interruption should doubtless be below the frequency
of the lower audible limit.   Noises of a slightly different kind
from those used might be produced by the irregular striking of
the keys of the piano or organ.   Can the rat be made to respond
to such " noises "?

Even the results already obtained on the white rat, indicat-
ing certainly considerable difference in the perception of noises
and of tones, will present difficulties of no small importance to
non-resonance theories of hearing.

A CUBAN CHIMPANZEE[1]

DR. LOUIS MONTANÉ

Professor of Anthropology at the University of Havana

Translated from the Spanish by C. S. Rossy[2]

In a notable report on " The order of the Primates: an anatomical parallel between man and apes " (Paris, 1877), Broca, in discussing the phenomena of gestation and the evolution of certain parts of the foetal membranes in the Primates, states that in this connection one can say very little about the anthropoid apes, because these animals do not reproduce themselves in captivity, and that " the little that is known of them has been observed from some female killed while in gestation." For this reason, the procreation and birth of a chimpanzee in Cuba constitutes a scientific event worthy of registration in the annals of natural science. According to our knowledge, it is the first time that an anthropoid ape has been born in captivity. The following data have been obtained concerning the family of the anthropoid ape to which we refer.

Jimmy, the father, came from London to Havana in 1914. This adult chimpanzee, 11 to 12 years of age, measures in height 1 meter and 13 centimeters. He is irascible and wild.

Cucusa, the mother, an adult chimpanzee from Sierra Leona, 12 to 14 years of age, is a beautiful specimen of anthropoid ape. She measures 1 meter and 30 centimeters, and her thoracic perimeter reaches 90 centimeters. Cucusa had previously indulged in amorous relations with Chimpí, a chimpanzee which lived in the park of the "Quinta Palatino," the estate of Dona Sra. Rosalia Abreu, from 1904 to 1914. He was a notable anthropoid on account of his intelligence. Because of certain intimate abnormalities of his physical constitution, Chimpí had no succession. He died at the age of 14 years as the result of acute myelitis, according to the reliable data revealed at an autopsy made by Dr. Raimundo Menocal.

[1] A paper read before the Cuban Society of Natural History, " Felipe Poey," on October 30, 1915.

[2] In this translation a few paragraphs which lacked scientific value have been omitted. The original article was published by *El Siglo* XX, Havana.

Lastly, the young chimpanzee, product of the relations between Jimmy and Cucusa, was baptized with the name of Anumá (a Simian divinity of India). It was born on the 27th of April, 1915, a date from now on memorable in the calendar of births of anthropoid apes.

About Jimmy I have very little to say, except in reference to the original posture that this ape takes in the act of reproduction. It is known that even in their most intimate acts the apes show the least possible modesty; and, due to this peculiarity, observers have been able to be present during the act of generation, *coram populo*, and to witness the classic position, *more canum*, in this interesting species of animals. Jimmy, however, presents an exception to this classic position. When this master and lord of the cage experiences ardent desires of possession (and this happens very frequently), he sits on the floor, stretches his legs out close to each other, and strikes the floor with the dorsal side of the hands, the fingers relaxed. This signal must be well known to the female, because, whenever she is surprised by it, she turns her head and, without the slightest vacillation, very passively comes to the male, who is waiting in the posture already described. Then she turns her back to him and sits on his thighs, opening her legs at the same time that she executes a movement of inclination towards Jimmy's feet,—prostrating herself, in other words, in the attitude of a Mussulman praying. During the act, the female remains passive until the end, the male assuming all the active part of the function.

With regard to Cucusa, pregnancy was first suspected in the month of August, 1914, because, at the catamenial period, the genital turgency was moderated while there was also a decrease in the flow of blood. These symptoms were significant, as it is known that at these periods the development of the external genital parts reaches a voluminous size. During this period also, Cucusa's usual joviality disappeared; at the same time, she was losing appetite, showing a certain dislike for food, which was expressed sometimes in actual vomiting.

Soon there could be no doubt as to her true condition, as the mammary glands were becoming more prominent and the abdomen was showing already a sensible volume; furthermore, all signs of catamenia disappeared during the last three months of pregnancy.

This last fact definitely settles the doubt expressed by Broca in his report on the order of the Primates: " Regarding the anthropoids, the question of the catamenial flow has remained doubtful up to the present time, as there has been no occasion to study female adults in captivity." Cucusa, in her normal condition, sometimes has had very abundant losses of blood. Another fact which should be mentioned, being of interest to naturalists, is that, contrary to what is observed in the case of most mammals, sexual relations between Jimmy and Cucusa continued during the whole period of gestation, both day and night.

Finally, nine months after the first visible symptoms were observed, Cucusa gave birth to Anumá on the 27th of April, 1915. This event established the duration of gestation of the anthropoids, which up to the present has been unknown, al- though suspected to be approximately as long as we have in- dicated.

———————

The parturition of the anthropoid ape must have taken place between 5 and 6 o'clock in the morning, as at 6 o'clock the young ape was first noticed, resting on the contracted legs of the mother and still joined to her by the umbilical cord. His body was completely hairless, with the exception of the head, on which hair was abundant. His eyes were wide open and his gaze indicated bewilderment.

The attitude of the mother at the moment of birth escaped observation. Nevertheless, everything has led us to believe that the obstetric posture of Cucusa was a crouching position, as is the case among other apes.

At 7 o'clock in the morning the umbilical cord appeared sepa- rated from the mother, but still adherent to the umbilicus of the young chimpanzee. No one assisted in the severing of the umbilical cord. The placental extremity, together with pieces of the membrane and two clots of blood, was found on the

mattress on which the mother was lying. In one of these clots, the eminent histologist of the faculty of medicine, Dr. Valentín Castanedo, discovered a placental cotyledon, which was shown in the preparation presented to the " Sociedad Poey." It is regrettable that we have not been able to obtain the placenta in this case, as very little is known concerning the placentae of the anthropoid apes.

(The author here quotes a statement from Madame Louise Toussaint[3] regarding the custom among apes of eating part of the placenta after parturition, and then severing the umbilical cord.)

Bouchacourt[4] emphasizes the fact that all animals after parturition eat their placentae, just as the birds eat the shells of the eggs after the hatching of the young.

We are, therefore, led to believe that Cucusa ate the placenta, as all other apes (monkeys) have done which have given birth to young in the park of the " Quinta Palatino."

During the first two days after parturition, Cucusa, somewhat fatigued, often lay down on her back. She lost very little blood. From the third day, she could easily climb to the board which was fastened high above her bed and which served as a resting place. Lactation began on the second day. Sixteen days after birth, that is, on the 13th of May, there was a normal return of catamenia with an abundant flow for twenty-four hours, but without external genital turgency.

The umbilical cord, dry and flattened, continued to adhere to Anumá for approximately thirty-six hours after birth. We took care to preserve it and find that it measures 70 centimeters. Through the examination of Dr. V. Castanedo we have learned that it contains the normal human constituents.

When Anumá was two months old four incisors appeared, two in the upper jaw and two in the lower jaw. During the third month the remaining incisors developed and, during the fourth month, four molars followed.

Anumá is at present six months old and measures in height 53 centimeters. The circumference of the head is 33 centimeters and the thoracic perimeter is 37 centimeters.

[3] Toussaint, Louise. Causeries d'une accoucheuse. Paris, 1910.
[4] Carnot, Dr. Paul. Opoterapia. Paris, 1911.

THE REFRACTIVE POWER OF LENS AND FLUID MEDIA OF THE MAMMALIAN EYE

STELLA B. VINCENT

In the paper on the mammalian eye in this Journal, vol. 2, p. 249, there are errors in the figures for the refractive indices. Mr. H. M. Johnson has kindly called my attention to this and I am very glad to give the corrections. The figures for the lens were omitted from the table and the confusion is caused by misplaced headings. The refractive figures for the horse have been shifted to the raccoon and this is also true of the description of the sensitive area of horse in column three. For fear that there might be other errors I have carefully verified all the factual material in the tables from the original articles. The figures below as they should have appeared in the original table are taken from Gustav Freytag, Die Brechungsindices der Linse und flussigen Augenmedien bei Katze und bei Kainichen, *Arch. f. verg. Opth.*, 1910, Vol. 1.

	Refractive Index Aqueous Humor	Refractive Index Vitreous Humor	Refractive Index Lens
Ape..................	1.33322	1.3338	1.4245 (Matthiessen)
Cat..	1.33009	1.33006	1.4465 (11 mos.) 1.4514 (7 yrs.)
Dog.................	1.3349	1.33483	1.4498 (1.25 yrs.) 1.4666 (15 yrs.)
Horse..............	1.33378	1.3338	1.4338 (10-12 mos.) 1.4484 (22 yrs.)
Rabbit.............	1.33069	1.33045	1.4174 (9 days) 1.4652 (5.50 yrs.)

REACTIONS OF PARAMOECIUM CAUDATUM TO LIGHT

A. C. WALTON

Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College. No. 279

The experiments of Engelmann, Jennings, and Mast have demonstrated that Paramoecium shows neither orienting nor directive responses to light. Mast (1911, p. 134), who has recently studied this question with care, makes the following statement: "At noon on a perfectly clear day in July I arranged a double convex lens 10 cm. in diameter so as to focus the direct rays from the sun on a slide under the microscope. The light was passed through distilled water in order to cut out the heat rays. The light at the focal point was at least 500,000 ca. m. in intensity. This extremely intense light was repeatedly flashed upon the Paramoecia as they swam about under the microscope, but there was no evidence of any response whatever. It is altogether probable, then, that the power to respond to light is not common to all protoplasm."

The above statement and that of Engelmann, that Paramoecium bursaria, a species containing chlorophyl, is positively responsive to decreases of light intensities only when the oxygen content of the water is below normal, have seemed to me to allow further work along the line of intensity reactions in Paramoecium. The investigations of Hertel (1904) and of Oettli (1910) have shown that Paramoecium is responsive to ultra-violet rays and to heat rays. Why may it not react to visible rays whose wave lengths are between those of ultra-violet and heat?

Apparently no work has been done on the activating effect of such light stimuli on the ciliary apparatus of Paramoecium, though much has been done on the directive and orienting effect of such stimuli. If different light intensities do cause an increase or decrease in the ciliary motion of Paramoecium, it might be exhibited in either of two ways, or by a combination of the two:—(1) by causing increased or decreased rapidity in the beating of the cilia, driving the animal along its normal spiral pathway at different rates of speed; (2) by widening or narrowing the curve of the spiral and hence decreasing or increasing the forward advance of the animal while the rate of motion is unchanged; or (3) by a combination of a change in the rapidity of the ciliary action and a change in the diameter of the spiral pathway. With the view of testing out these possibilities, the following investigations were undertaken under the direction of Dr. G. H. Parker, to whom the writer wishes to express his thanks and appreciation for the careful supervision of the results embodied in this article.

The animals used were all Paramoecium caudatum, obtained from sixteen different cultures, and kept under varying conditions of light. Individuals from three cultures that contained conjugating lines were used at the same time as those from non-conjugating lines, and careful records were kept to see if the physiological factor was in operation. Some cultures were kept in darkness for twelve hours preceding the trials, while other cultures were exposed to day light or electric light for the same period. The animals were placed in a hanging drop of water one-half inch in diameter and so arranged on the stage of the microscope that all light rays except those coming through the condenser were entirely excluded. The observations were conducted at a magnification of 25 diameters and camera tracings were carefully made of the paths of the animals during their exposure to the stimulus. The observations were all for a period of one-half minute and the traced paths were carefully measured with a planimeter. The stimulus consisted of a 32 c.p. Mazda bulb mounted on a sliding base and the intensities of the stimulus varied from 5 to 1422 candle-meters, gained by moving the light through the space between a point 15 cm. and another 250 cm. from the microscope. A cooling stage, through which cool distilled water was run, was used to prevent

heating.   The experiments were carried on in a darkened room so that the only possible light rays were those from the electric light used to illuminate the animal.

The size of the hanging drop was such that the path of the animal was very free from the sudden swervings due to hitting the boundaries of the drop.   At least one minute was always allowed, for the purpose of overcoming the mechanical stimulation due to the transfer of the animal to the hanging drop, before any measured observations were taken.   Some series were made in which the maximum stimulus was the first used and then the intensities were gradually decreased until the minimum intensity was reached.   Other series were run in the opposite direction, while a third set consisted in sudden jumps from one extreme intensity to the other.   All records were made in a room in which the temperature was always between 21° and 22° C.

The experiments were first made with the object of measuring the possible effect of the various light intensities upon the width of the spiral pathway.   Animals were placed either in water or in weak gelatin solutions, which slightly retarded their speed, and careful measurements of the widths of the spirals, under various intensities of light were made.   There was no measurable difference in the width of the spirals, no matter what intensity of stimulus was used, but a measurable change in speed was found, which must have been due to a change of ciliary activity in response to a change in the stimulus.   The greater the intensity of the light used, the faster the animal moved, hence the greater the ciliary activity.

The distances of the light from the hanging drop and the corresponding intensities of the light were as follows:—

Distance in cm......	15	25	50	75	100	125	150	175	200	125	250
Intensities in C. M..	1422	512	128	58	32	20.5	14.2	10.5	8	6.5	5.1

The average rate of speed of the animals in response to each intensity, irrespective of conditions preceding the trials as regards the light environment, and including animals from both conjugating and non-conjugating lines, was as follows:—

Intensities in C. M..	1422	512	128	58	32	20.5	14.2	10.5	8	6.5	5.1
Average velocity in cm. per min.	8	7.95	6.95	6.35	6	5	4.75	4.50	3.75	3.5	3

These averages are based on the results of 500 trials at each of the eleven intensities of light and contain the individual records that do not harmonize with the final conclusion, namely, that a higher intensity of light is accompanied with a higher rate of locomotion. In a series of 200 trials, animals were started under the highest intensity of light and carried through each intensity to the opposite extreme and back to the starting point. In a second test a similar course was run except that it started and ended with the lowest intensity of light. The results of these two series are shown in the form of curves of response in Fig. 1, in which the intensities are plotted as abscissae and the distances in centimeters per minute as ordinates.
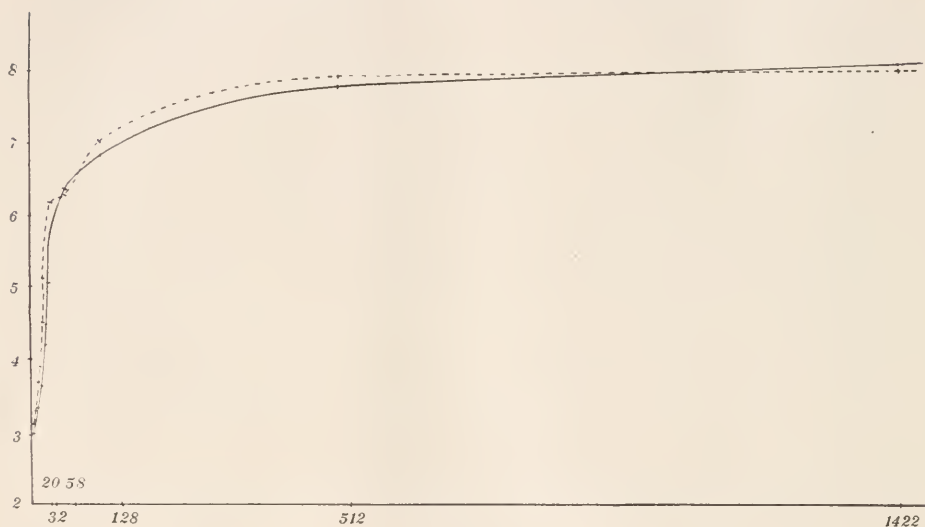
FIGURE 1

The heavy line represents the curve of response for the animals that began at the lowest intensities and the broken line that for animals which began at the highest intensities. These two curves practically coincide, thus showing, among other things, that the mechanical stimulation of placing the animal in the hanging drop did not cause an abnormal movement at the beginning of a series of trials.

Trials were also made in which the stimulus was changed suddenly from one extreme to the other. The response of the animals in such cases was different from that which the pre-

vious work had led me to expect.. In the beginning no change in the response of the animal to the increase or decrease of the stimulus was observable. The rate at which the animal had been traveling before the change in stimulus was made, was continued, and this lasted sometimes for as long as two minutes after the change had been made. If, however, the new stimulus was maintained for a longer period, a change in the rate of locomotion was noted, and gradually the response became the one found to be normal for the given intensity of stimulus. This slowness of response to sudden changes of the light may perhaps account for the fact that former observers have not noted the increased speed of Paramoecium in response to an increase of the light stimulus.

Another curious fact was observed in the behavior of animals that were undergoing conjugation. In such cases about 40 per cent of the animals were entirely irresponsive, or only very slightly responsive, to any change in the intensity of the light stimulus. Often the difference in response was noticeable only when the records for the two extremes of intensities were compared. In non-conjugating lines only 10 per cent of the individuals were poorly responsive to changes in the intensity of the light.

In 2 per cent of the animals tested there was found negative, or rather inhibitory, response to increased light. The greater the intensity of the light, the slower the locomotion until at the upper limit (1422 C. M.) practically all movement ceased. The power of motion was slowly regained as the intensity of the light was decreased.

There were no differences found between the responses of the animals kept in daylight, in electric light, or in darkness for the twelve hours preceding an experiment.

Both fresh and stagnant water were used in order to ascertain whether the amount of oxygen present has any effect on the activity of Paramoecium, but no such effect could be detected.

Although the light was also used to illuminate certain portions of the field to a greater extent than other portions, there was absolutely no evidence in the motions of Paramoecium of a directive or an orienting effect of this unequal lighting.

The conclusions that I have been led to in this study of the reactions of Paramoecium in response to increases and decreases of the light are as follows:—

(1) In 55 per cent of the animals from conjugating lines and in 85 per cent of the animals from non-conjugating lines tested, there was increased rate of locomotion in response to increased light intensity.

(2) In 2 per cent of the animals tested the response to increased intensity indicated inhibitory influence; the greater the light intensity, the slower the locomotion.

(3) In 40 per cent of the animals from conjugating lines, there was no response, or at best a feeble one, to any change in the light intensity. This fact points towards the conclusion that the physiological state of Paramoecium at the time of conjugation is such that the threshhold of light stimulation is raised beyond the intensities used in these experiments.

(4) No evidence was found that the amount of light to which the animals had been exposed before the tests had any effect on the subsequent response to the stimulus.

(5) Responses to sudden changes of intensity in the light were only gradually effected.

(6) Paramoecium responds in essentially the same way to the same intensity of stimulus, irrespective of the previous intensity to which it has been exposed, provided only that it be given time to adjust itself to the new condition.

BIBLIOGRAPHY

ENGELMANN, T. W. Ueber Licht- und Farbenperception niederster Organismen.
1882. *Arch. f. d. ges. Physiol.*, Bd. 29, pp. 387-400.
HERTEL, E. Ueber Beeinflussung des Organismus durch Licht, speziell durch
1904. die chemisch wirksamen Strahlen. *Zeit. f. allg. Physiol.*, Bd. 4, pp. 1-43, Taf. 1.
JENNINGS, H. S. On the Motor Reactions of *Paramecium*. *Science*, N. S., Vol.
1899. 9, pp. 367-368.
1900. The Behavior of Unicellular Organisms. *Biol. Lect., Mar. Biol. Lab. Woods Hole*, 1899, pp. 93-112.
1901. On the Significance of the Spiral Swimming of Organisms. *Amer. Nat.*, Vol. 35, pp. 369-378, 11 figs.
1904. The Behavior of Paramecium. Additional Features and General Relations. *Jour. Comp. Neur. Psych.*, Vol. 14, pp. 441-510, 17 figs.
1904[a]. Contributions to the Study of the Behavior of Lower Organisms. *Publ. Carnegie Instn.*, Washington, No. 16, 256 pp., 81 figs.
1906. Behavior of the Lower Organisms. New York, 8 vo., 366 pp.
MAST, S. O. Light and the Behavior of Organisms. New York, 8 vo., xi+ 410 pp.
1911.
1911[a]. The Effect of Light on the Movement of the Lower Organisms. *Scient. Amer. Suppl.*, Vol. 72, pp. 77-78, 4 figs.
OETTLI, M. Kleine Schulversuche. Die Thermotaxis der Paramaecien. *Monatsch.*
1910. *nat. Unterr.*, Bd. 3, p. 508, 1 fig.

A CRITICISM OF THE TROPISM THEORY OF JACQUES LOEB[1,2]

W. von BUDDENBROCK

Heidelberg University

CONTENTS

INTRODUCTION

There are two classes of biological investigators. One is concerned with *facts;* the theories which are based upon known facts serve him only to explain facts, to condense them into some general aspect, so that a deeper insight into the meaning of the whole problem may be gained. Even when his work lies along theoretical lines, to him facts are of the first importance. Should a fact be discovered which contradicts the theory, then the theory must suffer.

To the other kind of investigator the insignificant isolated facts are of no importance. His soaring mind desires universal recognition for the results of his achievement. The glittering *theory* is everything to him, the facts only its servant. If the fact does not suit, then it will be forced into the Procrustean

[1] The literature of the whole subject may be found in Loeb's paper: Die Tropismen, in Winterstein's Handbuch der vergl. Physiologie, Bd. 4, 1913.

[2] The original text of this paper is published in the *Biol. Centralblatt*, Bd. 35, Nr. 11, 1915.

bed of the theory or else so superficially studied that at first one is hardly aware of the discrepancy which lies deeper.

The crowning example of a theory which exerts such tyranny over facts is the so-called *tropism theory*, whose principal supporter is J. Loeb. To the criticism of this theory and, if possible, its refutation, the following pages are devoted.

The tropism theory has already been criticized by various writers (Jennings, Radl, etc.). They, however, always content themselves with pointing out that certain isolated cases do not harmonize with the theory. The most important general arguments have not yet been presented. Besides this, in his last publication in the Handbuch der vergleichenden Physiologie of Winterstein, 1913, Loeb shows that these criticisms have not affected him in the slightest degree, for he still reiterates the same opinions. For this reason a further investigation of the subject seems justified.

The word *tropism* denotes only a simple fact of observation. Many lower animals have the peculiarity of either creeping in a straight line away from or toward a source of energy, or a point from which light, heat, chemical energy, etc., radiates, or of choosing a path which is at right angles to the energy rays. These movements of orientation, which are also present in the lower plants, are termed *tropisms*, and are further known as photo-, chemo-, thermo-tropism, according to the kind of energy. Such lower animals can be drawn in a definite direction just as surely as a physicist can deflect a magnetic needle; and their behavior, giving so strongly the impression of being purely physical, has led the fathers of the tropism theory to regard the whole phenomenon as something very simple, whose solution may be found without any regard to the complicated structure of the organisms themselves.

To show how such an attempt has been made, the positive heliotropism of the winged aphid is cited, using Loeb's own words. He writes: " Two factors determine the progressive movement of animals under these conditions. One is *the symmetrical structure of the animal* and the second is *the photochemical action of the light.* * * *

The symmetrical structure of the animal is expressed anatomically in that, as is well known, the right and left body halves are symmetrical. But in my opinion, such symmetry exists not

only in an anatomical sense, but in a chemical sense; by which I mean that *symmetrical body regions are chemically identical* and have the same reactions, while *asymmetrical body regions are chemically different*, and in general have quantitatively or qualitatively different reactions. * * * If now more light falls on one retina than on the other, the chemical reactions also, for example the organic oxidations, will be more accelerated in one retina than in the other, and correspondingly greater chemical changes will occur in one optic nerve than in the other.

This inequality of the chemical processes spreads from the sensory to the motor nerves and finally to the muscles with which the latter are connected. We conclude from this that with an equal illumination of both retinas the symmetrical groups of muscles of both body halves are influenced chemically in the same way and so are in the same state of contraction; while, if the reaction speed is unequal, the symmetrical muscles on one side of the body are in greater activity than on the other side. The result of such unequal activity of the symmetrical muscles of both body halves is a change in the direction of the movement of the animal.

This alteration of the direction of the movement can either cause the head to turn toward the source of light, so that consequently the whole animal moves in the direction of the source of light; or else to turn the head in the opposite way and the animal moves in the opposite direction. * * * As soon as this has happened the two retinas are equally lighted and the (symmetrical)[3] muscles in both body halves once more work with the same strength. In consequence there is no longer any reason that the animal should deviate from this direction to one side or the other. It is therefore automatically led to the source of light. The will of the animal, which in this case dictates his direction, is the light, as it is gravity in the falling of a stone or the movement of the planets." (1909, pp. 9-14.)[4]

Jennings has aptly termed this theory, the *"theory of local actions,"* because it does not regard tropism as a movement of the animal as a whole, but as a movement of both *body halves,* which work against each other. This we must remember as an

---

[3] Italics and (symmetrical) added by the present author.

[4] Loeb, Jacques. Die Bedeutung der Tropismen für die Psychologie. Vortrag gehalten auf dem VI. Internationalen Psychologenkongress zu Genf. 1909.

important characteristic of the tropism theory, and also, that in direct consequence of this, according to the theory, the turning of the animal must always be around an axis which lies in the plane of symmetry that separates the two body halves.

A second, perhaps even more important characteristic of the theory is the complete *disregard of special structure*, which simply does not exist for Loeb and his followers. We need know only that the organism is symmetrical,—the theory is just as applicable to protozoa or larvae of the simplest structure as to the most complicated Metazoa—and that the organism reacts to the particular energy; all else accounts for itself. Whoever reads Loeb's writings might readily conclude, from different expressions that are found here and there throughout, that he is fighting against the conception that regards the actions even of the lower animals as voluntary acts of the will, and *denies that they are involuntary*. This, of course, is not the case, and is meaningless. Involuntary action is an undeniable fact of observation, which expresses itself in the phenomenon that under definite conditions all individuals of a species do the same thing; no one questions the existence of involuntary action, even though he may hold the view that not all the actions of the lower animals are involuntary.

Loeb has rather set himself the task of explaining *the mechanism of this involuntary action and by factors that work mechanically*. He attacks those who would explain the action by other means; above all he objects to the conception of tropisms—and especially of reflexes—as *originally individual actions which have shown themselves to be useful and in the course of time through habit and inheritance have become mechanical and involuntary*.

For a thorough understanding of the following criticism this view of Loeb's must be kept clearly in mind.

OUTLINE OF THE ARGUMENTS AGAINST THE TROPISM THEORY

To refute the tropism theory three lines of argument will be advanced:

1. We shall first show that the theory cannot explain all tropisms, for two reasons, (a) in many cases the necessary condition premised by the theory—namely, energy rays—may be absent, and yet actual tropisms occur; (b) in other cases, al-

though the necessary conditions are present, the tropisms occur in a way that openly contradicts the theory.

2. In the second place, it will be shown that even in cases which are apparently in agreement with the theory, the theory cannot furnish an adequate explanation of the tropisms.

3. Finally we shall set forth certain arguments which must be brought against the theory on biological grounds.

The examples that are used in the following arguments deal exclusively with heliotropism and geotropism, for to these belong the most numerous and the most exact phenomena of the whole subject. Whether chemotropism and especially thermotropism belong at all in this category is doubtful, in my opinion; galvanotropism certainly is a pure laboratory product, which for the biologist is of no interest, in so far as he wishes to study the animal, and not merely the chemical properties of protoplasm.

CASES OF TRUE TROPISMS IN WHICH THE CONDITIONS PREMISED BY THE THEORY ARE ABSENT

Tropisms without rays of energy.—I repeat again that by tropism is understood an involuntary movement definitely directed with respect to a source of energy. Such a phenomenon, notably, is the geotropism of certain aquatic invertebrates. It is either positive, making the animal creep perpendicularly downward, or it causes a horizontal movement, (diatropism) at right angles to the axis of gravity, the result of which for the organism is the so-called maintenance of equilibrium. In the majority of these cases, and to these we shall confine ourselves, the geotropism is bound up with definite sense organs, the so-called *statocysts*, with whose structure I shall assume the reader to be acquainted. It has been shown that their function depends directly upon the fact that the heavy statolith exerts a mechanical stimulus upon the sensory epithelium of the statocyst. The whole action of the apparatus, which is to bring the animal into a definite position with respect to gravity, then takes place because this mechanical stimulus acts in a direction determined by gravity, in consequence of the moveability of the statolith, which always seeks the lowest point in the wall of the statocyst cup. The theory of statolith pressure is demonstrated by Kreidl's famous experiments with iron statoliths in crustacea, by which he showed with a magnet that the movements of the

animal differ according to the direction from which the attract-
ing force comes.   Prentiss[5] and I[6] have further shown that the
loss of the statoliths alone has the same effect as the loss of
the whole organ.[7]

There is here absolutely no such *action of energy on the living
tissue* as the tropism theory requires; the energy acts upon the
lifeless statoliths, and the whole phenomenon belongs in the
category of mechanical stimuli, and consequently is excluded
from Loeb's scheme.

Other phenomena that are often cited as tropic movements
that take place without the conditions assumed as necessary by
Loeb, but which are normal in other respects, are the clearly
defined avoiding reactions which infusoria exhibit toward harm-
ful stimuli.   When a number of these animals, for example,
Paramoecium or *Stylonych a*, are placed under a cover glass the
phenomena of chemo- and thermotropism may be readily studied,
as many textbooks state, and in green species heliotropism is
often manifested.

But since these animals are entirely asymmetrical in struc-
ture, the tropism theory is not applicable to them, because it
presupposes two symmetrical body halves or a radial plan;
so that these may be cited as further examples in which tro-
pisms occur without fulfilment of the required conditions.   The
method, however, by which the infusoria avoid the harmful
stimuli is not a swimming in a straight line away from the
source of energy, but the making of so-called *trial movements*.
These are, therefore, not true tropisms, as I would emphasize
in agréement with Loeb against Jennings, so that these cases,
like most trial movements, cannot well be used in criticism of
Loeb's theory.

[5] Prentiss, C. W.   The otocyst of decapod crustacea.   *Bull. Mus. Comp. Zool.*,
Harvard, Vol. 36, 1901.

[6] v. Buddenbrock, W.   Ueber die Orientierung der Krebse im Raum.   *Zool.
Jahrb., Abt. f. allg. Zool. u. Physiol.*, Bd. 34, 1914.

[7] According to E. P. Lyon the case is different in certain fishes, since here, when
the statoliths are carefully removed without injuring the sensory epithelium, no
resultant loss of function is observed.   The accuracy of this observation seems
doubtful to me, because blood clots, which are almost unavoidable in the statocyst
cup, apparently may assume the rôle of the statoliths.   For our present discus-
sion, however, the fish behavior is immaterial, since we have only to show in this
case that *certain* geotropisms, not all, belong in the category of mechanical stimuli.

CASES IN WHICH THE PREMISED CONDITIONS OF SYMMETRY AND
OF ENERGY RADIATION ARE PRESENT, BUT THE MOVEMENT
TAKES PLACE IN A WAY THAT IS CONTRARY TO
THE TROPISM THEORY

Sidewise movement of crabs. — Three examples only will be
cited of tropisms that take place in a manner that is contrary
to the theory. The clearest of these, already discussed by
H. S. Jennings, is the sidewise movement of crabs. The facts
may be stated in a few words: If a crab is stimulated in any
way, for example, by a strong light and from one side only,
there is *no* turning of the animal until its axis of symmetry
coincides with the ray of light, as the tropism theory requires,
but at once the crab moves sideways away from the light. This
cannot be explained at all by Loeb's theory; it shows, rather,
in the clearest way that the light does not act separately upon
the two body halves, but upon the body as a whole, and, in
consequence, a harmonious activity of all organs of movement
is the result. Loeb, indeed, makes some objections to this
criticism. He writes: " I am rather inclined to draw another
conclusion, namely, that in the first place, in crabs an entirely
different relation exists between the retina and the locomotor
muscles than in other crustacea and in most animals; and that
in the second place an especial peculiarity exists in regard to
the function of the two retinas, in that these do not behave as
symmetrical superficial elements. There is here, in my opinion,
a new discovery to be made." (1909, pp. 48-49.)

It will be seen later why Loeb suddenly calls to his aid the
special structure that he has hitherto neglected, but it would
be difficult to say that his reply has in any way weakened the
evidence against the theory. In this case an error has certainly
crept into Loeb's reasoning. His explanation means, in some-
what plainer words, that in the crab in supposed opposition to
other crustacea the eye is not only related with the legs of one
side, which causes a turning of the animal, but with the legs
of both sides, which results in another kind of movement. The
real meaning of the tropism theory is not, however, that light
may cause any *desired* movement, but that it does cause a
definite movement, namely, that which leads the animal away
from the light; and, as Loeb himself has emphasized again and
again, this is only possible, in accordance with his theory, when

the movement in a straight line toward or away from the light involves a *symmetrical muscular movement of both symmetrical body halves.* Now the sidewise movement of the crab, although it is a movement in a straight line away from the light, is caused by an *asymmetrical cooperation of both sides,* since, for example, in moving to the right, the legs of the left side push the body so that the extensors are in activity, while the legs of the right side move with the flexors doing the work. This is not explicable by the theory and can only be understood as a purposeful and elaborate corporate action of the animal. The disagreement with the theory could scarcely be greater. The assumption is also untenable that the action of energy upon a symmetrical form is here concealed by some hypothetical second factor. For since the light, if the action takes place according to Loeb's scheme, must cause a turning of the crab, then this second factor, which inhibits the turning, must, when left to itself, cause a turning toward the opposite side. This would mean then that the crab, when not stimulated by light, would move continually in a circle, an evident absurdity.

A second example of a tropism which occurs in a manner that contradicts the theory, in spite of the presence of all the premised conditions, is a peculiar phenomenon which may be observed in the starfish, and in a crustacean, and which I may call *changeable heliotropism.*

If a starfish is brought into a uniformly lighted field in which is a spot of light of different intensity, such as a deep shadow or a brighter light, *in both cases* the animal creeps toward this spot.[8]

Among the crustacea I have observed an analogous phenomenon in *Hemimysis lamornae.* This animal swims constantly back and forth in the aquarium, as far as the space permits, but always in a perfectly definite direction, forward toward the light coming from the window, backward away from it. This crustacean therefore changes the character of its heliotropism with each turn that it makes at the glass wall of the aquarium.

That one and the same animal should show both positive and negative heliotropism is in itself nothing remarkable and in nowise contradicts the theory, it is moreover of frequent occurrence.

---

[8] Plessner, H. Untersuchungen über die Physiologie der Seesterne. *Zool. Jahrb., Abt. f. allg. Zool.,* 33, 1913.

The changing of one kind of movement into another, however, is always correlated with the application of some new stimulus,[9] by means of which the physiological condition of the animal is so changed that the same optical stimulus now produces the opposite reaction. A good and clear example of this is furnished by certain other Mysidae (see footnote 12) which become positively heliotropic after lighting, negatively heliotropic after shading the field. But the change of movement observed in *Hemimysis* takes place *without* any alteration in the physiological stimulation, and in the starfish we see even that one and the same animal may be brought to either a positive or a negative reaction, according to the desire of the experimenter.

Now, according to Loeb's theory, we see in an animal a definite system of chemo-physical forces. When energy of definite constant amount acts upon such a system, the reaction must necessarily be certain and definite, i.e., with similar stimuli and similar physiological conditions in the animal, the movement must always occur in the same way. The case of *Hemimysis* is therefore not to be explained by the tropism theory.

Conversely: If two separate and distinct amounts of energy each compel a definite system of forces to make the same movement, by logic these two amounts of energy should be equally great.

This principle is overthrown by the case of the starfish, which, in the same physiological condition, is attracted by light as well as by shadow. It therefore follows that, either the starfish is not such a system of forces as Loeb assumes, or that the energy acts on the eye in an entirely different manner. What the meaning of the phenomenon is does not concern us here, we are content with the assertion that the cases of changeable heliotropism cannot be explained by the tropism theory.

The impossibility of explaining the turning around the horizontal cross axis. The turning around a horizontal cross axis is a phenomenon which nearly all Metazoa exhibit in their *heliotropic* and *geotropic* movements, and it will be recognized as a third example of tropisms which take place in a manner

---

[9] This need not always be an external stimulus. It is also conceivable that in the course of individual development the physiological condition may be altered by the internal changes that are going on. The behavior of many larvae which, without outward cause, change their heliotropism after a certain age, serves as an example.

entirely contradictory to the theory, although all the necessary conditions of the theory are present. Beginning with the *diahcliotropic* movements of crustacea, it should be noted that many species, marine as well as fresh water forms, always swim with their backs turned toward the light (the " light-dorsal reflex "). They move, therefore, at right angles to the rays of light, a true diatropism. By arranging the lights so that the aquarium can be lighted either from above or from below, a sudden illumination from beneath causes the animal, which has been swimming dorsal side up, to turn over on its back, so that the dorsal surface, now down, is still turned toward the light. This, however, need not contradict the tropism theory, for the elongated crustacea always turn over on their backs by turning around the longitudinal axis which lies in the plane of symmetry. Now, if we assume for the sake of simplicity that the original position[10] is somewhat oblique, the theoretical scheme may be applied as follows: Unlike illumination of the two symmetrical body halves results in a turning of the organism until it reaches the final position, symmetrical with the rays of energy. The short-bodied compressed crustacea, however, behave in a very different manner on account of their structure, turning over on their backs by turning a somersault. The amphipod *Hyperia* always does this, the larvae of *Squilla* very often, and these are only two examples of a very frequent occurrence. Such a somersault utterly disregards all the preconceived rules of the tropism theory in that there is no turning of the body around an axis in the plane of symmetry. There is instead, a turning around a horizontal cross axis *perpendicular* to the plane of symmetry, through which no plane can be passed dividing the body into two symmetrical halves, as the theory requires. It is therefore utterly impossible to bring this movement into harmony with the theory, and yet it is a genuine tropism.

Exactly the same consideration applies to the *diageotropic* movements of those crustacea which swim ventral side up, manifesting the maintenance of equilibrium instead of the " light-dorsal " reflex. The crustacean *Palaemon* may be chosen

---

[10] The reversed symmetrical position, in this case with the plane of symmetry in the direction of the light rays, but with back turned away from the light, presents great difficulties for an explanation by the tropism theory (see p. 352).

as an example. As soon as this animal is removed from its normal horizontal position, with ventral side up, involuntary movements restore the original position. This kind of orienting movement can be reconciled with the tropism theory only when a turning around the long axis occurs. But place the *Palaemon* nearly perpendicular to the surface, and it will recover its normal position by turning around the horizontal cross axis, which, as we saw above, prevents any explanation by Loeb's theory.[11]

These diatropic movements cannot be ignored. They represent typical movements of orientation with reference to a source of energy, and are thoroughly genuine tropisms. Loeb must accustom himself to the idea that, in addition to the sidewise movements of crabs, there is another great category of phenomena which do not agree with his theory.

Without dwelling longer on the examples of diatropic phenomena, which after all, are relatively infrequent, let us consider any organism with positive or negative heliotropism which moves freely in space, perhaps swims. When the source of light is really on one side of it, the animal will conform entirely with the scheme of the theory by turning around a vertical axis which lies in the plane of symmetry, but if the light is either above or below it, then the animal will turn, as any experiment will show, around the cross axis, which is, as we know, contradictory to the theoretical expectations.

We see here once more what the observation of *Squilla* and *Palaemon* has already shown us, that in one and the same animal certain tropisms occur which *seem* to be explained by the theory, together with others which are seen at the first glance to be entirely inexplicable. Surely no one would wish to separate these two movements, the turning around the *vertical*, and the turning around the *horizontal* axis, or to assert that although the first is conditioned by the general laws of the tropism theory, the second requires a very different kind of explanation, namely that of the specific structure of the animal. No! Both movements, which frequently replace each other and can be combined in various ways, are *fundamentally alike*. Since it can

[11] *Palaemon* reacts also after loss of the statocysts, as I have shown, by means of the general position-reflex, which, since we know little about it in detail, may itself be open to explanation by the tropism theory.

be shown that one of these movements has nothing to do with the tropism theory, we shall come to the conclusion that the other, the turning around the vertical axis, is also only *apparently* connected with the tropism theory, but in reality is caused by the purposeful adaptive structure of the organism.

THE IMPOSSIBILITY OF EXPLAINING THE REACTION WHICH RESULTS FROM THE REVERSED SYMMETRICAL POSITION

In the above section we found for the first time an argument that is applicable to all tropisms. The turning around the horizontal axis furnished convincing evidence entirely contradictory to Loeb's theory, but it is different with respect to the turning around the vertical axis. In case that the evidence against the tropism theory already presented should be considered insufficient upon this point, (resting as it does, so far as this point is concerned, on reasoning from an analogy) we will now especially examine these movements, which were apparently the only ones Loeb had in mind. We shall show that even for these movements (of turning round the vertical axis) Loeb's assumption leads to consequences which contradict the facts; this will be shown first for a particular case,—that of the reversed symmetrical position.

If I take any bilaterally symmetrical negatively heliotropic organism and place it as exactly as possible so that the anterior end is turned to the light, the facts of the experiment are as follows: The animal turns itself very quickly through 180°, and swims, flies, or creeps away from the light. Now I ask you to consider that the whole principle of the tropism theory is founded upon the dissimilar action of energy upon both symmetrical body halves. In the present case there is no such dissimilar action, since both sides of the animal are stimulated by the light in exactly the same degree. In consequence, if the relations were actually what the tropism theory assumed, then a reaction would be either entirely lacking, or else would take place very gradually, after the animal had lost its symmetrical position through accidental, small movements. In other words: According to the tropism theory, the position with head turned away from the light for positively heliotropic animals, and that with head turned toward it for negative forms, must be a so-called "dead center" or point of no motion. An indisputable

line of thought, not to be answered by argument, mutatis mu-
tandis to be applied to every kind of tropism.

That a quick and precise reaction always takes place even
in the reversed symmetrical position, as every experiment proves,
can be only explained by the fact that the organism as a *whole*
is sensitive to the unusual position and reacts to it.   On no
account can the reaction be explained by the opposed actions
of the two body halves, for such actions would mutually destroy
each other.   This is the most generally valid argument that
can be brought against the tropism theory and it applies to all
existing tropisms.   The reaction which always may be observed
with the reversed symmetrical position cannot be explained by
any reflex mechanism, at least, very complicated hypothetical
assumptions would have to be made; it shows clearly that even
in the lower animals there are voluntary actions which take
place as a result of unpleasant sensations, or whatever one may
please to call them.

THE IMPOSSIBILITY OF EXPLAINING THE HARMONIOUS COORDI-
NATION OF THE MOVEMENT OF THE TWO BODY HALVES

The argument just presented, that the reaction of the animal
does not depend upon the independent action of the two body
halves but represents a harmonious working together of the
whole organism, applies, not only to the reversed symmetrical
position, but especially to almost every tropic turning around
the vertical axis.   If such a movement took place in accordance
with the scheme of the tropism theory, it might be compared
with a row boat containing two men, one pulling the right oar,
one the left.   If one pulls better or harder than the other, the
involuntary result is that the boat begins to turn.   Both sides
act without coordination and the turning is caused by the *differ-
ence* of the opposing forces of the two sides.   This case corre-
sponds exactly with the tropism theory, and is exemplified even
to the minutest detail in *galvanotropism*.

But there is another possibility for turning the row boat.
Should the oarsmen *intend* to turn around, then one of them
must row harder than before, while the other will either reverse
his stroke to help his partner, or row gently so as not to hinder
him.   This result is also a turning, but it is caused by the *co-
ordinated purposeful* working together of the two sides; in the

first case by the *sum* of both forces which work in the same direction, in the second case by the force of one side alone. *The criterion is that there is no opposed action of the two sides.* This case is exemplified in all tropisms which occur in nature and it evidently cannot be reconciled with Loeb's theory. Some examples will now be mentioned.

The first concerns the diaheliotropic movements of marine crustacea, the " light-dorsal " reflex which has already been described. Two years ago I showed that illumination from one side always produces a sidewise paddling of the swimmerets of *both sides with the same tendency*, a clearly coordinated and purposeful action which it is impossible to explain, or even to obtain, according to the tropism theory. Such an interaction of the musculature of the appendages of both sides may be observed in the entire animal kingdom in almost all movements involving a facing about. Until recently, however, very little interest has been shown in these matters, which are of great theoretical importance.

The second case, in which one side of the body moves while the other remains perfectly still, is naturally rarer. The best known example is the behavior of the Mysidae in response to light stimuli, studied by Bauer[12]. These peculiar animals are positively heliotropic after having been exposed to light, but are negatively heliotropic after shading; in the first case therefore, darkening, in the second case, illumination, is the stimulus that makes the animal try to escape. The escape takes place through the fact that the legs turned away from the stimulus have their movements inhibited, while those turned toward it keep on paddling, so that necessarily a turning away from the place of the stimulus results.

So much for the facts. If we try to find their meaning, it is clear, first, that the result is not unfavorable for Loeb, since *de facto* only those legs react which are connected with the stimulated eye, and therefore the movement *can* be regarded as not coordinated. On the other hand, it must be admitted that the movement, like that of the row boat, can just as well be regarded as a purposeful and coordinated one, since there is no hindering of one side by the other. We find ourselves to some extent on

[12] Bauer, V. Ueber die reflectorische Regulierung der Schwimmbewegungen bei der Mysideen, etc. *Zeitschr. f. allg. Physiol.,* Bd. 8, 1908.

neutral ground in regard to this interesting question.   We cannot prove that the phototropism of the Mysidae is evidence against the theory, but neither can Loeb show that it is evidence in his favor.

THE IMPOSSIBILITY OF FINDING THE AXIS OF TURNING

The three last-mentioned arguments against the tropism theory have been unaccountably overlooked by most critics until the present time.   The same is true of a fourth which will be considered next.

Any bilaterally symmetrical organism that is sensitive to light will serve as an example, but to select one of Loeb's own, let us take the winged aphid.   If this insect is illuminated from the left side only, (meaning that the source of light is neither above nor below, but exactly on a level with it), it will turn immediately and fly in a straight line to the source of light.   This is a very clear case of heliotropism, in Loeb's sense.   Illumination of one side, result: unequal movement of the two sides until a position is reached which is symmetrical with respect to the source of light; finally, flight in a straight line to the light.

Now how much of this can the tropism theory explain?   Evidently, setting aside some considerations to be discussed later, only the point that the two sides of the body move differently. Now from this, logically, a turning of the whole organism around *some* axis lying in the plane of symmetry, xy, must result, which turning continues until the plane of symmetry coincides with the plane xyL (L = point of light).   But that is all that can be obtained from the tropism theory!   The theory does not reveal around which one of the innumerable axes of this plane a turning takes place.   And yet, in order to reach the source of energy, the turning must be around a *definite* axis, namely, one perpendicular to the line joining the organism with the source of energy.   Any theory which deals earnestly with the present problem should explain how the turning takes place around just this one axis, or in other words, how the movement can occur in a few definite flight-muscles out of a great number.   Were Loeb's theory our only resort it would be necessary to assume a miracle to understand how the aphid ever gets to the light.   If point A is the animal, point L the light, and if I assume that the turning required by the theory is ended, and

therefore the line AL lies in the plane of symmetry of the animal, the animal can then assume different positions according to the axis around which it has turned. Consequently, without disregarding the conditions of the theory, it can move, according to the direction of its long axis, along any line running from A out into the plane of the paper, only one of which, AL, leads to the light. There could be no clearer demonstration of the inability of the tropism theory to furnish an explanation which is clearly its function to give. That a direct movement toward the light actually takes place is not to be explained by such physico-chemical assumptions as Loeb makes, it shows rather, that in the interior of the organism is a *purposefully functioning mechanism*, which, in response to the light stimulus, sets the locomotor organs into such activity that a general movement toward the light must follow. The morphological-physiological structure of the animal is consequently responsible for the occurrence of the tropism, and this structure must be investigated in every separate case.

THE DISAGREEMENT OF THE TROPISM THEORY WITH THE PRESENCE OF A REFLEX ARC

The question now arises of the relation of the tropism theory to the special structure of the animal, or in other terms: if it can be shown that the stimulus from the eye traverses a definite path, a so-called reflex arc, how does the tropism theory apply to this fact?

The unprejudiced observer will certainly be inclined to consider that the cause of the tropism is this reflex arc, which somewhat resembles the works of a clock where one wheel clutches another until the hands move, and that any farther explanation of this phenomenon is superfluous.

On the other hand, in looking through Loeb's writings, we are astonished to find that his opinion is quite different. This is most clearly shown in the case of the crab's sidewise movement, the facts of which we have already considered. Jennings having previously made the criticism that the behavior of this animal could not be harmonized with the theory, Loeb replied in the following words, which have already been quoted on p. 347: " I am rather inclined to draw another conclusion, namely, that in the first place, in crabs an entirely different relation exist

between the retina and the locomotor muscles than in other crustacea and in most animals; and that in the second place an especial peculiarity exists in regard to the function of the two retinas, in that these do not behave as symmetrical superficial elements."

He therefore not only does not deny the existence of the reflex arc, but uses it to explain the existence of the phenomenon, and yet he still stands by the tropism theory *in toto*. The solution for this enigma has escaped his recent critics; it will only be discovered by recalling the historical development of the tropism theory which may be told as follows: The phenomenon which shows the peculiarities of tropic movements in the clearest and sharpest manner is undoubtedly *galvanotropism;* the theoretical estimate of the remaining tropisms was then made by analogies drawn from this first phenomenon. Now the relations in galvanotropism are of a very special character. It does not occur in nature and is a pure laboratory product. So far as it is concerned, the animal is no machine with the definite tasks of the maintenance of its own life and the propagation of the species, but is solely a *symmetrical form the two sides of which possess a similar chemo-physical structure.* Expressions like adaptation and function are not needed here, and if a future chemist should ever succeed in producing from inorganic matter an animal like Faust's homunculus, this being would have no relation to function, natural selection, adaptation, etc., but would infallibly manifest the phenomena of galvanotropism. The organism in this case might be compared with a crystal, which does in fact possess a structure, from which on the application of certain energies definite resultant phenomena are manifested, but to which the conception of adaptation would be wholly inapplicable.

The fundamental mistake which Loeb and his followers make is to apply indiscriminately what they find true for galvanotropism to all tropisms that occur in nature. The idea of adaptation is here no empty delusion. If Leob actually denied the statement that *the animal is a machine adapted for self-maintenance and for the propagation of the species,* then no further discussion would be possible, but for his own sake, and for the sake of his reputation as an investigator of nature, I assume that he does not gò so far. If, however, he is prepared to admit

the above statement, then in return we can assure him that we
regard the actions of lower animals just as he does, as involuntary,
and that for the most part we reject any idea of free will; he
must then discuss certain questions with us.

For example: The eye of the heliotropic *Balanus* larva is of
little use in enjoying the beauty of the surrounding scenery; we
assert this because we, like Loeb, deny the larva's higher intel-
ligence and free will. In consequence, we are forced to the view
that the purpose of the eye, for it must have some purpose, is
to enable the heliotropic reflex to take place, at least we know
of nothing else for which the eye might serve. It therefore fol-
lows that the entire reflex arc, which alone it is that makes the
eye capable of functioning, is purposeful. In going so far we
finally cannot escape the view that the cause of the tropism is
just this mechanism of the reflex arc, so adaptive in construc-
tion and in function, and that energy plays no other rôle than
to set the apparatus in motion.

If Loeb replies to this deduction that all tropisms must then
have a biological use, the following is my answer: The contrary
assertion is in no way proved; if in many cases the tropism seems
useless or even harmful for the animal, it is highly probable that
we either do not understand what its use is, for we know pain-
fully little of the normal needs of the lower animals,[13] or it may
be, that during the experiment the experimenter has kept the
animal under unnatural conditions, a case that is only too
frequent.

To condense and recapitulate the foregoing argument: The
facts are, that light, with the help of the eye and the associated
reflex arc, starts a definite movement, of which light is one
condition, the reflex arc the other condition of its occurrence.
No conclusion can be reached from this statement, either for
or against the tropism theory. The latter theory acquires mean-
ing only when to the facts we add a definite definition of the
expression " animal," defining it simply as a form with definite
chemo-physical structure, without any reference to the purpose-
ful nature of its structure. Upon this form, then, the blind
natural orce acts ust as iron upon a magnetic needle, and so

---

[13] A more detailed consideration of this point would carry us too far. I will,
however, call attention to the valuable work of Franz, "Die phototaktischen Er-
scheinungen im Tierreiche und ihre Rolle im Freileben der Tiere," *Zool. Jahrb.,
Abt. f. allg. Zool.*, Bd. 33, 1914.

we get a tropism.   This definition of an animal, however, is false, and, in consequence, so are the conclusions that are drawn from it.

The animal is rather a mechanism of purposeful adaptive construction for the tasks of self-maintenance and reproduction. This is an unassailable truth; therefore it follows that the separate organs, for example, the eye, have a definite purpose, as the adaptive structure of the eye well shows, and even though this eye causes nothing but a heliotropic movement, in the last analysis, the reflex arc which enables the movement to take place must be considered as a purposefully constructed mechanism. Therefore this very mechanism is the cause of the tropism and the tropism theory is entirely superfluous.   This argument refutes the tropism theory so far as those lower animals are concerned whose eyes are only heliotropic in function.

One exception must be made.   In highly developed sense organs the matter is somewhat more complicated.   If, for example, an eye is adapted for perceiving images as well as for allowing heliotropic movements, one might assume that here *image perception alone is the purpose of the eye*, while heliotropism is but one of nature's unintended by-products.

In this case, one might almost assent to Loeb's view, were it not for those arguments already known to us which are based upon the details of the movement, and which entirely refute the theory.   The existence of a reflex arc makes the theory superfluous, at least in many cases, and robs it of any content. Tropism then finds its cause in the *reflex arc* itself.   It can neither be " explained " away nor denied, it is a simple fact of observation which leaves no room for a theory.

In all further cases, where such a reflex arc is not clearly demonstrable, but a nervous system exists which connects muscles and sensory epithelium, it is most probable that only our lack of operative skill prevents us from finding the reflex arc, and that it is perhaps never absent.   This again lessens the theory's right to exist.   I should like to bring such a case under closer consideration because it demonstrates so clearly the entirely unproved assumptions upon which the supporters of the tropism theory depend.   Davenport (1897) writes in regard to the negative heliotropism of the earthworm: "*The sun's rays may fall horizontal and at right angles to its axis.   Then the rays strike it* (*the earthworm*) *laterally or in other words, it*

is lighted from one side and not from the other. Since now the protoplasm of both sides is adapted to an equal amount of light, the side that is least lighted is nearer to the optimum strength of light. Its protoplasm is in a phototonic condition, while the strongly lighted side has lost its phototonic condition. Therefore the darkened muscles are in a condition to contract normally, and the brightly lighted ones are relaxed. *Under these conditions the animal turns toward the darker side. * * *"* " Dichtung und Wahrheit,"—poetry and truth—might be placed as a title above this entire statement. Truth is found only in the italicized[14] first and last sentences. What lies between can only be admired as evidence of a richly endowed imagination, it has no scientific value. We know nothing about what strength of light the " protoplasm " is adapted to. Its phototonic condition is completely hidden from us and consequently also the action of light upon darkened and lighted muscles. What we really know is that in and beneath the epithelium of the earthworm cells are found whose structure certainly indicates that they are sensitive to light, that from them nerves run to the ventral nerve cord, and other nerves from there to the muscle-layer of the skin, further, that the whole tropism ceases if I destroy the ventral nerve cord, so that we may suspect the existence of a reflex arc: epithelial cells sensitive to light, sensory nerves, ventral nerve cord, motor nerves, and muscle layer. Without hesitation I leave it to the reader to decide which of the two possibilities, the reflex arc or Davenport's assumption, is more probable. A certain possibility remains for an explanation in Loeb's sense. Assuming that the criticisms made above are unfounded, and referring exclusively to those cases where no reflex arc is at present demonstrable, then, from this standpoint, the tropism theory is master of the situation.

I wish here to draw attention to two tropisms of this kind (with no demonstrable reflex arc). The *first* concerns the reactions to the stimuli of gravity of such animals as are known to have no statocysts, especially those which still manifest geotropism even after the removal of these organs. The *second* concerns the growth phenomena of certain hydroid polyps which result in placing the animal in the direction of the rays of light.

---

[14] The italics and the words (the earthworm) are the present author's.

In both cases we are entirely unable to analyze the phenomenon if we wish to rest on a basis of *fact*. Nothing is more characteristic of the tropism theory than the fact that it flourishes best in these darkest corners of our knowledge. It is far easier to construct a theory in regard to things of which one knows practically nothing than about things which have been studied thoroughly, for then the theory is in continual danger of being impaled upon the rough edges of facts. These two tropisms would be insufficient to impale the theory were it not for the other arguments which are available as evidence in this case.

THE IMPOSSIBILITY OF EXPLAINING THE PURPOSEFUL NATURE OF TROPISMS

After having considered the arguments against the tropism theory from the morphological side, we shall now take up an argument from the biological side, namely, the purposeful nature of tropisms. It is usual to try to solve the problem of such movements as are seen in tropisms, by considering the structure of the animal as a *given premise*, and by limiting one's self to the movement as determined by certain elements of this structure and by definite external stimuli. The purposeful nature of the movement for the whole organism is then seen as a consequence of the structure. Purposefulness is therefore, wherever demonstrable, also a mere fact of observation, about whose origin we need not trouble further.

Loeb, however, takes an opposite view. For him, the structure of the organism is a negligible quantity which he quite overlooks in reaching after the higher spheres of physical chemistry, the universal panacea of modern investigation. The corner stones of the tropism theory are merely the symmetry of the animal and blind unorganized natural force, e.g., light. If from the interaction of these two factors a truly purposeful action results, it is most astonishing and some explanation is absolutely demanded from Loeb. His only possible means of escape is the selection theory, toward which, by the way, he takes a very peculiar and extraordinary position.

On one hand he denies any value to selection and writes: " Whoever does not want to waste his time in an idle play of words will do well to analyze instinct in the same manner as is done for occurrences in the inorganic realm, where expres-

sions like adaptation and natural selection are demonstrably useless and where the only concern is to make clear the mechanism of the occurrence," (1913, p. 452). I find, however, another place where he openly states: "that species manifesting tropisms which would be incompatible with the reproduction or maintenance of their kind must die out," which is in principle an affirmation of the idea of selection.

Whatever Loeb's position toward Darwin may be, it is certain, whether he admits it or not, that he needs Darwin as an ally, if he intends to explain the purposeful nature of tropisms.

It is all the same to us whether harmful tropisms, the existence of which we can rightfully contest, occur together with indifferent and useful ones, if only the origin of the useful tropisms can be established.

Some examples will now be given of tropisms which serve some purpose for the whole organism.

There are many animals in which the tropism takes the form of a movement of flight to avoid an enemy's attack. Certain species of *Cypris* living in open water are rendered positively geotropic and negatively heliotropic by mechanical disturbances; that is, they seek the deepest and darkest part of the water. On the other hand there are inhabitants of dark localities, which, when disturbed, respond with positive heliotropism, thereby avoiding an animal which is burrowing in the mud.

In other cases the tropism of food getting may be seen. Loeb himself gives as an example the behavior of the young caterpillar of *Porthesia*, which, creeping out of its winter nest can only find the young leaves at the tip with the aid of positive heliotropism.

One case should be mentioned where movements of this kind occur in response to need of air, for example, the water scorpion, *Nepa*, after using up its air becomes negatively geotropic and positively heliotropic,[15] and it thus rises to the surface of the water where it can get a new supply of air. In the same category probably is the positive heliotropism of the Daphnids, described by Loeb, which they manifest when certain acids, especially carbonic acid, are added to the water. This tropism evidently aids the animal in seeking fresher water levels.

[15] Baunacke, W. Statische Sinnesorgane bei den Nepiden. *Morphol. Jahrb.*, *Abt. Anat.*, 1912, Bd. 34.

Finally, there are many cases in which positive heliotropism forces great masses of young larvae to make purposeful movements which scatter them abroad in the water. There are many more examples and they will certainly increase in the future as our knowledge of the mode of life of the lower animals becomes more profound.

How can Loeb, if he stands by the tropism theory, explain the evidently purposeful nature of these tropisms?

The exact course of action in such movements must be considered if one is really to understand them. In the case of the *Porthesia* caterpillar hunger is the conditio sine qua non for the occurrence of the tropism, and this, in its turn, leads the caterpillar to the nourishing leaves. We have here a physiologically harmful condition, which of necessity causes a movement which ends the harm. Hunger is therefore to some extent its own physician!

Few words are required to show that this is evidently not a simple but a very complicated occurrence. If we wish to explain its origin with the help of the selection theory then it must be assumed that an elimination of unfit individuals takes place in two ways. On the one hand, all those caterpillars must perish which do not move directly toward the light but which move in a diaheliotropic manner, and of the selected individuals all must die which manifest the tropism under other circumstances than those of hunger. For should the impulse remain after the twigs are stripped bare death must surely follow.

In both these cases the survivors would be only a small minority, and with such a decimation it would be astonishing if there were any *Porthesias* left.

Discussions of the selection theory never lead to an entirely certain conclusion, but always to probabilities. I believe I have shown that in our case the possibility of an explanation by selection is very slight. It will naturally be even slighter if we consider combined tropisms like those of the water scorpion and the *Cypris*. Loeb has not concerned himself in any detail with the problem of the purposeful nature of tropisms. But it is not without amusement that we note that he, who regarded the consideration of the question of selection as " a loss of time in an idle play of words," should be forced to an ultradarwinian conclusion by a logical analysis of his own theory.

SUMMARY AND CONCLUSIONS

The tropism theory is not applicable to all tropisms for the following reasons:

1. In many cases the conditions premised by the theory are absent, and yet true tropisms, that is, involuntary movements regulated by a source of energy, take place. Example: The *action of energy* in geotropism *is lacking* in so far as it is connected with the presence of statocysts. The movement is the result of a mechanical stimulus caused by the statoliths.

2. In many cases, although the conditions premised by the theory are present, the tropisms take place in a manner that contradicts the theory. Examples: (a) Sidewise movement of crabs; (b) changeable heliotropism of certain marine animals; (c) turning around the horizontal cross axis not in the plane of symmetry, to be observed in all tropic movements.

There remain now, as possibly to be explained by the theory, only those cases in which *symmetrical animals manifest a turning around the vertical axis*. But here also the theory is unsatisfactory, because:

3. The theory cannot explain the reaction which results from the position of reversed symmetry.

4. The theory cannot explain the coordinated working together of the two sides of the body.

5. The theory cannot tell why the turning always takes place around the axis which is perpendicular to the line joining animal and source of energy; in other words, it especially cannot explain how the animal finds its way to the source of energy.

6. The presence of a reflex arc in many cases renders the theory entirely superfluous and without meaning, for the movement is already satisfactorily explained by the reflex arc itself.

7. The theory cannot explain satisfactorily the undeniably purposeful nature of many tropisms.

On the other hand, one positive result of our investigation is that wherever tropisms occur a purposeful adaptive mechanism for movement is found which has the task of guiding the animal to the source of energy, and that during the movement the organism always acts as a whole. We shall therefore adhere to our old opinion that tropisms, like all other reflexes, were originally individual actions, which, in the course of time, have become mechanical and involuntary. This view will not con-

tent everybody, for it requires the acceptance of certain un-
proved assumptions, but at least it is not contrary to facts.

It seems to me of the utmost importance that tropisms should
not be taken out of the class of other reflexes. If we observe
the reactions of the animal to light, from the simplest sensory
reflex up to image perception there is a continuous chain of
increasingly complex reflexes, whose common attribute is that
with the light stimulus definite muscles become active. Phy-
siologically, therefore, these movements are all alike; it is con-
sequently inadmissable to explain some of them in a way that
contradicts what is true of all the others.

It is hoped that the arguments here brought together will be
sufficient to make the tropism theory disappear from zoological
literature.

The theory is useful only in so far as it shows that the appli-
cation of the inorganic sciences to the problems of biology is
of very limited range.   I do not wish to be misunderstood upon
this point.   There are certain problems, and many of them of
great importance, which can only be solved with the aid of
chemistry and physics.   But such problems always concern
merely the study of *single organs*, perhaps of muscle, which is
evidently a chemical energy-machine, or of the alimentary
tract, which represents a chemical manufactory.   Here and in
a thousand analogous cases, with which naturally the physiology
of the senses belongs, the physical chemist finds a rich field of
activity.   Just as soon, however, as we observe many organs
working together, whether in a system of organs or in a whole
organism, we are confronted everywhere, in the morphological
structure as well as in all physiological processes, or the so-
called " psychic " actions of the animal, by *adaptations of pur-
poseful nature*. Whoever denies this, only shows that he is
insufficiently acquainted with facts. Purposeful structures,
however, cannot be explained by physical chemistry.   The
chief fault of Loeb and his followers is that they have overlooked
this point.

We have found it universally true that in all tropisms the
fundamental mechanism of movement is adaptively constructed,
for the purpose of leading the animal toward or away from the
source of energy.   Loeb's attempt to refer the actions of the
lower animals to chemo-physical processes should therefore be

disregarded for the future. The trend of his investigations is not only unfruitful in itself, but it leads to a shallow rather than to a deeper conception of the whole of biology, since it inclines to regard the whole problem as solved just as soon as the chemo-physical side of it is explained.

The statement, for example, that the spermatozoa of the fern are attracted by malic acid seems to those of this temper as a most satisfactory view. The " mechanism " of the occurrence is explained and one turns contentedly to other things. But what is actually gained? The problem really consists in the fact that the archegonium secretes just that substance to which the spermatozoon reacts. It is a most delicate adaptation, such as we find everywhere with closer observation, but whoever limits his view to chemo-physical processes will pass by this main problem without even seeing it. Biology is above all a historical science, it deals with things which have taken place, the investigation of which must be carried on necessarily from other points of view than the investigation of inorganic material. Physics and chemistry teach us chiefly to recognize the means which nature uses to attain any purpose in the realm of living matter, they cannot reach the deeper problems. Only when the physico-chemist is convinced of this can he work successfully within the field of biology.

NOTES

NOTES ON THE BEHAVIOR OF CERTAIN SOLITARY BEES

PHIL RAU AND NELLIE RAU

Colletes compactus[1]

The September afternoon was bright and sultry, with a temperature of perhaps 85°, as we trudged up a deep little valley between heavily wooded hills, where a tiny brook ran away from a spring. As we stepped over the stream, the hum and blurr of swarming insects attracted us. There at the side of the water was a swarm of *Colletes* bees, perhaps two hundred in number, buzzing, flying, wheeling, dancing, weaving in and out, all in a chosen spot a few inches above the pebbles at the water's edge, and in an area about two feet across. The excitement was riotous, dancing and mating, dancing and mating. The males were far in excess of the females, apparently in about the proportion of three or four males to one female. The females were not so active as the males, but sat down more often upon the rocks as if in quiet and meek anticipation of attention. And usually they rested only a few seconds before their mates arrived, often from two to five males struggling together for the possession of one female. I am not sure whether the female's deliberation was of psychological or physiological causes; matings were not seen to take place on the wing, but she was of heavier build than the male and also was frequently laden with pollen; this may have hindered her participation in the merry dance. They were so intent upon their frolic that we could pick them up easily with the forceps, and our presence scarcely disturbed them; when we stepped into the very midst of the swarm they scattered a little—of necessity—but returned and concentrated on the same spot as soon as we removed ourselves.

[1] We are indebted to Mr. J. C. Crawford for the identification of the three species herein mentioned.

We could see no reason why this spot should be more agreeable to them than any other. Some lime had been thrown over the rocks at this point, but we could not see why this should attract them, since they paid it no heed. Other lime-dumps were near by, which did not attract them.

Calliopsis nebraskensis Cfd.

Some little solitary bees, *Calliopsis nebraskensis* Cfd., often busy themselves upon a bare spot in our field. They live in holes in the ground, and while they are solitary in habit they often exist in communities, i.e., several holes occur near together, but we have not ascertained whether this is because they prefer the community life, or whether merely the desirable features of the sunny bald spot has brought them near to each other.

These holes are always found closed and covered with a little mound of loose, well-pulverized earth. Not infrequently one sees this loose soil move, but evidently the occupant of the hole is only pushing up more dirt from below. Only rarely does one see her come tumbling out through the top of the mound, gather herself together and shake off the dust all in an instant, while the loose dirt again closes behind her, and dart off on the wing. It is a wise precaution that she keeps her nest always covered, for I have seen vandals prowling about these homes more often than I have seen the rightful owners. In fact, I long thought that these burrows and mounds actually belonged to certain tiny black-and-red wasps, who make very bold in the liberties they take about them.[2]

Now these little bees have one strange antic which has aroused our curiosity a number of times. First, one's attention is attracted to some little object buzzing around on the dusty ground, in the manner of an insect which has fallen upon its back and is struggling to get on its feet. It is a pair of these little bees, clasping each other by the legs, ventral to ventral, and with their bodies curved, so that the two united form almost a ring. Thus they continue buzzing and spinning and tumbling about on the dusty ground, whirling 'round and 'round in small circles near the same spot. In its intensity the struggle has much the appearances of a miniature dog-fight. I have never been so

---

[2] This was later identified as the parasitic bee *Sphecodes sp.* by Mr. S. A. Rohwer.

fortunate as to see the beginning of one of these performances, but they have continued for thirty seconds to a minute after discovery.

At first we thought it was a mating performance, but later we found a pair in actual copulo, sitting quietly on the ground, the male surmounting the female with the abdomen curled underneath hers to effect the union. The duration of this mating was perhaps five minutes. But what the significance of this whirligig struggle may be we have not yet determined. At the conclusion of the performance they have always separated and instantly darted away with a buzz, so we have failed even to determine the sex of the performers. Is it a friendly or an antagonistic encounter, a sexual or merely social or platonic frolic? There may be some of the elements of courtship about it, but so far as we have seen it does not immediately precede or follow mating.

Megachile brevis Say.

We were plodding along the railroad track one hot, mid-July day, hunting for ground-wasps, when a little creature emerged from a crack in a tie at our feet and darted away on the wing. It was a little leaf-cutter bee, Megachile brevis Say. After one or two minutes we spied it returning, coming up the track from the east; it located its particular crevice without the least difficulty, entered, reappeared after a few moments and went off directly down the track to the east again. Soon she returned, coming straight along the track as before, and entered her hole without displaying the least confusion. This time she remained in for five minutes, and even a heavy train passing on the parallel track and shaking the earth perceptibly did not alarm her away.

When next she emerged she sailed directly west, with a dash. She flew with a characteristic gait, neither gliding nor zig-zag, but a combination of the two, like a boy on skates making a smooth, gliding stroke, first with one foot and then the other. She flew about twelve or fifteen inches above the ground, and kept pretty accurately to the same level. After ten minutes she reappeared, coming down the track between the rails, carrying her bit of green leaf, about one-half inch long. This time

she approached from the west (a new direction), and she betrayed extreme confusion, flying back and forth in the region of her tie and finally alighting on a weed near by to rest and readjust her burden and get a better grip upon it with her hind pairs of legs. At this point a train dashed by, passing over her very tie, shaking it violently, and causing her to disappear for seven minutes. Then we spied her up the track, hunting eagerly over another tie which had a wire over it, just like her own. Furthermore, she was searching over *only* the south end and west side of the ties (this was the location of her nest in her own tie); then she seemed to give it up and dashed off down the track to a few feet beyond her nest and resumed the searching, then gradually worked her way back, circling low over the south end of many ties until she came to her own which she recognized at once and wearily entered, carrying all the time her green leaf. After a four-minute rest she dashed off westward again, this time for a fifteen-minute journey. Upon her return she repeated exactly the performance of searching over the ties a little west, then east of her nest, and then working back to the middle position, where lay her nest. At each trip she brought her load of leaf. As she emerged from her crevice after five minutes we caught her and dug out her nest, a neat little pack of leaves about three-fourths inch long.

It seems to me that she was quick to make use of her newly-acquired knowledge that she could rely upon the rails as guide-lines to her home, and not look to the right or the left of the track. She searched only in the two directions of a straight line, which is far simpler than to search in all directions of the compass, as her ancestors must have done. For is not this deliberate search on either side of her nest analagous to the flight of orientation, commonly seen in the homing of bees and wasps? Is it not, in fact, itself a flight of orientation so simplified and so deliberately executed that we are able to follow each movement?

SETTING REACTIONS OF BIRD DOGS TO TURTLES

HAROLD C. BINGHAM

Several years ago an incident was reported to me regarding the setting response of a chicken dog to a snapping turtle. Mr. W. W. Azeltine, the reporter of the incident, was an experienced hunter and had had extensive experience with various types of dogs. His interesting account of the incident was recalled recently when, with a different dog, I observed a similar response.

In this note, I shall describe the two incidents that have come to my attention. They are significant, it seems, when one considers that both dogs were accustomed by nature and training to trail and "set" only warm blooded representatives of the higher vertebrates. In each of the incidents, the dog evidently confused the trail of a turtle with that of a prairie chicken. The habitual method of trailing and setting prairie chickens was characteristically adopted in response to the trail of a cold blooded vertebrate.

According to Mr. Azeltine's narrative, he was hunting with a mongrel, Prince, in which shepherd and setter blood apparently predominated. He had used the dog two seasons and in a section of the country where prairie chickens were abundant. The dog had had some experience with quail but, within the knowledge of the narrator, with no other species of this class of game birds. He regarded the dog as having an unusually reliable " nose."

While hunting on a fair day, Prince characteristically assumed, at the edge of a field of stubble, a solid setting posture. When encouraged to advance upon the expected game, the dog was unusually reluctant making the hunter look for a bird to flush at any moment. Prince, holding closely to the trail, was urged slowly across the field of stubble and into the long grass of a slough. At the end of the trail, he came upon a snapping turtle, from which he turned at once and began hunting.

After this experience, Prince was similarly fooled two or three times. Always he left the tortoise with indifference as soon as he reached the end of the trail.

The owner of an Irish setter reported to Mr. Azeltine similar experiences with his dog.

My own observation of this confusion of turtle and chicken trails occurred quite recently in the same section of the country, but prairie chickens had become scarce. I was hunting behind a yearling dog, Heinie, on the first day of the hunting season. I had owned the dog after he was approximately four months old. His ranging privileges had been rather restricted and only permitted under my own observation.

According to the fancier who sold Heinie, the male parent of the dog was a setter and the mother was a pointer. Heinie resembled the pointer stock, but his hunting was typically that of the setter. He relied chiefly upon trailing and, in comparison with other dogs I have used, his ability to locate game was rather inferior. In trailing, however, he was a moderately reliable young dog.

Heinie's first experience with prairie chickens came only a short time before his reaction to the trail of the land tortoise. In a field of stubble he had "set" quite satisfactorily a covey of chickens. Following the shooting, one of the escaped birds was being sought in the moderately high grass of an adjoining pasture. Heinie had been unable to locate it and we were leaving when he suddenly assumed the setting attitude. It was strikingly similar to his behavior not more than thirty minutes earlier and, despite the fact that we were some three or four hundred yards from the place where we had watched the chicken down, I thought he had located it. Obviously, Heinie was even more earnest and excited than in his previous reaction to the covey of chickens. He trembled characteristically and, as before, moved forward cautiously. So low did he crouch that at times his belly actually touched the ground. The direct trail that the dog seemed to be following made me suspicious and the outcome became even more doubtful when the distance reached something like one hundred yards. It was probably one hundred fifty yards before we came upon the maker of the trail—a sluggish land tortoise.

Upon reaching the animal, Heinie gradually relaxed from his tense setting attitude.   In a half skulking response, he sniffed briefly and somewhat fearfully at the turtle, turned away abruptly, and went about his hunting apparently indifferent to his new acquaintance.

Announcement of Change in Subscription Price

of the

Journal of Animal Behavior
and the Behavior Monographs

Because of increased cost of manufacture, the management of the Behavior Publications has voted to increase the regular subscription price to $5.00 per volume.

Beginning with volume 7, 1917, the subscription price of the Journal of Animal Behavior, postpaid to all points in the postal union, will be $5.00.

Beginning with volume 4, the subscription price of the Behavior Monographs, postpaid to all points in the postal union, will be $5.00.

On the above subscription price, a discount of 10% will be allowed to book dealers and magazine agents.

All orders for the Journal or the Monographs should be addressed to

The Journal of Animal Behavior

Emerson Hall   Cambridge, Mass.

LITERATURE FOR 1915 ON THE BEHAVIOR OF THE LOWER INVERTEBRATES

W. H. TALIAFERRO

From the Zoölogical Laboratory of the Johns Hopkins University

Allen (1) finds that *Planaria dorotocephala* reacts both positively and negatively to a stream of water. " The sign of the reaction may differ depending upon the velocity of the current." In such cases the author finds that they are positive to the stronger current and negative to the weaker one, and that often when a given specimen is reacting negatively to a weak current it can be made positive by increasing the velocity of the current. A positive reaction can be changed to a negative one by a change in the composition of the aquarium water and can be again reversed by the resumption of the former conditions. Similar reversals can be effected by sudden temperature changes.

The sudden appearance and disappearance of vast numbers of *Folliculina* on the aquatic plants along the shores of the Chesapeake Bay and its branches that were noted by Andrews (2) in 1912 and 1913 occurred again in 1914. The time of appearance and disappearance differs in successive years. The author is of the opinion that the large numbers of this protozoan are due more to immigration from without than to the division of the organisms that have already settled on the plants. " It is suggested that conditions of food possibilities are determining factors in these inroads into the brackish fauna."

Bittner, Johnson, and Torrey (3) hold that the one thing fundamental to all tropism hypotheses is that the movements in orientation should be predictable as to direction, and they

try to show that such is the case in the reactions of *Allolobophora sp.* to light. They find that there is a tendency for this animal to swing the anterior end in regular alternation from side to side in successive extensions and a tendency in orientation to light for the animal to swing directly away from the source of stimulation. As one would expect from the action of these two tendencies they find that the anterior end of the worm is swung away from the light most frequently when it is directed toward the light and least frequently when it is directed away from the light at the moment the light is turned on.

In a paper on the physiology and histology of the statocysts of *Pecten*, Buddenbrock (4) finds that this animal in directing its course makes use of two different methods. There is (1) vertical steering (Vertikalsteuerung) in which the animal can direct itself in any direction in relation to gravity by turning about its transverse axis, viz., the axis which passes in general between the right and left valves in an anterio-posterior position. In this mode of steering the animal uses the so-called " position reflex " and the reflex from the left statocyst. Then there is (2) side steering (Seitensteuerung) in which the animal can direct itself in any direction in a horizontal plane by turning about its vertical axis, viz., the axis passing through the center of the animal perpendicular to both valves. In this method the animal uses the reflex from the left statocyst alone. In no case is a reflex from the right statocyst used. This lack of function corresponds to its degenerate histology. The same author (5) gives a very extensive criticism of Loeb's tropism theory. Space will not permit a consideration of his various arguments against this theory.

In a paper which deals chiefly with the cytology of the different stages of the encystment of *Amoeba proteus*, Carter (6) gives some details of the behavior during the process of encystment. The animal becomes sluggish and exudes a slimy mucous substance, which causes diatoms, debris, etc., as well as cast off waste products to adhere to the animal and thus form a protective wall. The Amoeba as well as the mass of debris then assumes a spherical form.

Cary (7) (8) finds that although regeneration can take place normally in *Cassiopea xamachana* without the influence of the marginal sense organs, the rate of this regeneration is decidedly

lower in the absence of such influence. The rhopalia likewise
seem to have some influence on certain metabolic activities.

Child (9) by means of his "differential susceptibility to cyan-
ide" method and Lillie's indophenol method of determining
intracellular oxidations, finds that there is a metabolic gradient
in the unfertilized egg of the star fish which coincides in direction
with the axis determined by the excentric position of the nucleus.
This gradient disappears in the bipinnaria larvae as metamor-
phosis approaches.

Crozier (10) finds that *Holothuria surinamensis* "is reactive
to tactile, vibratory, photic and chemical stimuli. It is practi-
cally indifferent in a sensory way, to heat." The following is
the order of decreasing sensitivity of parts of the animal: " ten-
tacles > anterior end > posterior end > papillae, pedicles (podia) >
mid-body surface." Also he (11) finds that the Cuvierian organs
of *Holothuria captiva* are expelled in response to mechanical
but not to various chemical stimuli. He then takes up the
mechanism of the discharge of these organs and the cause of
their adhesiveness after the discharge. In continuing his work
on the latter organism he (12) finds that it is sensitive to light
and shading over its entire surface and concludes that photic
orientation in this animal is in accord with Loeb's definition of
negative phototropism. The same author (13) gives a note
on the behavior of a species of *Ptychodera* and another (14) on
the rhythmic pulsation of the cloaca of *Stichopus moebii*.

Garrey and Moore (15) have attempted an experimental
analysis of "the normal progressive movements of the earth-
worm" in regard to such things as the initiation of peristalsis,
rôle of ventral nerve, etc.

Hirsch (16) has made a very careful study of the biology of
nutrition of carnivorous gastropods. The work is too extensive
to do more than call attention to the original article.

Hutchison (17) finds that M/100 and M/50 NaCl, M/3000
CaCl$_2$, M/50 KNO$_3$ and distilled water, by increasing the heat
resisting powers, exert a protective action on a pure race of
Paramoecium caudatum grown in an alkaline medium. On the
other hand M/4000 CaCl$_2$, M/100 NaCl and distilled water
exert an adverse effect on a pure race grown in an acid medium.
The author is of the opinion that these "experiments seem to
point to the conclusion that certain properties of the medium

are important factors in the heat resistance of *P. caudatum*, and that such properties will predetermine whether a given salt solution will have a favorable or unfavorable effect." In general he finds that there is no decided effect on heat resisting powers produced by continued exposure to moderately high temperatures.

Hyde and Spreier (18) find that light has a stimulating effect on the reproductive power of *Vorticella* up to a certain optimum, and that the yellow and green rays are more effective than the red or blue.

Jordan (19) gives some observations on the movements, etc., of *Mactra inflata* while burying itself in the sand.

In a popular paper Kanda (20) briefly considers reactions to gravity "in animals from the unicellular organism to man" and concludes that the behavior of all of these points to the truth of the statocyst theory as opposed to the mechanical, pressure, or resistance theories.

Kellogg (21) gives a very thorough description of the ciliary mechanism of a large number of *Lamellibranchs*. In discussing the action of these mechanisms in food collection and the removal of the material not used as food the author concludes, " Volume alone determines whether the collected foreign matter that reaches the palps shall proceed to the mouth or shall be sent from the body on outgoing tracts." For this reason a *lamellibranch* can feed only in comparatively clear water and not in the presence of a large amount of suspended matter. (With the exception of the genus *Macoma*).

According to Kepner and Rich (22) the proboscis of *Planaria* possesses an instinct to ingest objects and the control of this instinct lies not in the dorsal ganglia, " but in a region of the body anterior to and quite near the base of the proboscis."

In a note Kepner and Taliaferro (23) find that the natural habitat is an important factor in the physiological tone of *Rhabdococles* when kept under laboratory conditions and hence is a determining factor in their reactions.

Kühn (24) has made a study of the resting condition during hibernation of the snail *Helix*.

Loeb and Wasteneys (25) in a study of the relative effect of various parts of the spectrum for the orienting reactions of the sessile hydroid *Eudendrium* find that the most effective region

is in the blue at λs 4735 Å. u.   This is approximately the same region found by Blaauw for seedlings of *Avena*, viz., λs 4780 Å. u. The regions in red, orange, and yellow, it is maintained, have practically no effect on either *Avena* or *Eudendrium*.   Loeb and Wasteneys conclude that, " The heliotropism of the sessile animal *Eudendrium* and that of the sessile plant *Avena* are therefore identical even as regards the most efficient wave length." These authors (26) in another article, conclude that in plants as well as in animals " There seem to exist two types of heliotropic substances, one with a maximum of sensitiveness (or absorption) in the yellowish green (near $\lambda = 534 \ \mu\mu$) and the second with a maximum of sensitiveness in the blue (near $\lambda = 477 \ \mu\mu$)."   According to them the distribution of these two photosensitive substances is without reference to the systematic boundaries of the two groups.

Mast (27), in studying the relative stimulating efficiency of spectral colors for fifteen species of organisms finds that with the exception of two forms they fall into two groups.   In the first group, viz., *Pandorina*, *Eudorina* and *Spondylomorum*, the region of stimulation begins in the blue between 430 and 440 $\mu\mu$ and ends in the red at about 640 $\mu\mu$, the maximum being in the green between 530 and 540 $\mu\mu$.   In the second group, viz., *Trachelomonas*, *Phacus*, *Euglena* (five species), *Gonium*, *Arenicola* larvae, and earthworms, the region of stimulation begins in the violet between 420 and 430 $\mu\mu$ and ends in the green near 520 $\mu\mu$; the maximum being in the blue between 480 and 490 $\mu\mu$. The author also finds that the maximum region of stimulation for *Chlamydomonas* is in the green very near 510 $\mu\mu$ and for the blow fly larvae approximately at 520 $\mu\mu$.   No difference in the relative efficiency of these different regions was found for a given species either when it was tested under different conditions of illumination and temperature, or when the organism reacted negatively or positively.

Paul (28) points out that *decapods*, because of their hard integument and peculiar vascular system, run great risk from hemorrhage in the injury of one or more of their appendages.   He then shows how this is guarded against by self-amputation and makes a very careful study of the processes involved in this act and later regeneration.   " Valvular action of the diaphragm at the breaking plane plays a greater part in stopping of hemorrhage

after self-amputation than clotting." The same author (29) continues his work on the self-amputation of appendages in a number of *decapod crustacca* by making a comparative experimental study of the reflexes, etc., involved in this act.

Pearse (30) gives some interesting facts concerning the habits, courtship, copulation, etc., of the fiddler crabs *Uca pugnax* and *U. pugilator*.

Pecker (31) has made an extensive study of the modification of *Colpoda* and its cysts under the action of blood serum.

Phipps (32) finds that several species of *amphipods* with which he worked are negative both with reference to light intensity and direction of rays, the latter being the more efficient as a stimulus. The sign of the reaction can be reversed in most cases by treatment with certain depressing agents, which effect seems to be due to changes in certain metabolic processes.

According to Polimanti (33) weak mechanical stimulation with a glass rod causes *Planaria* to lengthen and show flight movements while strong mechanical stimulation is followed by complete immobility. From this the author holds that a weak stimulus causes an excitation in the tonus of the animal while a strong stimulus causes inhibition. He also concludes that the mechanism of inhibition in its last analysis is one of fatigue.

In a study of the function and structure of the grasping organ of *Dendrocoelum lacteum*, Redfield (34) finds that this organ " is used to seize and hold material on which *D. lactcum* feeds. It is stimulated to activity by appropriate materials applied to the receptors located on the anterior part of the worm." These receptors probably are on the grasping organ itself. The organ may be used in some forms of locomotion but this certainly is not one of its essential functions.

Root (35) gives an account of the life history and the reactions to food of the *suctorian Podophyra collini n. sp.*

Schwartz and Safir (36) find that when the fiddler crab is placed in a wooden box it tries to escape by moving persistently toward some definite corner. The direction of this movement is conditioned to a large extent by the comparative symmetry of the two chelipeds, the dextrous males going to the right, etc. If the corner to which a given specimen moves is closed by a glass plate the animal will learn to go in some other direction which offers the possibility of escape. The rapidity of this habit

formation varies in direct proportion to the number of trials. The chief factors in the formation of this habit are sight and touch, especially the former. The habit persists after a lapse of ten days but it can be unlearned " although previous experience seems to have no influence on the rapidity of unlearning."

Welch (37) in an extensive study of the *Enchytraeidae* of North America gives a number of experiments on the reactions of *Lumbricillus rutilus n. sp.* to a number of stimuli found in its environment. As this species is found in one of the sewage disposal plants of Chicago, the author gives a discussion of the relation of the behavior of this animal with respect to the work done by the disposal plants and concludes that the worms facilitate the oxidation of unstable organic matter and increase the putrescibility of the sewage.

Wilhelmi (38) gives a note on the function of the grasping organ or sucking pit (Sauggrube) of fresh water *triclads*.

REFERENCES

1. ALLEN, G. D. Reversibility of the Reactions of Planaria dorotocephala to a Current of Water. *Biol. Bull.*, **29**, 111-128.
2. ANDREWS, E. A. Distribution of Folliculina in 1914. *Biol. Bull.*, **29**, 373-380.
3. BITTNER, L. H., JOHNSON, G. R., and TORREY, H. B. The Earthworm and the Method of Trial. *Jour. Animal Behav.*, **5**, 61-65.
4. BUDDENBROCK, W. v. Die Statocyste von Pecten, ihre Histologie und Physiologie. *Zool. Jahrb. Abt. f. Zool. u. Physiol.*, **35**, 301-356.
5. BUDDENBROCK, W. v. Die Tropismentheorie von Jacques Loeb. *Biol. Cent.*, **35**, 481-506.
6. CARTER, L. A. The Cyst of Amoeba proteus. *Proc. Roy. Phys. Soc.*, **19**, 204-212.
7. CARY, L. R. The Effect of the Removal of the Marginal Sense Organs on the Rate of Regeneration in Cassiopea xamachana. *Science, N. S.*, **41**, 471.
8. CARY, L. R. The Influence of the Marginal Sense Organs on Functional Activity in Cassiopea xamachana. *Proc. Nat. Acad. Sci.*, **1**, 611-616.
9. CHILD, C. M. Axial Gradients in the Early Development of the Starfish. *Amer. Jour. Phys.*, **37**, 203-219.
10. CROZIER, W. J. The Sensory Reactions of Holothuria surinamensis Ludwig. *Zool. Jahrb. Abt. f. Zool. u. Physiol.*, **35**, 233-297.
11. CROZIER, W. J. A Note on the Physiology of the Cuvierian Organs of Holothuria captiva Ludw. *Amer. Jour. Physiol.*, **36**, 196-202.
12. CROZIER, W. J. The Orientation of a Holothurian by Light. *Amer. Jour. Physiol.*, **36**, 8-20.
13. CROZIER, W. J. The Behavior of an Enteropneust. *Science, N. S.*, **41**, 471-172.
14. CROZIER, W. J. The Rhythmic Pulsation of the Cloaca of Holothurians. *Science, N. S.*, **41**, 474.
15. GARREY, W. E. and MOORE, A. R. Peristalsis and Coordination in the Earthworm. *Amer. Jour. Physiol.*, **39**, 139-148.
16. HIRSCH, G. C. Die Ernährungsbiologie fleischfressender Gastropoden. *Zool. Jahrb. Abt. f. Zool. u. Physiol.*, **35**, 359-504.
17. HUTCHISON, R. H. The Effects of certain Salts, and of Adaptation to High Temperatures, on the Heat Resistance of Paramoecium caudatum. *Jour. Exp. Zool.*, **19**, 211-224.

18. HYDE, I. H. and SPREIER, C.   The Influence of Light on Reproduction in Vorticella. *Amer. Jour. Physiol.*, **36**, 398-399.
19. JORDAN, H.   Ueber die Art, wie Mactra inflata sich in den Sand einwühlt. *Zool. Jahrb. Abt. f. Zool. u. Physiol.*, **35**, 298-300.
20. KANDA, S.   Geotropism in Animals. *Amer. Jour. Psych.*, **26**, 417-427.
21. KELLOGG, J. L.   Ciliary Mechanisms of Lamellibranchs with descriptions of Anatomy. *Jour. Morph.*, **26**, 625-701.
22. KEPNER, W. A. and RICH, A.   Food Reactions of the Proboscis of Planaria. *Science, N. S.*, **41**, 473.
23. KEPNER, W. A. and TALIAFERRO, W. H.   Preliminary Report on the Relations Between the Reactions of Rhabdocoeles and Their Environments. *Science, N. S.*, **41**, 473-474.
24. KÜHN, W.   Aus dem Leben der Weinbergschnecke. *Umschau*, **19**, 372-374.
25. LOEB, J. and WASTENEYS, H.   The Relative Efficiency of Various Parts of the Spectrum for the Heliotropic Reactions of Animals and Plants. *Jour. Exp. Zool.*, **19**, 23-35.
26. LOEB, J. and WASTENEYS, H.   The Identity of Heliotropism in Animals and Plants. *Science, N. S.*, **41**, 328-330.
27. MAST, S. O.   The Relative Stimulating Efficiency of Spectral Colors for the Lower Organisms. *Proc. Nat. Acad. Sci.*, **1**, 622-625.
28. PAUL, J. H.   Regeneration of the Legs of Decapod Crustacea from the Preformed Breaking Plane. *Proc. Roy. Soc. Edinburgh*, **35**, 78-94.
29. PAUL, J. H.   A Comparative Study of the reflexes of Autotomy in Decapod Crustacea. *Proc. Roy. Soc. Edinburgh*, **35**, 232-262.
30. PEARSE, A. S.   On the Habits of Uca pugnax (Smith) and U. pugilator (Bosa). *Trans. Wis. Acad. Sci. Arts, Letters*, **17**, 791-802.
31. PECKER, S.   Die Änderung von Colpoden und deren Cysten unter dem Einfluss von Blutserum. *Pfluger's Arch.*, **163**, 101-146.
32. PHIPPS, C. F.   An Experimental Study of the Behavior of Amphipods with Respect to Light Intensity, Direction of Rays and Metabolism. *Biol. Bull.*, **28**, 210-223.
33. POLIMANTI, O.   Ueber bei Planarian beobactete Tonusschwankungen. *Zeit. f. Biol.*, **66**, 127-135.
34. REDFIELD, E. S. P.   The Grasping Organ of Dendrocoelum lacteum. *Jour. Animal Behav.*, **5**, 375-380.
35. ROOT, F. M.   Reproduction and Reaction to Food in the Suctorian, Podophrya. collini n. sp. *Arch. f. Protist.*, **35**, 164-196.
36. SCHWARTZ, B. and SAFIR, S. R.   Habit Formation in the Fiddler Crab. *Jour. Animal Behav.*, **5**, 226-239.
37. WELCH, P. S.   Studies on the Enchytraeidae of North America. *Bull. Ill. State Lab. Nat. Hist.*, **10**, 122-212.
38. WILHELMI, J.   Einige biologische Beobachtungen an Süsswassertricladen. *Zool. Anz.*, **45**, 475-479.

LITERATURE FOR 1915 ON THE BEHAVIOR OF SPIDERS AND INSECTS OTHER THAN ANTS

C. H. TURNER

Sumner High School, St. Louis, Mo.

TROPISMS AND RELATED PHENOMENA

Essenberg (33) finds that the back-swimmers are negatively geotactic, negatively geotropic, positively phototactic and positively rheotactic, and that the water-striders (34) are positively phototactic, negatively geotactic, positively thigmotactic and positively rheotactic.

Krecker's experiments (73) show that *Hexagenia variabilis* behaves as though it were negatively anemotropic, negatively geotropic and negatively phototropic.

According to Blackman (14) a strong light causes *Pityogenes hopkinsi* to stop work; but frequent repetitions of the stimulus soon produce no visible effect on the animal.

Hargitt (56) finds in the mourning-cloak butterfly a dominance of the chemotropic response to food and a slight negative phototropism, and Howlett (65) discusses the chemical reactions of fruit-flies.

According to Zetek (130) phototropic responses dominate the flight of the malaria spreading mosquitoes.

Turner states (119) " The ant-lion may be considered positively geotactic, positively thigmotactic and negatively phototactic, with the reservation that all of its movements cannot be explained as tropisms in the Loebian sense."

Girault (49) placed some specimens of *Trichogramma minutum* in a glass jar which was equally lighted on all sides. They climbed the sides of the jar; and, when it was slowly reversed, they turned so as to continue upwards. Evidently they are negatively geotactic.

McDermott (84) caused a warm current of air to impinge on a dish containing material attractive to flies. The enticed flies would walk along until within two or three centimeters of the

point where the air struck the dish. There, facing the current they would pause with outstretched wings. Sometimes two or three would be in a row. Either a sudden stopping of the current or increasing the temperature to forty degrees centigrade would cause them to disperse.

Kincaid (69) finds that the color of the environment of the larva has a pronounced effect upon the color of both larva and pupa of the thistle butterfly. Caterpillars of this species were placed in boxes of the following colors; pearl gray, lavender, crushed apricot, blue, pink, green and black. The larvae placed in the gray boxes became light gray. Those in the black boxes became black and formed black chrysalids with a sprinkling of gold. Those in the green boxes turned black; but their chrysalids were dark brown. Those in the blue boxes acquired brown bodies with bluish spines and their chrysalids were brown with gold spots. Those confined to the lavender and to the pink boxes developed stripes about the color of the boxes; but the chrysalids of the first were light tan with gold spots and those of the latter almost all gold. Those in the apricot boxes evolved stripes and spines that matched perfectly the color of the box and the chrysalids were the exact color of the box, with two rows of gold spots. The adults did not seem to be affected at all by the color of the environment of the larvae.

OLFACTORY SENSATIONS

Small drops of coal oil and of ammonium were placed on the upper edge of an aquarium containing water-striders. When the insects approached these substances, they waved their antennae and dropped into the water. These reactions caused Essenberg (34) to predicate a sense of smell to water-striders.

To test the olfactory sense of beetles, McIndoo (85) isolated them in small triangular boxes with netting bottoms. He used 434 individuals belonging to eleven species and eight families. From some he removed the antennae; from others, the elytra; from others, the wings; from others, one or more legs. " Four unmutilated species responded to odors more slowly than did members of the same species with amputated antennae. . . . Five species without antennae responded to odors as promptly as did the same species unmutilated. . . . Two species without antennae responded to odors more slowly than did the same

species unmutilated.   Six species so mutilated that most of their olfactory pores on the elytra and wings were prevented from functioning responded from two to five times more slowly than did the same species unmutilated, or with the antennae pulled off.''   These results prompted the conclusion that the antennae have no olfactory function and that the pores found on the peduncles of the elytra, on the dorsal surfaces of the wings, on the trochanters, tibiae, and sometimes the femurs and tarsi, and perhaps on the mouth appendages, are the true olfactory organs of beetles.   This is in accord with the same investigator's work on the Hymenoptera, which was reviewed in this journal last year.

These experiments of McIndoo are painstaking and his anatomical studies of what he calls olfactory pores are excellent; but, the serious student, who is acquainted with the experiments of Forel and others who '' claim that the antennae are the organs of smell,'' will not be convinced that the last word has been said on the subject.   They do not seem to have met the following criticisms raised by Forel* several years ago:—'' To demonstrate the sense of smell, our two physical distant senses, vision and hearing, must be eliminated with certainty.   But that is not sufficient.   Innumerable chemical substances included in either air or in water in a state of gas (free or absorbed) can, as is known, and as I have already pointed out at the commencement of these experiments (1878), while exercising in any way some corrosive action, irritate nerve terminations other than those of olfaction, and that (at least so far as concerns man) generally in a painful or at least a disagreeable fashion.''   '' If we are content, as our predecessors have often been, and as Graber is again, to bring close to the animal certain substances which are odorous to us, and see whether or not it avoids them, we have not demonstrated olfaction at all.   We have simply shown that these substances have irritated the animal in one way or another.   If the animal comes up to them instead of avoiding them we have proof that the irritation is agreeable to it.   That nearly approaches olfaction, but is by no means proof of it, for certain irritations can be agreeable, without, for all that, being olfactive.   It is necessary, then, as I have said, to show that the irritation in question allows

---

* Forel, August.   The Senses of Insects.   Translated by Macleod Yearsley. Methuen & Co., London, 1908, p. 74–76.

the animal to recognize such or such matter, to distinguish it from others in a constant and indubitable fashion. Then we have a right to speak of olfaction, and it is even in my opinion the only proof, the only definition of the sense we have."

OTHER SENSES

1. *Auditory Sense.* When a metallic sound is made the water striders move backwards. If a buzzing insect drops into the water, the striders rush towards it; but, they do not respond to a dead insect that falls into the water. These facts induced Essenberg (34) to believe that water-striders can hear.

2. *Tactile Sense.* By means of a tuning fork and of a straw attached to an electric vibrator, Barrows (12) has given a brilliant confirmation of what Dahl* discovered long ago; i. e., that spiders reach their prey by following the radius that vibrates the strongest. By amputating first one leg and then another, he demonstrated that the sense of touch is not confined to any pair of legs.

3. *Vision.* Works on color vision and form-perception have appeared by Buttel-Reepen (20), Frisch (41) and Stellwaag (114).

MATING BEHAVIOR

Awati (4) describes the mating behavior of the apple sucker and of the pear sucker; Back and Pemberton (5, 6), of the Mediterranean fruit-fly and of the melon-fly; Blackman (14), of *Pityogenes hopkinsi*; Chapman (23), of *Agrilus bilineatus*; Fuller (43), of some South African termites; Funkhouser (44), of *Vanduzea arquata* Say; Gerhardt (45), of crickets and locusts; Hancock (55), of pink katydids; Kennedy (68), of dragon-flies; Rau (102), of *Dichromorpha viridis*; Turner (120), of the camel cricket; and Williams (127), of the pea thrips.

It is well known that the phosphorescence of the Lampyridae is a courting device. Blair (15) informs us that among the British forms it is the female that does the active courting, while in America it is the male. He also reminds us that we do not know the function of the phosphorescent light in those few forms that do not belong to the Lampyridae.

Schwarz (106) remarks that the mating behavior of *Catocala*

* Dahl, Frdr. Beiträge Zur Biologie der Spinnen. *Zool. Anz.,* VII Johrg., 1883, No. 180, s. 591–595.

titania resembles that of the English sparrow. With his wings half spread, displaying the beautifully colored hind wings, the male performs many antics.

Sturtevant (116) has performed some experiments upon sex recognition and sexual selection in *Drosophilia ampeliphila*. By putting a female in one vial and a male in another and placing the vials mouth to mouth, with a cover glass between them, it was found that the male pays no attention to the female until the cover glass is removed. This observation, coupled with the fact that they mate in darkness, forces the conclusion that vision is not essential for their mating. Experiments demonstrated that the female will mate with either normal or mutilated males; but males with entire wings mate sooner than those with mutilated wings. Hence he concludes that the wings play a prominent part in arousing sexual excitement, but that there is no evidence of sexual selection. A specimen that is ready to mate will do so with the first member of the opposite sex that happens along.

MATERNAL INSTINCTS

Back and Pemberton (5, 6, 7) have discussed the ovipositing of the Mediterranean fruit-fly and the melon-fly; Blackman (14), of *Pityogenes hopkinsi*; Dunn (32), of *Dermacentor nitens*; Essenberg (34), of the water-strider; Fuller (43), of some South African termites; Hancock (55), of katydids; Kennedy (68), of dragonflies; Schwarz (106), of *Catocala titania*; and C. L. Turner (120), of the camel cricket.

Severin (107) thinks that the perception of the digestive fluids through the micropyle of the egg causes the larva of the leafovipositing Tachinidae to begin to free itself from the egg.

Hegner (58) so manipulated the eggs of the potato beetle that 35 batches were in the sunlight and 15 in the shade. All of the eggs in the shade hatched; but none of those in the sun, although 18 developed to the hatching point. Sections of the eggs showed that development had proceeded in the sunlight and that the failure to hatch was probably due to dessication. He concludes: " The advantage of concealment is not so great therefore as that secured by shielding the eggs from the dessicating properties of the sun."

By adding spiders to and abstracting spiders from the nests of mud-dauber wasps, Rau (101) demonstrated that sometimes

the spiders were removed and at others they were not. " In answer to the question suggested in the title we can only say that in most cases where the spiders were disturbed the owner was quick to detect it and frequently resented it. But, since, in her anger, she often threw away part or all of her own prey, we cannot determine whether or not she recognized her own, or merely responded, with alarm, to any meddling about her home."

FOOD PROCURING ACTIVITIES

Awati (4) describes the feeding behavior of the apple sucker and of the pear sucker; Clausen (24), of certain aphid feeding Coccinellidae; Cleare (25), of a butterfly injurious to the cocoanut palm; Funkhouser (44) ,of *Vanduzea arcuata* Say; Gillette and Bragg (46), of some Colorado aphids with alternating feeding habits; Girault (48), of the aphid-eating *Adalia* 15-*punctata*; H. A. B. (52), of a fruit-fly attacking papaws; Haddon (53), of the larvae of the glow-worm *Lampyris noctiluca*; Hewitt (61), of the stable-fly; Rau (102), of *Dichromorpha viridis*; Shannon (108), of syrphid flies; Williams (127), of the pea thrips; and Marcovitch (89), a mite, a chalcid fly, a fruit fly, and a caterpillar that feeds on the juniper berry.

Bromley (17) gives an extensive list of the prey of eighteen species of asilids.

Sanders (105) records the fact that the larva of the fruit-fly (*Xylena bethunei*) eats the pupae of *Malacosoma distria* and *M. americana*.

Girault (47) relates the case of a bird-bug (*Cimex hirudinia*) which forsook the swallows of the chimney for the people sleeping in the adjoining room.

By dissections, Wheeler (126) demonstrated that the food of the New Zealand glow-worm consists of insects. He thinks the larvae catch both creeping and flying hexapods in their glutinous webs.

Richardson (103) found the larvae of a wasp dwelling in passageways in the galls of *Holocaspis globosus* of the oak and feeding upon plant lice. From this he concludes that the adults attend to the young throughout the entire larval period. It is unfortunate that the colony was not kept under observation long enough to verify this conclusion.

By raising fleas in petri dishes, Lyon (82) discovered that the

fleas prefer, as food, dust from the room and dried insect skins to dry blood.

It is well known that crab-spiders (Thomisidae) frequent flowers for the purpose of preying on insects. Lovell (79) discovers that they feed on bumble-bees, honey-bees, butterflies, dragon-flies, large flies and wasps.

Rau (100) finds that both the larva and adult of the meal-worm eat feathers, seed and dead insects.

Zetek (130) states that the mosquitoes *Anopheles albimanus* Wied. and *A. tarsimaculata* Goledi prefer human blood to any other food.

According to Essenberg (34) the water-striders feed upon a large variety of animal food, most of which is captured upon the surface of the water. Food is never secured under water and the insect will not touch larval mosquitoes. They often rest quietly upon aquatic plants and catch mosquitoes by leaping upon them. In confinement they are cannibals.

Turner (119) finds that the ant-lion feeds upon a variety of small invertebrates that happen to fall into the pits which it forms in any kind of friable material that is protected from the rain. Two methods are used by the ant-lions in forming these pits. " Usually it furrows backward, excavating a series of concentric, adjacent, circles, each deeper than the last, and shovelling out the soil with its head. The front of the body is so curved as to make it easy for the dirt to fall forward on the head. In the second method, the larva simply burrows downward into the ground and tosses out the soil with its head until the sides of the pit become stable. Pits formed by the second method are usually subsequently enlarged. He confirms the often discredited statement of early investigators that this insect removes obstacles from the pit by backing up the side thereof with the object balanced on its abdomen.

Lloyd (77) describes a species of caddis worm (*Ganonema nigrum*) which in its habits is unlike all others except a New Zealand species (*Triplectides obsoleta*) described by Hudson in 1904. Instead of constructing the orthodox dwelling of con-glomerated stones or twigs or tubes of silk, it selects a short twig from the stream bottom, hollows it from end to end, and lines the cavity with silk. When this tube becomes too short, the insect glues it, end to end, to another twig and treats the addition

in the same manner it did the first twig.   If the added piece is
too long it is shortened by girdling.   The food consists of powder
rasped from submerged wood.

Noyes (93) has made a careful study of the net-spinning caddis-
worms of Caseadilla creek.   She demonstrated, experimentally,
that they will construct tubes even in still water; but that nets
are only formed in the presence of a current.   The different
species of Hydropsyche construct similar nets, and the net-
building behavior is as follows:—1. They construct nets by either
day or night.   2. Two and a half to three hours is the average
time required to complete a tube.   3. No temporary construc-
tion threads are used.   4. There is no definite order in which the
threads are woven.   5. Particles are removed from the nets with
the mouth parts and not with the dorsal tufts of hairs on the
anal legs.   6. The front legs and the mandibles are used for
holding particles in position until they are fastened in place with
silk.   7. They are never too busy weaving to stop to capture
food that adheres to the net.   She confirms Siltala's statement
that the food of these forms is both animal and vegetable.   In
fall and winter diatoms form the bulk of the food; in spring and
summer minute animals predominate.   At all times a moderate
amount of algae is consumed.

<center>ANTHOPHILY</center>

As a result of ten years devoted to their study in Maine and
Massachusets, Lovell (78, 80) reports the discovery of 332
species of anthophilous beetles belonging to 127 genera and 29
families.   This is 47 species more than Knuth records for all of
North America.   He writes: " In all of the families, in most of
the genera and in very many of the species in which anthophily
occurs this habit has been acquired independently; but in the
case of *Gnathium* and *Nemognatha* it probably arose before the
genera were differentiated.   Except in these two genera and to
a less extent in *Chauglignathus* and *Lepturini* the modifications
induced are obscure and indistinct; from which it may be in-
ferred that anthophily among the Coleoptera is of compara-
tively recent origin.   The primitive Coleoptera lived largely
upon the ground and were carnivorous, but as they learned to
search for prey on plants and to feed upon vegetation anthophily
became correspondingly common.   As pollinators of flowers the

anthophilous beetles are of little significance. The enormous devastation of the vegetative organs of plants by beetles both in the larval and the adult stages, the consumption and waste of pollen and nectar, the destruction of the petals and other floral members, the absence of hair for holding the pollen and their indefinite manner of flight are factors which greatly reduce their value as pollen carriers. Floral structures show absolutely no response to the visits of beetles, and there is no reason to suppose that the development of the anthophilous flora would have varied in any respect had entomophily never arisen among the Coleoptera.''

HIBERNATION

Frohawk (42) discusses the hibernation of *Vanessa antiopa* and Nicholson (92), that of *Vespa vulgaris.*

According to Blackman (14) *Pityogenes hopkinsi* hibernates in the larval pupal and also the adult stages.

Recently three investigators have discussed the overwintering of the house-fly and they are not in accord. Lyon (81) used thirty-seven lots of 100 pupae. Some were placed in wet sand and some in dry, some in wet manure and some in dry, some in moist loam and some in dry, and some in leaf mould. Two series were placed out of doors, one in a sheltered spot and the other in an unsheltered position; a third series was placed in a greenhouse and a fourth in a cellar. No adults emerged from the jars placed out of doors; but, by the first of December, 210 had emerged from the pupae placed in the greenhouse and 367 from those stored in the cellar. The pupae that did not emerge were found to be dead. "It would seem therefore that the appearance of the seemingly freshly-emerged adults in any considerable numbers during the late winter should be accounted for in some other way" than supposing they have over-wintered in the pupal stage.

Skinner (111) after asserting that Dr. Moncton Copeman and Mr. E. Austin claim that the adult house-fly does not hibernate in England, expresses the belief that it does not do so in Philadelphia. He bases his conclusion upon his observation that the flies seen in the Academy of Science during the winter look as though they have just emerged.

Hewitt (60) writes: " I think we are still justified in regarding the dormant and periodically active states during the over-

wintering period as the usual occurrence in northerly latitudes. In no case have I been able to find in England or Canada living pupae of *Musca domestica*, under outdoor conditions, during the winter. Nor has it been possible in my breeding experiments in Canada and England to carry insects through the winter in the pupal stage. . . . Until evidence is secured of the insect overwintering in the pupal stage, we shall be justified in believing, from the facts available, that in northern latitudes *M. domestica* is accustomed normally to winter in the adult stage. In more southerly latitudes, where the temperature is much higher, and where the activities of the flies are practically continuous throughout the winter months, one would expect the occurrence of insects in an active condition and of the various stages of development during this period."

ECOLOGY

Forbes (38) urges students of economic entomology to study ecology. Defining ecology "as the relation of organisms to their environment, organic and inorganic, and any and all organisms, man included—man, indeed, as by far the most important living factor, from whatever view point," he insists that these relations are three: 1st, interactions (dynamic relations); 2nd, space relations (static relations); 3rd, successional relations (genetic relations). The dynamic factor is the only one that interests the economic entomologist; and twentieth century man, as a dominant species, is an important element of that factor.

Shelford (109) reminds us that scarcely any of the pests of forage and garden crops are forest animals and that only a few of the orchard and small fruit pests are strictly so. These pests naturally fall into those that frequent moist places and those that prefer higher and drier ground. The original home of the former was the lowland about streams, lakes and marshes; while the latter originated on the steep lake and river fronts and on exposures of bare rock. Hence, originally our pests were crowded into the cracks of the forest and scattered along the river margins of the great plains. With the clearing of the land and the planting of crops the habitats of these pests were expanded.

Banks (8) writes: " Since the main orders of insects have existed on the earth the gross outlines of the continents have

changed several times and between these changes there were migrations and dispersals, just as there is to-day. So that to-day each continent has insects which by their structure and origin are isolated from other insects around them and find their relations only in insects of distant countries." In western North Carolina there is a species of *Panorpodes*, a genus whose only other habitat is Oregon and Japan. In the southern Appalachians there is a spider (*Hypochilus*) which occurs elsewhere only in Colorado and which has a closely related genus in North China and New Zealand. In eastern S. America there is a handsome genus of ant-lions (*Dimares*) unlike anything else in S. America, but is so closely related to species of a genus found in Africa, Arabia and Ceylon that one loathes to separate them. Evidently the types of insect fauna do not agree with those of mammalian and avian fauna. There are three major types of insect fauna; (1) the microtypal, including insects of Europe, N. America, N. Asia, a considerable element of Andean America, many species in India, Insulidae and New Zealand, a distinct representation in Australia and a poor development in Africa; (2) the African or Gonwandan, with its present home in Africa, but strongly developed in Australia and almost as well developed in Insulidae and Ceylon, plainly present in India and noticeable in the Americas; (3) the Brazilian, with its center in Brazil. The third is a recent development; the other two are of ancient origin.

Banks analyzes the present insect fauna of the U. S. A. into the following elements. (1) Genera which are the relicts of a very ancient fauna which existed when the land masses were of a different formation from now. These are isolated in our fauna and are mostly examples of discontinuous distribution. (2) Genera representing relicts of an ancient invasion from S. America possibly through the West Indies, after S. America had been connected with Africa or a Pacific continent. These genera are isolated systematically in our fauna; they are forms that look out of place among our insects and are usually represented in northern Europe neither by recent forms nor by fossils. (3) Genera originating in this country from an insect fauna of which the elements " 1 " and " 2 " are relicts. These are confined to the United States and their affinities are with S. American or Asian insects rather than with those of Europe. " I consider

that this fauna had a long period of quiet development and be-
came very extensive. The miocene fossils perhaps represent
this fauna." (4) Genera and derivatives representing the hol-
arctic fauna forced southward by the advance of the ice-sheet.
These are the forms that show the relationship of our insect
fauna to that of northern and middle Europe. The bulk of
many large families belong here. (5) Genera representing a
comparatively recent influx from the American tropics, a migra-
tion still in progress. He gives examples of all of these elements
and closes his article with: " I doubt not but there are other
elements also in our fauna; but I think these are the most notice-
able, and sufficient to show that the Nearctic insect fauna is
not a realm, but a conglomeration of several such realms."

LETISIMULATION

Chapman (23) states that when touched the adult *Agrilus
bilineatus* letisimulates and drops to the ground.

According to Essenberg (34) death feigning is a characteristic
of the water-strider. It crosses its forelegs and becomes per-
fectly rigid.

Turner (119) finds that the ant-lion letisimulates so perfectly
that one can cut off the tips of its legs and even of its mandibles
without inducing a response. All death-feigning poses are not
death attitudes. " In the ant-lion letisimulation seems to be
but an exaggeration and prolongation of the pause made by
most animals when they are startled. The total behavior of
the death-feigning ant-lion supports Holmes's contention that
' the instinct of death-feigning is connected with much that is
called hypnotic in the lower animals,' and endorses James, when
he says: ' It is really no feigning of death at all and requires
no self-command. It is simply terror paralysis which has become
so useful as to become hereditary.' "

MISCELLANEOUS ACTIVITIES

Commensalism. Diguet (31) describes a case of commensalism
between a spider and a beetle and another species of spider and
ants. The beetles and ants seem to remove the remains of the
numerous flies that become ensnared in the web.

Knab (70) records a case of commensalism in *Desmometropa*.
Disease Spreading Activities. Articles on the relation of flies

to diseases have been published by Hadwen (54), Hewitt (62), McShane (86), Mitzmain (90), and anonymously (1,2). Notes on the malaria spreading mosquito have appeared by Carter (22). Wheeler (125) has discussed ants and bees as bearers of pathogenic micro-organisms.

Locomotion. Zetek (130) found that the mosquito *Anopheles* migrates from the marshes to town at dusk and from the town to the marshes at dawn. Lloyd (77) says the wood-boring caddis worms studied by him crawl with a jerky motion. Mann (88) mentions a tick, found in the Sinaitic Peninsula and Arabia, which travels after its host at the speed of a man.

Longevity. Back and Pemberton (5, 6) discuss the duration of life of the Mediterranean fruit-fly and of the melon-fly; Girault (48), of *Adalia* 15-*punctata*; Lyon (82), of the cat flea; Rau (100, 102), of the meal worm and of *Dichromorpha viridis.*

Migrations. McAtee (83) describes a remarkable flight of caddis flies and chironomids; Webster (123) mentions migrating swarms of the milk-weed butterfly which he noticed at Ames, Iowa, August 30 and at Waterman, Illinois, September 18, 1915.

Memory. See Rau (101) and Sturtevant (116) under maternal instincts.

Barnard (11) noticed a butterfly attempt to feed from the brightly colored eye of a peacock's feather on a man's hat.

REFERENCES

1. ANON. Flies as a Factor in Infant Mortality. *Penn. Health Bulletin,* No. 69.
2. ANON. House Flies as Carriers of Disease. *Nature,* **95,** 289-292.
3. ALEXANDER, C. P. The Biology of the N. A. Crane Flies. *Jour. of Entom. and Biol.,* **7,** 1-9, 141-160.
4. AWATI, P. R. The Apple Sucker, with Notes on the Pear Sucker. *Ann. App. Biol.,* **1,** 247-266.
5. BACK and PEMBERTON. Life History of the Mediterranean Fruit Fly from the Standpoint of Parasite Introduction. *Jour. of Agri. Research,* **3,** 363-374.
6. BACK and PEMBERTON. Life History of the Melon-Fly (*Bactrocera cucurbitae*), *Jour. of Agri. Research,* **3,** (1914), 269-274.
7. BACK, E. A. and PEMBERTON, C. E. Susceptibility of Citrous Fruits to the Attacks of the Mediterranean Fruit Fly. *Jour. of Agri. Research,* **3,** 311-330.
8. BANKS, NATHAN. Geographical Distribution of Neuropteroid Insects, with Analysis of the American Insect Fauna. *Ann. Entom. Soc. of America,* **8,** 125-135.
9. BANKS, NATHAN. Miscellaneous Notes. *Proc. Entom. Soc. of Washington,* **17,** 146-147.
10. BARBER, H. S. The Breeding Place of *Dermestes elongatus.* *Proc. Biol. Washington,* **27,** 145-146.
11. BARNARD. A Mistake of a Butterfly. *Nature,* **96,** April, 15.
12. BARROWS, WILLIAM. The Reactions of an Orb-Weaving Spider, *Epeira scloptera,* to Rhythmic Vibrations of the Web. *Biol. Bull.,* **47,** 316-332.

13. BISHOPP, D. and PARMAN. Notes on Certain Points of Economic Importance in the Biology of the House-Fly. *Jour. of Econ. Entom.*, **8**, 54-71.
14. BLACKMAN, M. W. Observations on the Life-History and Habits of *Pityogenes hopkinsi* Swaine. *New York State College of Forestry, Technical Publication*, **16**, 11-66.
15. BLAIR, K. G. Luminous Insects. *Nature*, **96**, 411-415.
16. BROCHER, F. Researches sur la Respiration des Insectes Aquatiques Adultes. Les Dyticides. *Ann. Biol. Lacustre*, **7**, 5-39.
17. BROMLEY, STANLEY W. Asilids and Their Prey. *Psyche* (1914), **21**, 192-198.
18. BRAUN, A. F. Life Histories of N. A. Tineida. *The Canad. Entom.*, **47**, 104-108.
19. BUDDENBROCK. W. Ueber das Vorhandensein des Lichtdruckenreflexes bei Insecten sowie bei dem Krebse *Branchipus grubei. Sitsungsberichte Heidelberger Akad. d. Wiss.*, Ab. **1**, 10 pp.
20. BUTTEL-REEPEN, H. Haben die Bienen einen Farben und Formsinn? *Die Naturwissenschaften*, **13**, 80-82.
21. CALLARD, M. Appetite of Slugs for Green Material. *The Zoologist*, 1915, 159.
22. CARTER, H. R. Notes on Anopheles Production from a Malarial Survey. *Amer. Jour. of Trop. Diseases and Preventive Medicine*, **2**, 753-758.
23. CHAPMAN, R. N. Observations on the Life History of *Agrillus bilineatus. Jour. of Agri. Research*, **3**, 283-294.
24. CLAUSEN, C. P. A Comparative Study of a Series of Aphid-Feeding Coccinellidae. *Jour. Econ. Entom.*, **8**, 487-491.
25. CLEARE, L. D. A Butterfly Injurious to Cocoanut Palms in Br. Guiana. *Bull. Entom. Research*, **6**, 273-278.
26. CONSTANT, A. F. The Habits, Life-History and Structure of the Bloodsucking Muscid Larva (*Protocalliphora azurea*). *The Jour. of Parisitology*, **1**, 34-150.
27. COOK, A. J. The Relation of Bees to Agriculture. *Mo. Bull. State Com. of Horticulture*, **4**, 426-427.
28. CRIDDLE, N. Some Inhabitants of a Sand Plain in June. *The Canad. Entom.* **47**, 24-30.
29. CUTHBERT, H. G. Selective Instinct in Bees. *The Irish Naturalist*, **24**, 188-189.
30. DAVIS, J. J. Cages and Methods of Studying Underground Insects. *Jour. of Econ. Entom.*, **8**, 140-149.
31. DIGUET, LEON. Nouvelles Observations sur le Mosquero ou Nid D'Araignees Sociales. *Bull. de la Societe Nationale D'Acclimatation de France*, **62**, 240-249.
32. DUNN, L. H. Observations on the Preoviposition, Oviposition and Incubation Periods of *Dermacenton nitens* in Panama. *Entom. News*, **26**, 214-219.
33. ESSENBERG, C. The Habits and Natural History of the Backswimmers, *Notonectidae. Jour. of Animal Behav.*, **5**, 381-390.
34. ESSENBERG, C. The Habits of the Water-Strider *Gerris remiges. Jour. of Animal Behav.*, **5**, 397-402.
35. FANTHAM, H. B. Insect Pests and War. *Nature*, **95**, 265-266.
36 FELT, E. P. The Gall Midges of the Pine. *Bull. Brooklyn Entom. Soc.*, **10**, 74-76.
37. FLOERSHEIM. Some Notes on the Papilionids. *The Entomologist London*, 1915, 225-229.
38. FORBES, S. A. The Ecological Foundations of Applied Entomology. *Ann. Entom. Soc. of Amer.*, **8**, 1-19.
40. FOSTER and JONES. The Life History and Habits of the Pear Thrips in California. *U. S. Dept. of Agri., Bull.*, 173.
41. FRISCH, K. VON. Der Farbensinn und Formsinn der Biene. *Zool. Jahrb.*, Abt. f. Allegmein Zool., **35**, 1-183.
42. FROHAWK, F. W. Hibernating Examples of *Vanessa antiopa. The Entomologist London*, 1915, 242-243.
43. FULLER, CLAUDE. Observations on some South African Termites. *Ann. of the Natal Museum*, **3**, 329-504.

44. FUNKHOUSER, W. D.   Life History of *Vanduzea arquata Say* (Membracidae). *Psyche*, **22**, 183-199.
45. GERHARDT, W.   Copulation und Spermatophoren von Grylliden und Locustiden. *Zool. Jahrb. Abth. f. Syst.*, **36**, 1-64.
46. GILLETT and BRAGG.   Notes on Some Colorado Aphids Having Alternate Food Habits. *Jour. of Econ. Entom.*, **8**, 97-103.
47. GIRAULT, A. A.   A Birdbug Attacking Human Beings. *Entom. News*, **26**, 221-222.
48. GIRAULT, A. A.   Duration of the Pupal Stage of *Adalia* 15-*punctata*. *Entom. News*, **26**, 223.
49. GIRAULT, A. A.   Geotaxis in *Trichogramma minutum* Riley. *Entom. News*, **26**, 131.
50. GIRAULT, A. A.   Larva of *Heliotus obsoluta* Fabricius Eats a Larva of *Empretia*. *Entom. News*, **26**, 226-227.
51. GLASER, R. W.   Bacterial Diseases of Caterpillars. *Psyche*, **21**, 184-190.
52. H. A. B.   A Fruit Fly Attacking Papaw Fruits. *Agri. News Barbados*, **14**, 106.
53. HADDON, K.   On the Methods of Feeding and the Mouthparts of the Larva of the Glow-Worm (*Lampyris noctuluca*). *Proc. Zool. Soc. London*, 1915, 77-85.
54. HADWEN, S.   Warble Flies.   A Further Contribution on the Biology of *Hypoderma lineatum* and *H. bovis*. *Parisitology*, **7**, 331-338.
55. HANCOCK, J. L.   Pink Katydids and the Inheritance of Pink Coloration. *Entom. News*, **27**, 70-82.
56. HARGITT, C. W.   Observations on the Behavior of Butterflies. *Jour. of Animal Behav.*, **5**, 250-257.
57. HARGRAVES, E.   The Life-History and Habits of the Greenhouse White-Fly (*Aleyrodes vaporarium Westd.*). *Ann. App. Biol.*, **1**, 303-334.
58. HEGNER, R. W.   The Advantages Chrysomelid Beetles Secure by Concealing Their Eggs. *Psyche*, **22**, 24-27.
59. HEWITT, C. C.   An Early Reference to the Relations of Insects to Disease. *The Canad. Entom.*, **47**, 396-399.
60. HEWITT, C. C.   Notes on the Pupation of the House-Fly (*Musca domestica*) and Its Mode of Overwintering. *The Canad. Entom.*, **47**, 73-78.
61. HEWITT, C. C.   Observations on the Feeding Habits of the Stable-Fly. *Trans. Royal Acad. of Canada*, **8**, 37-42.
62. HEWITT, C. C.   The House Fly.   Its Structure, Habits, Development, Relation to Disease and Control.   Cambridge, 382 pp.
63. HEWITT, T. R.   The Larva and Puparium of the Fruit-Fly. *Agri. News Barbados*, **14**, 313-316.
64. HIRST, S.   On Some New Acarine Parasites on Rats. *Bull. Entom. Research*, **6**, 183-190.
65. HOWLETT, F. M.   The Chemical Reactions of Fruit-Flies. *Bull. of Entom. Research*, **6**, 297-306.
66. HYSLOP, J. A.   Observations on the Life History of *Mercantha contracta*, *Psyche*, **22**, 44-48.
67. ILLINGWORTH, J. F.   Notes on the Habits and Control of the Chicken Flea (*Echidnophaga gallinacea*). *Jour. of Econ. Entom.*, **8**, 492-495.
68. KENNEDY, C. H.   Notes on the Life History and Ecology of the Dragonflies (Odonata) of Washington and Oregon. *Proc. U. S. Nat. Hist. Mus.*, **49**, 259-345.
69. KINCAID, E.   The Effect of Color on the Thistle Butterfly. *Nature Study Review*, **11**, 340-341.
70. KNAB, F.   Commensalism in Desmometopa. *Proc. Entom. Soc. Wash.*, **17**, 117-121
71. KNAB, F.   The Secretions Employed by Rhynchophorous Larvae in Cocoon-Making. *Proc. Entom. Soc. of Wash.*, **17**, 154-158.
72. KNAB and BUSCH.   Mosquitoes and Sewerage Disposal. *Jour. of Agri. Research*, **2**, 333-338.

73. Krecker, F. H. Phenomena of Orientation Exhibited by Ephemeridae. *Biol. Bull.*, **29**, 381-388.
74. Kreuger, E. Physiologisch-Biologiche Studien-Ueber die Bedeutung der Luft des Elythrabraums bei Dysticus. *Acta Universitasis Lundensis (nova series)*. **10**, No. 13, 20 pp.
75. Leceaga, E. How War Has Been Waged in Mexico against the Mosquito. *The Amer. Jour. of Tropical Diseases and Preventative Medicine*, **2**, 118-123.
76. Leuderwandt, H. Zur Lebensweise Brasilianischer Cincindeliden. *Zeit. f. Wiss. Insektenbiol.*, **11**, 25-27.
77. Lloyd, J. T. Wood-Boring Trichoptera. *Psyche*, **22**, 17-21.
78. Lovell, J. H. A Preliminary List of the Anthophilous Coleoptera of New England. *Psyche*, **22**, 109-117.
79. Lovell, J. H. Insects Captured by the *Thomisidae*. *The Canad. Entom.*, **47**, 115-116.
80. Lovell, J. H. The Origin of Anthophily among the Coleoptera. *Psyche*, **22**, 67-84.
81. Lyon, Harold. Does the House Fly Hibernate? *Psyche*, **22**, 140-141.
82. Lyon, Harold. Notes on the Cat Flea (*Ctenocephalus felis Bouche*). *Psyche*, **22**, 124-132.
83. McAtee, W. L. A Remarkable Flight of Caddis Flies and Chironomids. *Science*, **42**, 694-695.
84. McDermott, F. A. Notes on the Reaction of the House-Fly to Air Currents. *Jour. of Animal Behav.*, **5**, 73-74.
85. McIndoo, N. E. The Olfactory Sense of Coleoptera. *Biol. Bull.*, **28**, 407-460.
86. McShane, H. the *Phlebotomys papatsch* the Transmitter of the Three Days Fever. *Amer. Jour. of Trop. Diseases and Preventative Med.*, **2**, 815-818.
87. Macfie, J. W. S. Observations on the Bionomics of *Stegomyia fasciata*. *Bull. Entom. Research London*, **6**, 205-230.
88. Mann, W. M. A Cursorial Tick. *Psyche*, **22**, 60.
89. Marcovitch, S. The Biology of the Juniper Berry Insects, with Description of New Species. *Ann. Entom. Soc. of Amer.*, **8**, 103-188.
90. Mitzmain, M. B. An Experiment with *Stomoxys calcitrans* in an attempt to Transmit a Filaria of Horses in the Philippines. *Amer. Jour. of Trop. Diseases and Preventative Med.*, **2**, 759-763.
91. Nanayama, S. Notes on the Life-History and Habits of the Rose Scale *Aulacaspis rosae*. *Jour. of Entom. and Zool.*, **7**, 45-54.
92. Nicholson, C. Hibernation of Vespa vulgaris. *The Entom. Record*, 1915, 115-116.
93. Noyes, Alice A. The Biology of the Net-Spinning Trichoptera of Cascadilla Creek. *Ann. Entom. Soc. Amer.*, **7**, 251-271.
94. Nutall, G. H. F. Observations on the Biology of the Ixodidae; Artificial Parthenogenesis in Ticks. *Parasitology*, **7**, 408-461.
95. Pearse, A. S. and White, Gertrude M. Recent Literature on Tropisms and Instinctive Activities. *Psychol. Bull.*, **12**, 231-290.
96. Pictet, A. Reactions Thermotropiques chez les Insectes (Resume). *Compt. Rendu Sciences de la Soc. de Physique et d' Histoire Naturelle de Geneve*, **31**, 54-56.
97. Pierce and Cushman. A Few Notes on the Habits of Parasitic Hymenoptera. *Proc. Entom. Soc. of Washington*, **17**, 164-167.
98. Ping, C. Some Inhabitants of the Round Gall of the Goldenrod. *Jour. of Entom. and Zool.*, **7**, 161-179.
99. Rattray, R. H. Notes on the Larval and Pupal Stages in some of the Sesiidae. *The Entomologist*, London, 1915, 9-12.
100. Rau, Phil. Duration of Pupal and Adult Stages of the Meal Worm *Tenebro obscurus* Linn. *Entom. News*. **26**, 154-157.
101. Rau, Phil. The Ability of the Mud-Dauber to Recognize Her Own Prey. *Jour. of Animal Behav.*, **5**, 240-244.
102. Rau, Phil. The Longevity and Mating Habits of *Dicromorpha viridis* Scud. *Entom. News*, **26**, 27-28.

103. RICHARDSON, C. H.   An Observation on the Breeding Habits of *Stigmus conestogorum* Rohwer. *Psyche*, **22**, 104-105.
104. RUGGLES, A. G.   Life History of *Obera tripunctata*. *Jour. of Econ. Entom.*, **8**, 79-85.
105. SANDERS, GEO. E.   Carnivorous Habits of *Xylina Bethunei* G. & R. *Canad. Entom.*, **47**, 183-184.
106. SCHWARZ, ERNST.   Observations on the Habits of *Catocala titania* Dodge. *Entom. News*, **27**, 67-69.
107. SEVERIN, HENRY H. P. and HARRY C.   The Stimuli which Cause the Eggs of the Leaf-Ovipositing Tachinidae to Hatch. *Psyche*, **22**, 132-137.
108. SHANNON, R. C.   Captures of the Syrphid Fly *Merapiodes villosus*. *Proc. Entom. Soc. of Washington*, **17**, 147-148.
109. SHELFORD, V. E.   Suggestions as to the Original Habitat and Distribution of Various Native Insect Pests. *Jour. of Econ. Entom.*, **8**, 171-174.
110. SJOSTEDT, Y.   La Construction des Nids chez les Insectes. *Revue Gen. des Sciences Pures et Appliques*, **26**, 85-90.
111. SKINNER, HENRY.   How does the House-Fly Pass the Winter? *Entom. News*, **26**, 263-264.
112. SNYDER, T. E.   Biology of the Termites of the Eastern United States, with Preventative and Remedial Measures. *Bureau of Entom., U. S. Dept. of Agri.*, Bull. 94, 13-85.
113. STELLWAAG, F.   Ueber das Biogenetische Grundgesetz im Leben der Insektenstaaten. *Naturwiss. Wochensch.*, **14**, 426-427.
114. STELLWAAG, F.   Zum Farbensinn der Bienen Liefert Kranichfeld in Biologischen Zentralblatt. *Naturwiss. Wochenschrift*, **14**, 427-428.
115. STEPHEN, J.   Die Spinnkunst der Raupen. *Natur, Halbmonatschrift f. alle Naturfreunde*, 1915, 427-430.
116. STURTEVANT, A. H.   Experiments on Sex Recognition and the Problem of Sexual Selection in *Drosophilia*. *Jour. of Animal Behav.*, **5**, 351-366.
117. TORRE BUENO, J. R. de la.   Phototropism in Heteroptera. *Bull. Brooklyn Entom, Soc.*, **11**, 90-96.
118. TURNER, C. H.   Literature for 1914 on the Behavior of Spiders and Insects other than Ants. *Jour. of Animal Behav.*, **5**, 415-445.
119. TURNER, C. H.   Notes on the Behavior of the Ant-Lion with Emphasis on the Feeding Activities and Letisimulation. *Biol. Bull.*, **29**, 277-307.
120. TURNER, C. L.   Breeding Habits of *Ceuthophilus latens*, the Camel Cricket. *Bull. Wis. Nat. Hist. Soc.*, **13**, 32-41.
121. WALLENGREN, H.   Physiologischbiologische Studien ueber die Atmung der Aeschnalarven. *Acta Universitatis Lundensis*, **10**, No. 8, 28 pp.
122. WASMANN and VALKENBURG.   Ein Neues Buch Ueber das Leben und Wesen der Bienen. *Die Naturwisssh.*, **38**, 485-488, 497-500.
123. WEBSTER, F. M.   Migrating Notes on the Milkweed Butterfly. *The Canad. Entom.*, **47**, 406.
124. WEISS, H. B.   Notes on the Tropic Reactions of *Macrodactylus subspinosus*. *The Canad. Entom.*, **47**, 152.
125. WHEELER, W. M.   Ants and Bees as Carriers of Pathogenic Micro-Organisms. *Amer. Jour. of Trop. Diseases and Preventative Med.*, **2**, 160-168.
126. WHEELER, W. M. and WILLIAMS, F. X.   The Luminous Organ of the New Zealand Glow-Worm. *Psyche*, **22**, 36-43.
127. WILLIAMS, C. D.   The Pea Thrips (*Kakothrips robustus*.) *Ann. App. Biol.*, **1**, 222-246.
128. WOODWORTH, C. W.   The Rate of Hatch of Scale Insect Eggs. *The Canad. Entom.*, **47**, 98-99.
130. ZETEK, J.   Behavior of *Anopheles albimanus* Wied and *tarsimaculata* Goeld. *Ann. Entom. Soc. of Amer.*, **8**, 221-271.

LITERATURE FOR 1915 ON ANTS AND MYRMECOPHILS

MORRIS M. WELLS
University of Chicago

Bonner (1) presents a careful study of the wintering activities of Formica *picea*, beginning his observations in January. At this time the moor in which he made his studies was frozen solid to a depth of 10-15 cm. The air temperature in the day time was about 7° centigrade but it dropped to −10° at night. Nests of F. *picea* were chopped out of the frozen sphagnum and the ants were often found clumped together in the center of the nest and apparently frozen solid. An hour in a warm room restored them to normal activity. Bonner found that the large ants tended to form the center of the clump in the winter nest while the smaller, younger ones were often outside and perhaps not in the main clump but scattered through the galleries. Bonner also reports some experiments performed to determine the effect of submergence in water upon ants. His results confirm those of other workers who have found that ants can live under water for hours in some cases.

Bonner (2) discusses the matter of the parasitism of Lasius *fuliginosus* on L. *umbratus* in connection with the color of the nest coverings and lining of the galleries and also with regard to the behavior of L. *fuliginosus* toward Claviger *longicornis* which latter is a normal guest of L. *umbratus*. He experimented by placing a specimen of C. *longicornis* in a nest of L. *fuliginosus*. The ants touched the beetle but did not pay any special attention to it. Two weeks later he took the beetle out of the nest. It had not been harmed. Bonner thinks that the beetle may start development in the umbratus nest but that the larger number of host individuals present with the coming in of *fuliginosus* may result in conditions that are more favorable to the development of the beetle than those existing in the nest when L. *umbratus*

is in charge. This suggestion is made by Bonner to explain the finding of over 100 specimens of C. *longicornis* in a *fuliginosus* nest by Rosenberg in 1911. The difference in the color of the *umbratus* and the *fuliginosus* nests he attributes to the oxidation of the nest materials which at first are light and yellowish but later turn black

Brun (3) published this book in 1914. It is a critical experimental study of ant behavior and a contribution to the mneme theory. It is listed here as it is a work that should not go unrecorded in a list of ant literature.

Crawley (5) records observations regarding the behavior of fertilized females of Lasius *umbratus*. He states that such females at once devour one or more workers of L. *niger* if the latter are available. The author thinks that this act produces the proper odor, physiological state or other condition necessary for the acceptance of the *umbratus* female into the nests of L. *niger*. He found that queenless colonies of L. *niger* accepted these queens readily while they usually killed queens that were introduced into their nest before they had eaten a niger worker. Even L. *niger* colonies with queens did not kill the *umbratus* queens for some time if the latter had previously eaten a niger worker.

Crawley (6) here gives a list of ants collected in British Guiana by Mr. E. Bodkin. With many of the species he gives rather full habitat and breeding notes making the paper one of considerable interest.

Davis (7) found on July 26, 1914, on Long Island, a nest of Formica *fusca* var. subsericea that measured 18 feet in diameter. He noted that while the ants of this species are usually not very pugnacious those of this nest seemed to be quite vicious. The nest was in an open wood of pines and oaks. It was apparently the work of one colony.

Donisthorpe's book (8) on ants has received mention in the Entomological Record (1915) p. 237 and in Science (1916) p. 316-18. These reviews have been extremely favorable. The book stands out as the important publication on ants in the year 1915. As is to be expected in so large a publication many phases of the subject of ants and their relationships are discussed. In general the material can be divided into a first part which deals with the external and internal anatomy of ants, a second part that treats of ant physiology and a third division that dis-

cusses fully the psychology of ants. The book contains many original observations on the behavior of ants especially in the section devoted to Lasius. In the psychological discussion the author speaks of the ants throughout as though they were possessed of human consciousness. This is hardly justifiable at the present stage of our knowledge.

Donisthorpe (9) here records observations on the marriage flights of Donisthorpe sp. (Lasius sp.). He calls attention to the fact that these flights seem to be timed to some extent by weather conditions such as temperature, humidity, etc.

Elliott (10) describes fungi found in the nests of two British ants (Lasius *niger* and L. *umbratus*). The characteristic fungi were found in all the nests examined and no other species were found. The author thinks that perhaps the ants weed out the foreign species

Emery (11) in 1908 and 1909 succeeded in starting two experimental societies of Polyergus *rufescens*. These colonies were united in 1910 and the single resultant colony has been kept going since that time. In the present paper the author tells of taking the nest of Amazons into his garden where he opened it and allowed the ants to explore the surrounding territory. He was thus enabled to make detailed observations on the behavior of the ants. He observed them while they raided colonies of Formica *fusca* var. *glebaria* and F. *rufibarbis*. In July 1914 the ants were allowed to establish themselves in the soil in a courtyard of his villa. For the remainder of the summer and up to Oct. 2, the ants made sorties into the surrounding territory but got no plunder as there were no nests of slave species in the yard. Emery believes that workers of the Amazons, leaving the nest singly, discover nests of slave species and returning, determine at least the initial direction taken by the army when it goes out. He noted that most of the sorties occur late in the afternoon, usually between 4:20 and 7:00 P. M.

Flint (12) records observations made every night for nearly two months on movements of Lasius *niger americanus* at Bloomington, Ill. It was frequently noted that on warm nights when the ants were very active they would attack and kill many small insects that came near their nests.

Jones (13) in a short paper includes ants among the insects that carry the spores of pear blight in California. The list given

by him is as follows: honey-bees, flies, ants, pear thrips, and apple aphids.

Mann (14) here gives some ecological data that is of value. In the main the paper is concerned with the description of a new species that is, according to the author, an addition to the species that occur at isolated points on the north coast as relicts of the ancient coastal plain fauna.

This paper by Mann (15) is largely a description and listing of other insects that the author has found in the nests of ants in Hayti. There are however occasional notes concerning the behavior of the ants and their guests. He records the following families of insects as occurring as guests in the nests of ants: Gryllidae, Cercopidae, Membracidae, Lathridiidae, Bethylidae, Syrphidae.

Morrill (16) in working on remedies for the suppression of the damage of the harvester ant in Arizona, reports that he has found that Carbondisulphide cannot be forced into the galleries of the ants even with a high pressure pump. He found that London purple kills the ants readily and with little expense attached to the treatment of the soil. He states that $1.17 worth of the poison killed the ants in ten acres of ground where the nests of the ants were estimated to occupy one and one fourth acres.

In this paper Morrill (17) reports that carbondisulphide can be used successfully in combating the harvester ant in Arizona if the liquid is introduced into the nest and the hill then covered with a galvanized tub.

Smith (18) states that termites are damaging the lemon trees in the vicinity of Germantown, California.

In this account by Snyder (19) we have a very important and valuable addition to our knowledge of the biology of our North American termites. The account is based largely upon investigations carried on in 1910 and 1911 as to the character and extent of damage done to telephone and telegraph poles, mine props, etc., by wood boring insects. The investigation showed termites to rank among the most destructive agencies attacking crude and finished forest products. The species that he has considered are distributed widely over the United States.

The booklet is divided into a number of sub heads as follows: Classification, history, biological experiments, communal organization, polymorphism (different castes), life cycle, canni-

balism, situation of the different forms in the nest, the nuptial flight, the establishment of new colonies, the royal pair and other reproductive forms, association with ants, termitophilous insects, parasites, damage to forest products, preventatives, remedies and immune woods. The paper contains reports upon a considerable number of experiments of one kind and another. There are also recorded many interesting original observations. Concerning the relation of termites to ants the author says that while ants and termites are commonly found inhabiting the same log or stump, yet ants are the enemies most to be feared by termites, as they will capture and carry away the members of a disorganized colony. Ordinarily the relations between termites and ants seem to be neighborly and peaceful. If the termite colony is opened up and disorganized, the ants at once take advantage of the opportunity and carry away the termites which offer but little resistance. Ants of several species may be attracted to such a helpless colony from a distance. The soft bodied soldiers are apparently not very effective in such an emergency, although in the narrow channels of the colony, where the powerful head with open mandibles is the only front presented to the marauding ants, they afford some protection to the colony.

Two species of carpenter ants (Camponotus *pennsylvanicus*, Mayr and Cremastogaster *lineolata* Say) are the ants which more commonly have been found associated with termites in eastern U. S. The latter species, due to its small size and rapid movements is a most formidable enemy.

Ants greatly diminish the number of the colonizing individuals at the time of the swarm, carrying them away as they are running about on the ground. Soldiers and workers guard the breaches from which the sexed adults have emerged.

Theobald (20), describes several new species of Myrmecophilous aphides and gives some behavior notes.

Turner (21) watched the mating activities of Lasius *niger* in St. Louis on Sept. 17, 1913. The entire mating behavior except the copulatory act was observed. In discussing these activities he points out that they are not readily explainable upon the basis of simple tropisms. He states that at this time he observed Formica species, present at the mating activities of Lasius, to be eating the Lassius males and sometimes the females also.

Wheeler (22) outlines the question of the spinning of cocoons by ant larvae and calls attention to the fact that in the families Dorylinae, Myrmicinae, and Dolichoderinae the larvae never spin cocoons before pupation. He further points out that he has already published evidence as shown by the ants found in Baltic amber that there must have been forms with naked pupae at least two million years ago. This would seem to settle conclusively, in the negative, any question as to the recent origin of the non-spinning habits of certain ant larvae. The fact that the mature ant larvae cannot spin its cocoon without first being buried in a small mass of rubbish or in the earth makes it possible that the origin of the non-spinning habit is the result of a dropping out of this burying behavior upon the part of the adults rather than to a loss of spinning ability upon the part of the larvae. Wheeler cites a considerable list of ant species in which the larvae are great spinners but in which the spinning activities go toward the making of a nest for the entire colony and the larvae never spins a cocoon for itself. As an example of this altruistic behavior the author records some observations which he made in Australia on Oecophylla *virescens*. He spent some time observing under favorable conditions the nest making activities of this species which makes its nest by weaving together the leaves on a branch of a tree. The weaving is done by the adults but the larvae furnish the silk and are carried about in the mandibles of the adult and used as a shuttle until their supply of silk is exhausted. He noted also that young larvae were most commonly used. Most of the work is done from the inside of the nest and is therefore not easily observed. Wheeler, however, fortunately saw part of the work being done on the outside of the nest.

In the latter part of the paper Wheeler discusses briefly coloration of ants in general. 1. Some ants are white or light colored. These forms usually live in the dark. 2. A number of species exhibit a progressive development from red, brown or black to the interference colors. This is noticeable in ants living in hot dry sunny climates. Many of the Australian ants show interference colors. 3. There are large eyed tropical ants that are black and yellow with red spots and bands. Their general appearance is made more striking by the presence of a white or

golden pubescence. The ants in moist places usually show little or no pubescence.

Wheeler (23) here gives some habitat data along with a description of a new variety of Formica *fusca*. He found this new variety in a peat-bog near Petersham, Mass. The author also gives a list of the ants one is likely to find in the cold bogs of the Northern United States, and British America.

REFERENCES

1. Bönner, W. Die Ueberwinterung von Formica picea and andre biologische Beobachtungen. *Biol. Cent.*, **35**, 65-77.
2. Bönner, W. Der temporare soziale hyperparasitismus von Lasius fuliginosus und seine Beziehungen zu Claviger longicornis. *Zeit. f. Wiss. Insektbiol.*, **11**, 14-20.
3. Brun, R. Die Raumorientierung der Ameisen und das Orientierungs-problem im allegemeinen. Jena, Gustav Fischer, 1914, pp. VIII2+34. 5 figs. Bibliography with 124 titles.
4. Cornetz, V. Observations nocturnes de trajets de fourmis. *Rev. Suisse Zool.*, **22**, 581-95.
5. Crawley, W. C. A remarkable marriage flight of ants and some theories. *Entom. Record*, **27**, 205-6.
6. Crawley, W. C. Ants from British Guiana. *Ann. and Mag. of Nat. Hist.*, London, **17**, 366-78.
7. Davis, W. T. A Long Island ant's nest 18 ft. in diameter. *Jour. of N. Y. Ent. Soc.*, 1915, 69.
8. Donisthorpe, J. K. British Ants, Their life history and Classification. Wm. Brendon and Sons, Ltd. pp. XV+373; 18 pls. 92 figs.
9. Donisthorpe, H. Marriage flights of Donisthorpea species on August 8th. *Entom. Record*, **27**, 206.
10. Elliott, J. S. Bayliss. Fungi in the nests of ants. *Trans. Brit. Mycol. Soc.*, **5**, 138-42.
11. Emery, C. Histoire d'une societe experimentale de Polyergus refescens. *Rev. Suisse. Zool.*, **23**, 385-400.
12. Flint, W. P. On the capture of living insects by the cornfield ant (Lasius niger americanus). *Jour. Econ. Entom.*, **7**, 476-478.
13. Jones, B. J. The Natural modes of distribution of pear blight in California. *Mo. Bull. Com. Hort. Cal.*, **3**. Also U. S. Dept. Agr., **33**.
14. Mann, W. M. A new form of a southern ant from Naushou Island, Mass. *Psyche*, **22**, 51.
15. Mann, W. M. Some Myrmecophilous insects from Hayti. *Psyche*, **22**, 161-66.
16. Morrill, A. W. Ant, harvester, remedies. *U. S. Dept. of Agric.*, **32**, 549-50.
17. Morrill. Ants, harvester, remedies. *U. S. Dept. Agric.*, **33**, 57.
18. Smith, H. S. Termites (Insect Notes). *Cal. Comm. Hort.*, **4**, 53.
19. Snyder, T. E. Insects injurious to forests and forest products. Biology of the termites of the eastern United States with preventative and remedial measures. *U. S. Dept. Agric. Bull. Bur. Ent.* No. 94, Pt. 2. pp. V+13-88.
20. New Myrmecophilous aphides. *Entom. Record*, **27**, 52.
21. Turner, C. H. The mating of Lasius niger. *Jour. of Animal Behav.*, **5**, 337-40.
22. Wheeler, W. M. On the presence and absence of cocoons among ants, the nest spinning habits of the larvae and the significance of the black cocoons among certain Australian species. *Ann. of Entom. Soc. Am.*, **8**, 323-42.
23. Wheeler, W. M. A new bog Inhabiting variety of Formica fusca. *Psyche*, **22**, 203-6.

LITERATURE FOR 1915 ON THE BEHAVIOR OF VERTEBRATES

STELLA B. VINCENT

Chicago Normal College

SOUND

Mammals.—The auditory sensitivity of the white rat still continues to engage the attention of Hunter (13). The work here reported has its chief interest in the substantiation of his previous experimentation through the introduction of many and varied controls. The method and the apparatus was described last year. The rats failed to show, through any behavior, discrimination between the sound of a tuning fork 896 dv and the absence of the sound in 650 trials. Rats trained to react to a Galton whistle tone of 3906.07 dv would not react to a tuning fork 1152 dv plus 1280 dv or to the fork 1280 dv when each of these were substituted for the standard stimulus. The author says: " When a whistle of the same pitch was sounded in an adjoining room, so that the distance probably eliminated the noise factor, the rats failed; although they made a significantly larger per cent of correct reactions when the standard stimulus was decreased in intensity to match the intensity of the distant whistle. Further, these same rats reacted properly when either of the following noises were substituted for the standard whistle: (a) the rush of air through the whistle; (b) sound of rush of air made with lips; (c) clapping of hands. The rats reacted successfully to 1280 dv on the standard whistle *but failed when the same pitch* was sounded on the tuning fork."

He concludes "(1) There is a practical insensitivity to many pitches in the lower region of the scale for the white rat. This apparently goes along with a sensitivity to noise of the same predominant pitch.

"(2) Differences in total complexity and intensity may be considerable without making discrimination possible.

"(3) Apparent reaction to tones are most probably made to accompanying noises.

"(4) If after all there is a sensitivity to tonal stimuli as here tested, then, for the rat, tones and noises are very different classes of stimuli."

Miss Barber's work (3), from the same laboratory, was concerned primarily with the accuracy of the localization of sound and the relation of the intensity, absolute and relative, to the accuracy of this response. The apparatus was an octagonal shaped box whose floor was divided into 32 sections. This box stood on a table surrounded by a stimulus screen and the operator was invisible. The stimuli were tapping with an instrument whose predominant pitch was 256 dv, a tuning fork and an organ pipe of the same pitch, hissing through the teeth and tapping with a lead pencil. A regular order of presentations was followed in which each of the 32 sections of the box was given once every four days. There was an attempt made to control kinaesthetic, olfactory and visual clues. Only seven rats were used.

The writer while realizing the defects of the apparatus believes that the rat is able to localize noise with an average accuracy of two to four inches under the conditions of the experiment. She thinks that the auditory factor which in general determined the accuracy of the response was probably the relative intensity of the sound to the two ears. " The rats were not only unable to localize pure tones from tuning forks but absolutely ignored them."

CHEMICAL SENSITIVITY

Fish.—Wells, (36) using Shelford's apparatus and methods, reports some experiments which deal with the reaction of fresh water fishes to acidity and alkalinity. He finds that they select a slight acidity in a gradient when the other possible choices are neutrality and alkalinity but choose a slight alkalinity in preference to neutrality. The writer calls attention to the fact that the distribution of plankton in the lakes of Wisconsin and New York shows a very interesting correlation with the chemical reactions of the water of the lakes.

An experimental study of the movements of herring and marine fishes was undertaken by Shelford and Powers (25) at the Puget Sound Marine Station. This study is important because we do not know enough of the chemical condition of

the water and its effects upon the movements, migrations and general health of the animals. We should know more of the chemical conditions in which the animals breed in order to secure the preservation of their natural breeding grounds against the contamination which follows as a result of advancing civilization and industry. The study is extremely suggestive as to the physiological explanation of the migration of fishes, etc. The economic value of such work is not sufficiently appreciated. The authors say:—"The extreme sensitivity of the fishes studied as shown by their detection of slight deviations from neutrality, of temperature differences as small as .2 of a centigrade degree, of small fractions of a cubic centimeter per litre of hydrogen sulphide, etc., makes it very clear that there is no difficulty in fishes determining the direction to large rivers from hundreds of miles out at sea or finding their way into any bay or harbor which their particular physiological condition at the time demands."

OLFACTION

Mammals.—The only article dealing exclusively, or predominately perhaps one would better say, with olfaction in animal life is one by Seffrin (24). This investigation attempts to find odorous substances and the necessary amounts of each to cause a reaction. The registration of these reactions was by means of the breathing movements,—a method previously used in similar experimentation by Heitzenröder. The apparatus and method are fully described. He used such substances as ether, formaline, xylol, oil of rose, violet, extract of vanilla, etc., and also mixed odors of animal origin,—urine, blood, flesh extracts, etc. He found the dog less sensitive than man to the first class of odors but far more so to those animal odors more closely related to his life. Tables are given showing the amount of the stimulus and the time of the reaction.

VISION

Mammals.—In a paper included in the transactions of the Illuminating Engineering Society, Johnson (16) reports, with clear comments, some recent experiments of his own and others in the field of animal vision. De Voss and Ganson (8) publish some work on the color blindness of cats. They say:—"The term 'color blindness' is used in the title of this paper not

because color vision should be denied an animal as the result of a single investigation, no matter how carefully it may be conducted, but because the results of our experiments certainly make the term ' color blindness ' a less presumptuous one than ' color vision ' when applied to these animals.'' Colored papers which were tested by two observers by the flicker method were the stimuli. Nine animals in all had 100,000 trials—one cat alone had 1500 trials. Colors were first presented in easily discriminable pairs until the selection of the food color was rapid and accurate and then the distance between these colors was varied until confusion colors were found. When one cat confused certain colors the same colors were immediately given to another cat, called the follower, to confirm the results. Thirty consecutive choices with twenty-four right in a series was called a discrimination and six hundred failures counted as complete confusion. When such confusion colors were finally found they were then paired with grays of the same flicker equivalent. The authors say in conclusion:—'' It seems probable that cats cannot distinguish any one color from all the shades of gray under light adaptation. It seems probable that cats may be totally color blind by daylight.'' They also found that both red and blue had a low stimulating power and think that possibly cats have a shortened (gray) spectrum. Yet blue was not confused with black. The paper represents an enormous amount of work. The tables are all given.

Birds.—A preliminary report of the color vision of the Ring Dove is given by Yerkes (40). The birds were first tested for their reaction to achromatic stimuli. After two doves had been trained to discriminate a bright from a dark area of the same size they were tested for preference for spectral red 626 to 640 or spectral green 498 to 510. A modification of the Yerkes-Watson spectral color vision apparatus was used. The results for the two birds used differed and indicated that the values for these two wave lengths might be very different for the two birds.

Fishes.—One of the best papers published during the year is von Tschermak's excellent review of the results of his own investigations and those of others on the vision of fishes (29). Since the article itself is a summary it is difficult to characterize it. It treats of the physical conditions which affect vision in water,

brightness vision, questions concerning the color sense, adaptation of skin to the water ground, range of vision, monocular and binocular vision, position and movements of the eyes, and compensatory changes of the eyes in relation to equilibration. The object of the article as stated by the author is first to give a reliable account of the knowledge gained in the last ten years of the vision of fishes and second to awaken and stimulate interest in the many biological questions that still await solution.

TROPISMS AND ORIENTATION STUDIES

Observers have differed as to which end of Amphioxus is in advance during swimming. While working at the Bermuda Station Arey (1) had an opportunity to observe the swimming habits of a West Indian lancelet. He says that while Amphioxus can swim backward for short distances its normal orientation is with the anterior end in advance. Kanda (17) discusses geotropisms in animals with the different explanatory theories of the phenomena. He then attempts to connect the observed behavior in many forms with the statolith organs. Brun (4) gives a theoretical discussion of the orientation problem in general for all animals but the discussion is based upon some experimental work with ants.

Our common minnows usually keep in shallow water near the shore line and follow the tide in its movements. This behavior aids the fish in the escape from its enemies and the securing of food. Mast (18) studied the actions of Fundulus when trapped in pools which fill shallow depressions in the sand. He found that ordinarily their movements were regulated in some way by the ebbing and flowing of the tide as the behavior was quite different at different times of tide. The fish flop out of the pools and then with successive flops travel in a fairly direct course to the sea. No matter what the axial direction of the fish is as it falls the next flop will carry it on its course. The regulatory mechanism is uncertain. The author thinks that it cannot be vision or the slope of the land.

INSTINCT

A most interesting note on the maternal instinct of monkeys is given us by Yerkes (39). Gertie, a Rhesus monkey, for five weeks carried about with her the vanishing remains of a still

birth guarding it so carefully that it was impossible even by force to take it from her. Coward (7) writes in a vivid way of the repeated battles of a cock blackbird with its own reflection in the glass of a window—battles which were kept up through an entire mating season. There is an attempted analysis:—the accidental encounter, instinctive attack in rivalry, memory and absolute failure to profit by experience.

DEVELOPMENT

Fish.—White (37) describes the behavior of the Brook Trout embryo from the time of hatching to the absorption of the yolk sac. Among other things she relates that it reacts to touch and to mechanical jars immediately after hatching. She finds that the head is least sensitive to touch of any part of the body while the eye is insensitive. The embryo is photokinetic and negatively phototactic. It begins to respond to shadows about the fifth week and feeding reactions commence when about two months old.

GENERAL BEHAVIOR AND LEARNING

The progress in animal psychology in the last few years is reviewed in a clear way by Baege (2) and Hirshberg (10) gives a brief well phrased statement of some of the more recent methods and investigations with an estimate of the value of such work.

Mammals.—In a short paper Shepherd (27) reports some experiments designed to test adaptive intelligence in cats, dogs and monkeys. He also gives in another paper (26) his observations of the behavior of Peter and Consul—apes appearing on the vaudeville stage. These observations are based upon a single private examination and a few stage performances. Some titles are given of articles dealing with the Elberfeld horses (19), (23), (28), but it seems useless to burden our pages further with such futile discussion. Cole (6) reviews Hunter's work on the delayed reaction and McPheeter and Gregg's experiments with raccoons so far as they concerned his own previous work, with both critical comment and explanation of differences. Hunter (14), (15) replying to some statements made by Watson and Cole comes to the defense of his theory that the delayed reaction experiment with raccoons can be explained only by some process which functions as memory ideas do in human behavior. He emphasizes the fact that the ideational function which he ascribed

to the raccoons and to the child in his monograph on the delayed reaction was the residual effect of sensory stimuli, strictly sensory in content. Quite in a line with the above question are the experiments of Walton (35) who undertook to determine what would be the effect of diverting stimuli during delayed reaction with dogs. In the main there was an attempt to follow Hunter's methods and type of apparatus, i. e., the dogs were confined in a release box from which it was possible to see four compartments twelve feet distant. The animals were to choose the compartment after the light which indicated it had been turned off from one second to five minutes. After the reaction was learned and during this delay, visual, olfactory and auditory distractions were used. The experimenter differs from Hunter in concluding that though signs of orientation may be prominent in the dog such clues are not important for the success of the reaction in the animals used. It cannot too frequently be urged that in order to duplicate results apparatus and methods should be identical. It should also be reiterated that there is little doubt, at least with dogs, that no safe conclusions can be drawn as to cues when the operators are visible. They should preferably be out of the room. The method and the type of apparatus which had been used in the study of the dancing mouse were this year applied by Dodson (9) to his study of the relation of the strength of the stimulus to the rapidity of habit formation. By stimulus is meant here not the strength of the light to which the kittens were reacting but the strength of the punishment by the electric grill when they failed to choose rightly. The kittens of which there were eighteen were required to choose correctly between light and dark boxes and each cat was given ten trials per day until it had chosen correctly for three successive days. The difference in brightness to be discriminated in one series was very great, in another medium, and in another very slight. The experimenter thinks that the relation of the painfulness of the electrical stimulus to the rapidity of habit formation depends upon the difficulty of the visual discrimination. Hubbert (11) using albino rats studied the effect of age on habit formation. The apparatus concerned in the experimentation was Watson's circular maze with camera lucida attachment. Five groups of rats aged 25, 65, 200, 300 and 500 days, took part in the experiments. These groups numbered 27 and 28 animals

with the exception of the 500-day group in which there were only 12 rats. Among other things the writer says in her résumé of conclusions:—" Young rats learn the maze more rapidly than the old ones, the rapidity with which the habit may be formed decreasing with increase in age. The time for the execution of a perfect run increases with increase in age, the oldest group requiring twice as much time as the youngest. The most rapid stage of habit formation occurs earlier in the learning process of the younger animals than of the older." The same writer, briefly, in this paper, more fully in another (12), discusses the elimination of errors in the same maze. Her interest lay in the question whether, in learning the maze, the useless movements most closely connected with satisfaction—food—are the first to be eliminated or whether the useless movements most remote from the source of satisfaction—food—persist the longer.

The distribution of effort in learning has, in the past, engaged the attention of several in the animal field but Ulrich (30) this year has made a more extended investigation. He formulates his problem as an effort to determine how distributing the effort over one, three or five trials per day would affect the rapidity of learning, the degree of effort and the amount of retention. Another question which engaged him was, do the relations found true in the learning of one problem hold good when two or three problems are learned at the same time. The pieces of apparatus concerned in these problems were the latch box, the circular maze and the inclined plane box. The author says:—When trials are distributed over several days learning is more economical but more days are required to establish a habit than where several trials are given on one day. When three problems are learned abreast a much larger number of trials is required to learn each of the problems than would have been required if the animal had been allowed to learn only one problem at a time.

The behavior of the pig was studied by Yerkes by means of what he calls the multiple choice method (38). Yerkes says:— " The experimenter seeks in using the multiple choice method to present to his subject, no matter what its type, age or condition, a problem which may be solved by the perception of certain constant relations or group of relations within the reaction mechanisms. For example, the mechanism to be operated may, in the case of one problem, be the middle one of the group, and

the total number of mechanisms presented may vary from three to nine. Only by perceiving and appropriately responding to the relation which the experimenter designates as middleness can the subject solve the problem." The apparatus used with the pigs consisted essentially of nine stalls opening from a central yard by sliding doors which were controlled by an unseen operator. Each stall gave access, at the other end, through a sliding door controlled as before to a food trough. There was an arrangement by which the animal after choice returned again by a side way to the central court. The plan was to have the pigs learn four problems: (1) to choose the first door on the right; (2) to choose the second door on the left; (3) to take alternately the first door on the right and the first door on the left; (4) to take the middle door. In all cases it was planned to have other doors, from three to nine in number open while choice was being made. The two pigs which served in this experiment solved the first problem in 65 and 85 trials respectively. The second problem was solved more slowly because the habits formed in the previous experiment had to be broken up. It took 396 and 516 trials each. The third problem was solved also in 490 and 431 trials each. Problem four proved too difficult for the pigs. They could succeed when the open doors were few in number but when seven to nine doors were open they were confused. Yerkes thinks his results indicate an approach to free ideas if not the actual attainment of simple ideational behavior. Complete numerical tables are given. Would the practice were more prevalent.

Four articles by Vincent (31), (32), (33), (34), have to do with learning in mazes in which the sensory conditions were modified. In the first series of experiments the true path and the *cul de sacs* were made to differ in brightness, i. e., the true path was made as white and the *cul de sacs* as black as possible and *vice versa*. In the second series olfactory trails were laid in the first case in the true path in the second case in the *cul de sacs*. In the third series a maze was constructed having elevated pathways with no restraining, outside walls—a condition which forced the use of nose, feet and vibrissae and thus made the tactual control the important one. The fourth paper gives a comparative estimate of the relative effectiveness of these different senses as modes of control and includes also a brief discussion of the number and

distribution of the errors. The conclusions of all four studies are based upon (a) the time taken to learn the problem (b) the accuracy, initial, final and total, as shown by the number of the errors and (c) the development of speed both initial and final.

Birds.—Coburn (5) continues his study of the crow this year by using an adaptation of the multiple choice apparatus and method described for the pig in this article. There were nine compartments and doors. In this experiment there were from two to five doors open. Three problems were attempted:—to take the first door to the right, the second to the left, and the first to the left. Both birds learned one and three but in 500 trials had not solved two, i. e., to take the second door to the left. The reason for this is thought to be the disturbing habits set up in the first problem. This is the first of a series of papers using this method of which the one on the pig given above is the second.

GENERAL SUBJECTS

Piéron has given us in the last few years several papers which discuss in a theoretical way problems of significance for those engaged in animal psychology. One appearing this year (21) is a general review article of published statements, works and theories dealing with the modern objective attitude in psychology. It is based primarily upon Bechterew's work. Pieron attacks such questions as, why and how such an attitude attained such vogue, where it finds its chief value, how it has affected the methods and view points of modern experimental psychology and he makes an attempt to evaluate its postulates for psychology in general. In one of its meetings the French philosophical society devoted itself to the question of instinct. M. Piéron (20) submitted the following program for discussion:—

1, Examination of the criteria—often contradictory—utilized in the definition of instinct:—nervous localization, consciousness or unconsciousness, specific identity, immutability, finality.

2, The impossibility of distinguishing by the criteria, decisively, instinctive acts from reflex or intelligent acts.

3, The place of instincts in the behavior of animals and the social equivalent of instinct.

4, The problem—insoluble by science in its generality—of the origin of instinct.

Previous to this the same author reviewed in a general way

(22) articles and positions on the subject of mimicry. The treatment is philosophical as well as biological and its implications are of value to all students who are busy with comparative psychology.

REFERENCES

1. AREY, LESLIE B. The Orientation of Amphioxus During Swimming. *Jour. Exper. Zool.*, **19**, 37-44.
2. BAEGE, VON M. H. Die Moderne Tierepsychologie. *Naturwissenschaftliche Umschau* No. 10-11. *Beilage der Chemiker-Zeitung*, No. 141, S. 1-5.
3. BARBER, ALDA GRACE. The Localization of sound in the White Rat. *Jour. Animal Behav.*, **5**, 292-312.
4. BRUN, RUDOLPH. Das Orientierungsproblem in allgemeinen und auf Grund experimenteller Forschungen bei Ameisen. *Biol. Centrbl.*, **35**, 190-207.
5. COBURN, CHAS. A. and YERKES, ROBT. M. A Study of the Behavior of the Crow-*Corvus Americanus* Aud. by the Multiple Choice Method. *Jour. Animal Behav.*, **5**, 75-115.
6. COLE, L. W. The Chicago Experiments with Raccoons. *Jour. Animal Behav.*, **5**, 158-173.
7. COWARD, T. A. A Note on the Behavior of the Blackbird—A Problem in Mental Development. *Proc. Manchester Literary and Philosophical Soc.*, 1915, 1-8.
8. DeVoss, J. C. and GANSON, ROSE. Color Blindness of Cats. *Jour. Animal Behav.*, **5**, 115-140.
9. DODSON, J. D. The Relation of Strength of Stimulus to Rapidity of Habit Formation in the Kitten. *Jour. Animal Behav.*, **5**, 330-337.
10. HIRSHBERG, L. K. The Study of Animal and Human Behavior. *Sci. Am.*, **112**, 491-
11. HUBBERT, HELEN. The Effect of Age on Habit Formation in the Albino Rat. *Behav. Mon.*, **2**, pp. 55.
12. HUBBERT, HELEN. The Elimination of Errors in the Maze. *Jour. Animal Behav.*, **5**, 66-72.
13. HUNTER, W. S. The Auditory Sensitivity of the White Rat. *Jour. Animal Behav.*, **5**, 312-336
14. HUNTER, W. S. A Reply to Some Criticisms of the Delayed Reaction. *Jour. Phil. Psychol.*, etc., **12**, 38-41.
15. HUNTER, W. S. A Reply to Prof. Cole. *Jour. Animal Behav.*, **5**, 406.
16. JOHNSON, H. M. Some Recent Experiments on Vision in Animals. *Trans. Illuminating Engineering Soc.*, **6**, 502-514.
17. KANDA, SAKYO. Geotropism in Animals. *Am. Jour. Psychol.*, **26**, 415-425.
18. MAST, S. O. The Behavior of Fundulus with Especial Reference to Overland Escape from Tide-Pools and Locomotion on Land. *Jour. Animal Behav.*, **5**, 341-351.
19. MÜLLER, G. E. Ein Beitrag über die Elberfelder Pferde. *Zeit. f. Psych. u. Physiol. der Sinesorgane*, **73**, 258-264.
20. PIÉRON, M. H. La Notion d'instinct. *Bull. d. l. soc. franc. de Phil.*, **14**, No. 8.
21. PIÉRON, H. L'Attitude objective dans la psychologie moderne. *Scientia*, **17**, 119-133.
22. PIÉRON, H. L'Evolution de l'opinion scientifique actuelle sur la question du memétisme. *Scientia*, **14**, 453-462.
23. SCHNEIDER, K. C. Die rechnenden Pferde. *Biol. Centrbl.*, **35**, 153-160.
24. SEFFRIN, L. Uber die kleinsten noch wahrnehmbaren Geruchmengen einiger Riechstoffe beim Hund. *Zeit. f. Biol.*, **65**, 493-
25. SHELFORD, VICTOR E. and POWERS, EDWIN B. An Experimental Study of the Movements of Herring and other Marine Fishes. *Biol. Bull.*, **28**, 315-334.
26. SHEPHERD, W. T. Some Observations on the Intelligence of the Chimpanzee. *Jour. Animal Behav.*, **5**, 391-397.

27. Shepherd, W. T.   Tests on Adaptive Intelligence in Dogs and Cats as Compared with Adaptive Intelligence in Rhesus Monkeys.   *Am. Jour. Psychol.*, **26,** 211-217.

28. Sommer, R.   Anfangsunterricht bei den Elberfelden Pferden.   *Fortschritte der Psychologie und ihrer Anwendungen*, **3,** 135-149.

29. Tschermak, v. A.   Das Sehen der Fische.   Die *Naturwissenscheften*, **3,** 177-, *Rev. Zeit. f. Physiol.*, **33,** 282.

30. Ulrich, John L.   Distribution of Effort in Learning.   *Behav. Mon.*, **2.**

31. Vincent, S. B.   The White Rat and the Maze Problem—The Introduction of a Visual Control.   *Jour. Animal Behav.*, **5,** 1-24.

32. Vincent, S. B.   The White Rat and the Maze Problem—The Introduction of an Olfactory Control.   *Jour. Animal Behav.*, **5,** 140-158.

33. Vincent, S. B.   The White Rat and the Maze Problem—The Introduction of a Tactual Control.   *Jour. Animal Behav.*, **5,** 175-185.

34. Vincent, S. B.   The White Rat and the Maze Problem—The Number and Distribution of Errors.   *Jour. Animal Behav.*, **5,** 367-375.

35. Walton, Arthur C.   The Influence of Diverting Stimuli During Delayed Reaction in Dogs.   *Jour. Animal Behav.*, **5,** 259-292.

36. Wells, Morris M.   Reactions and Resistance of Fishes in their Natural Environment to Acidity, Alkalinity and Neutrality.   *Biol. Bull.*, **29,** 221-257.

37. White, Gertrude M.   The Behavior of Brook Trout Embryos from the Time of Hatching to the Absorption of the Yolk Sac.   *Jour. Animal Behav.*, **5,** 44-60.

38. Yerkes, Robt. M. and Coburn, Chas. A.   A Study of the Behavior of the Pig *Sus Scrofa* by the Multiple Choice Method.   *Jour. Animal Behav.*, **5,** 185-226.

39. Yerkes, Robt. M.   Maternal Instinct in a Monkey.   *Jour. Animal Behav.*, **5,** 403-405.

40. Yerkes, Robt. M.   Preliminaries to a Study of Color Vision in the Ring Dove. *Turtur risorius*.   *Jour. Animal Behav.*, **5,** 25-43.

DONALDSON'S " THE RAT "*

HARVEY CARR
University of Chicago

This work of Donaldson is a compendium of references and statistical data concerning the development of the Albino and the Norway rat. Its contents can best be described by an enumeration of the topics discussed:—Life History, Biology, Heredity, Anatomy, Physiology, Pathology, Classification, Growth of Body Weight, Growth of various Organs, and Growth in terms of Water, Solids, and Chemical Constituents. As a source of reference, this book will be invaluable to all investigators who employ the rat as their laboratory material. The author's name is a sufficient guarantee of the accuracy and completeness of this compilation of data.

* Donaldson, Henry H. The Rat, Data and Reference Tables, Memoirs of The Wistar Institute of Anatomy and Biology, No. 6. Philadelphia, 1915. pp. V+278.

CHILD'S "SENESCENCE AND REJUVENESCENCE" AND "INDIVIDUALITY IN ORGANISMS"*

C. JUDSON HERRICK

Students of behavior are perforce interested in the question of the underlying causes of behavior. Here, as in other fields of biology, there are doubtless many who would prefer to turn such problems over to the philosophers, whose special province it is to deal with questions of teleology and other basal postulates. But even philosophers need facts upon which to base their general reasoning. And the insistent intrusion into behavioristic literature of works on objective psychology and mechanistic conceptions of life, on the one hand, and of doctrines of orthogenesis and vitalism with their entelechies and other metaphysical daemons, on the other hand, shows that these theoretical questions not only lie in the background but often also in the foreground of research in behavior, sometimes playing a decisive part in the shaping of a research program.

Few investigations of recent times have yielded more positive factual contributions to the problems of the organization and fundamental behavior of living things than have those of Child as reported in the two volumes recently published by the University of Chicago Press and the extensive series of special papers upon which these volumes are largely based. Many phenomena which in the past have been confidently cited by the vitalists as demonstrative proofs of the impossibility of mechanistic explanations are in these works shown to be the natural expressions of a mechanism of extreme simplicity whose operations yield to experimental control and explanation with all desirable objectivity.

Some years ago Jennings summed up his very illuminating discussion of the regulatory processes in organisms in the aphor-

istic expression, " Behavior is regulation." Indeed, one may go further and maintain that regulation is the most character- istic of all of the distinctive vital functions. There is nothing which more clearly distinguishes a living body from a dead body than the ability of the former to adapt its behavior to changing environmental conditions, and yet during this adaptation to maintain its structural and functional pattern without funda- mental change.

The method of learning and many of the other questions with which students of animal behavior are concerned are, of course, special problems of regulation in the wide sense of the term; and it is therefore to be expected that any contribution to the nature of regulation in general will bear directly or indirectly upon the fundamental problems of comparative psychology. Child's work, accordingly, has both theoretical and practical value in the field of animal behavior.

The two books here reviewed present successive chapters in a single program of research. The first and larger volume on Senescence and Rejuvenescence gives a detailed analysis of the problem of organic constitution with experimental illustrations of some of its factors, notably those centering about the life cycle. The second book on Individuality in Organisms analyzes in more general terms the nature of the biological individual and the mechanistic factors which characterize it. Among the theses which are elaborated, the following are of especial interest from our point of view:

1. In discussing living things static formulations are incom- plete and meaningless without corresponding formulations in dynamic terms. " Life is not any particular reaction nor any particular substance, but a great system of processes and sub- stances. Structure and function are then indissociable." " In other words, neither structure nor function is conceivable except in relation to each other." The discussion takes its departure from the following definition, "A living organism is a specific complex of dynamic changes occurring in a specific colloid sub- stratum which is itself a product of such changes and which influences their course and character and is altered by them." (Senescence, p. 26.)

2. There are two factors in organic differentiation, (1) the amount of metabolism, and (2) the complexity of organization.

These are independent variables. The first factor can be meas-
ured directly in terms of the carbon dioxid output or oxygen
consumption of the tissue, and also indirectly by a very ingenious
method elaborated by Child which depends upon a differential
susceptibility of the tissue to various poisons. Tissues with
higher metabolic rate are more susceptible to certain concentra-
tions of potassium cyanide, alcohol, ether, and other drugs than
are tissues of lower metabolic rate. In many lower organisms
this difference in susceptibility can be directly observed through
structural changes caused by the drugs. The second factor is
expressed functionally by the range of diversity of behavior and
structurally by complexity of tissue and organ differentiation.

3. In general, young tissues have a higher rate of metabolism
and less complexity of organization than older tissues, other
things being equal. During the life cycle, from cleavage stages
of the egg to advanced senescence, there is a progressive reduc-
tion in the amount of metabolism per unit of weight and a pro-
gressive increase in complexity of permanent stable organiza-
tion; and throughout the cycle some parts of the body retain
their juvenile characteristics longer than others. Growth,
senescence, tissue differentiation, and regeneration all have
certain features in common, one of which is the progressive
stabilizing of the more labile embryonic protoplasm by laying
down a framework of relatively immobile structurally differ-
entiated substances. "According to this view, senescence is
primarily a decrease in rate of dynamic processes conditioned
by the accumulation, differentiation, and other associated
changes of the material of the colloid substratum. Rejuvenes-
cence is an increase in rate of dynamic processes conditioned by
the changes in the colloid substratum in reduction and dediffer-
entiation " (Senescence, p. 58).

4. The ripe germ cells are really " old " in the sense defined
above, i. e., their metabolic rate is low and their protoplasmic
structure is stable. By the act of fertilization the quiescent
germ cells are stimulated to a high rate of metabolism, with
corresponding transformation of their highly differentiated and
stable protoplasm into a less differentiated and more labile form.
Both fertilization and asexual reproduction are processes of
rejuvenescence. " If these conclusions are correct, agamic and·
gametic reproduction are fundamentally similar processes,

except for the fact that in gametic reproduction specialization of the reproductive cells has proceeded so far that the peculiar conditions associated with fertilization are necessary for the initiation of the process of regression and rejuvenescence. And if we accept this theory of reproduction, the Weismannian conception of germ plasm as a self-perpetuating entity, independent of other parts of the organism except as regards nutrition—in short, a sort of parasite upon the body—becomes not only unnecessary but impossible. Germ plasm is any protoplasm capable, under the proper conditions, of undergoing regression, rejuvenescence and reconstitution into a new individual, organism, or part " (Senecsence, p. 461).

5. It is suggested (Senescence, p. 463, Individuality, p. 205) that throughout the history of organic evolution there has been a progressive change in the organization of protoplasm of animal phyla analogous with that which occurs in the individual life cycle, from a relatively undifferentiated and mobile condition in lowest organisms (and in young parts of more highly specialized types) to a condition characterized by the fixation in protoplasm of stable structural elements which give to each species and organ its characteristic mode of behavior. This is the physical basis of differentiation. On the anatomical side this leads to the highly complex and diversified tissue types. On the behavior side it leads to progressive complexity in the inherited types of activity, which culminates in the instinctive reactions of higher animals. (Of course, in the higher organisms there is in addition to this stable framework of protoplasm and of behavior a more labile stuff which may be metabolically very active—see 9 below.) The more diversified life of higher organisms, therefore, rests upon a more diversified structural organization. And the advance in this organization is progressive in evolution. This is a non-metaphysical type of orthogenesis, which may be expressed by the proposition that in evolution the protoplasm of the race is progressively growing older. Parallel with this the behavior is becoming stabilized in more complex patterns Of course, not all of the protoplasm thus grows old, and the labile protoplasm of the " younger " type is the basis of that plasticity which makes advancement in evolution possible.

6. From the observed differences in metabolic rate in different

tissues it follows that every living body exhibits a metabolic gradient. There is in most plants and animals a primary axis with a high rate at the apical or head end and a diminishing rate as we pass away from this center. There are also various subsidiary metabolic gradients in addition to this primary axial gradient, the details of which we need not here enter upon.

7. The point of highest metabolic rate is a " center of dominance " in the sense that the physiological activities of all other parts of the body are to some extent regulated and integrated from this dominant center of highest metabolic rate. In all higher animals this center of dominance is in the brain and the chief mechanism of regulatory control is the central and peripheral nervous system. The nervous system, however, contributes nothing new in principle to what is found in plants and the lowest animals possessing no nervous organs whatever.

8. In organisms which lack highly differentiated nervous systems the controlling and integrating influence exercised by the center of dominance over other parts of the body diminishes with the distance of the parts from this center; and when by the growth of the body this distance exceeds a certain maximum the influence of the center of dominance is so reduced as to result in a " physiological isolation " of part of the body from this influence. In this case a secondary center of dominance may arise, subsidiary to which a complete new individual is constituted. This is the mechanism of asexual reproduction by fission and budding in plants and many lower animals. The regeneration of lost parts in invertebrates and lower vertebrates is possible by virtue of a similar but less complete physiological isolation of the region of injury. In higher animals, where the nervous system provides a more efficient apparatus of control from the primary center of dominance these phenomena of fission and local regeneration are not found, although even in man the phenomena of healing of wounds exhibit some small measure of physiological isolation and local control.

9. The characteristics of the center of dominance are dependent primarily upon its higher rate of metabolism. A high rate of metabolism may be effected by one of two types of mechanism, either (1) by relatively undifferentiated protoplasm, all of whose substance is relatively unstable and so capable of rapid chemical transformation (the " young " type of tissue), or (2) by organs

whose tissues possess a large amount of highly differentiated and relatively stable substance of low metabolic rate (the " old " type of tissue) and in addition a more labile substance which can be rapidly mobilized in functional activity without disturbing the pattern of the more stable framework. This second type is characteristic of the brains of higher vertebrates, where there is (1) a very definite stable and heritable organization which expresses itself functionally in the reflex and instinctive life, and (2) pervading this organization the more labile substance which provides for the individual modifiability of behavior, including the capacity of learning by experience and all higher conscious functions.

The preceding summary includes a few only of the important conclusions which Child draws from his experimental studies upon lower forms of life. It should be emphasized that these conclusions are not speculative, but rest upon a very large body of carefully controlled experimental work, only a small part of which is presented in detail in the two books here reviewed. The application of these fundamental principles of organic growth, reproduction, and regulation to the higher forms of behavior is not attempted in these works, though a few hints are dropped which give promise of possible applications in the realms of comparative neurology, psychology and sociology (see Individuality, pp. 173, 178, 188, 205). It is hoped that the author may himself elaborate these suggestions in more detail in subsequent publications

HERRICK'S "AN INTRODUCTION TO NEUROLOGY"*

HENRY H. DONALDSON

During the past twenty-five years the clinical neurologists have been losing faith in neuropathology as a prime method for the solution of their problems. Perhaps in the first place they were misled into hoping too much from this method. Be that as it may, there is now something of a tendency " to throw out the baby with the bath " and to reduce to a minimum the anatomical data which are utilized.

The anatomy of the nervous system both normal as well as pathological has suffered from this shift of interest. Of course, in this case, as always, there is some reason for the present state of affairs. In the first instance anatomical relations have been over-interpreted and further during the last two decades the finer anatomy of the nervous system has been so assiduously cultivated that the great mass of data collected was in danger of becoming a burden unless the facts could be classified and strung on a stout physiological thread.

The move toward this solution has been slow, and in the meantime the gap between neuro-anatomy and clinical neurology has remained only too evident.

Herrick's " Introduction to Neurology " helps to bridge this gap in a very satisfactory manner, for it presents the anatomy of the human nervous system in its physiological relations.

The book contains 137 illustrations, mainly Schemata, with full legends. Of the 338 pages of text, 45 pages are in fine print —used for the presentation of details—and 39 pages are given to a glossary-index containing concise definitions of all of the newer technical terms. Thus, within the remaining 254 pages on which the illustrations also appear, the author has succeeded in presenting the main facts of neurology as they stand to-day. This means compact writing. The book is avowedly an intro-

---

* Herrick, C. Judson. An Introduction to Neurology. W. B. Saunders Co., Phil. and London, 1915, p. 355.

duction or outline and this limitation is consistently kept in mind. It is so written, however, as to be instructive to the physiologist, clinician and psychologist, or in other words, any student who requires a concise statement of neurological facts. With each chapter goes a bibliography, and these bibliographies taken together comprise the titles of the important contributions to neurology.

Guided by the idea that the best understanding of the nervous system is to be had by viewing it as a mechanism at work, our author starts with the reflex circuit (a term preferred to reflex arc) as his unit, and proceeds to show how the entire nervous system can be regarded as arranged so as to furnish such reflex circuits, which increase in complexity as, one after another, the more cephalic divisions of the central system (medulla oblongata, thalamus and cortex), are involved in the reactions. This arrangement holds good for the entire vertebrate series, but, as we ascend in the scale, the increasing development of the cephalic divisions brings about responses better and better adapted to favor the welfare of the organisms as a whole.

The book opens with the statement of general biological ideas, nervous function and the characters of the neuron. Then the discussion of the reflex circuit, anatomical and physiological leads to an account of the general anatomy of the nervous system. This is followed by an examination of the larger divisions and parts. It is of interest here to note that while six chapters are required for even a brief description of the sources and pathways of incoming impulses, a few paragraphs amply serve to indicate the arrangement of the efferent neurons. The remainder of the text is given mainly to describing the arrangement and functional connections of those neurons which mediate between any incoming impulses and the neurons of final discharge (efferent neurons). This allotment of space alone serves to indicate the enormous relative development of the afferent and central divisions of the nervous system in the higher vertebrates.

In the course of the presentation our author elects to write the words neuron and axon (sic) without a final e. From Sherrington he adopts the terms receptor (exteroceptor; interoceptor and proprioceptor) for the sense organ; and effector for the organ of response. Moreover he has formulated a more precise use of the terms correlation, association and coördination, terms

sometimes indiscriminately applied.   The cells to which afferent impulses are delivered or between which they pass before they reach the neuron of final discharge, are called correlation neurons. This is the more general term.   But the activity of such correlation neurons in the cortex is linked with consciousness and these cortical elements are, therefore, distinguished as association neurons.

Coördination describes the orderly activity of effectors but whether we should distinguish coördination centers as a third class of central neurons seems doubtful, though our author does so (page 181).   As matters stand the typical group of coördinating neurons is represented by the cerebellum.   It will be noted that the expression reflex circuit has been used in place of reflex arc.   The analysis of the reflex by Dewey has drawn attention to the facts on which this change is based.   The same afferent axon by its collaterals delivers impulses to the correlation neurons in the region of its immediate entrance into the central system and at the same time by its main axon or other branches to more remote correlation neurons, so that impulses returning from the higher to the lower center find a prepared, rather than indifferent, neuron on which to act.   A like relation is found between the effector and the central neurons.   A circulation of impulses is thus suggested.   This is a concept of much value and on it our author lays due stress.

The convenient term reflex pattern is also utilized.   This term, suggested by Sherrington, was applied originally to the form of the functional response to a stimulus, but as such a response implies a structural basis more or less precise in arrangement it is hard to escape the use of the word pattern in the structural sense (p. 312).   The term is excellent, but it would be helpful if it could be so modified as to make precise in each instance the sense in which it is applied.   In the matter of technical terms the text follows the B. N. A. except in a few instances. The most notable departure is made in the case of the bundles of fibers which appear in the cross section of the spinal cord. As the analysis of the cord proceeded in the hands of the earlier anatomists, the names applied were largely based on the local relations.   The B. N. A. established the general term fasciculus for such bundles, but our author has advanced a step and while retaining the term " fasciculus " for the bundles composed of

fibers having various or undertermined functions, he has used the term " tractus " for those bundles, the connections of which are known, giving in the second part of the name the origin and termination of the constituent fibers, e. g., (1) Tractus spino-tectalis; (2) Tractus tecto-spinalis. It is not always easy to use a nomenclature so defined in such a way as to avoid criticism, but the introduction of the distinction which it allows is a definite advance.

In the presentation before us we find as distinctive features the emphasis placed on the reflex circuit, as the unit of functional response, and the application of the results of comparative anatomy to the appearances found in the human nervous system. Our author is peculiarly well qualified to write from this latter standpoint and he has used his advantage with discretion. From comparative anatomy come several general concepts which do not always appear in the text books. One of these is the concept of nerve components. The older descriptions assumed, for the most part, a uniform function for each of the spinal and cranial nerves. It has been shown, however, that bundles of fibers of diverse function are to be found in most, if not all, of these nerves; that in different vertebrates the same morphological nerve may have a different set of components and also that components of like functional value may connect with the central system by way of several different nerves. These relations serve to direct attention to the functional groups of fibers as contrasted with the structural groups, and the change in view has proved very helpful. Associated with these studies is the concept of the gray substance of the axial nervous system as comprising four functionally distinct cell columns in each lateral half. Enumerated from the dorsal to the ventral position, as they appear in a cross section of the cord or medulla, these cell columns are named somatic sensory, visceral sensory, visceral motor and somatic motor. The consequences of this arrangement are far reaching and are worthy of careful consideration from the standpoint of the clinician.

Comparative studies show also many remarkable variations in the central cell groups, especially in those of the bulb. Among the lower vertebrates, some forms depend for their principal reactions largely on a single sense and it often follows that this sense organ and its central connections are in such cases almost

monstrously developed.   Thus there are forms depending mainly
on the sense of smell or of taste or touch or vision and in each
instance showing a relative over-development of the neural
structures concerned.   The study of these and other instances
of unbalanced structure has furnished a clue to the significance
of various cell groups in the human bulb otherwise difficult to
interpret.   For example it has thus been possible to clear up
the arrangement of the nuclei of the vestibular apparatus—from
which the cerebellum has been elaborated, and also to interpret
such a cell group as the nucleus of the fasciculus solitarius, the
center of the taste (p. 234).   But the applications of these com-
parative studies extend still farther.   By their aid it is possible
to distinguish between the primitive thalamus (paleothalamus)
and the large additional mass (neothalamus), as it appears in
man and the anthropoids, with its various cell groups and highly
elaborated cortical connections.   Using like methods it has been
possible also to follow the evolution of the neopallium or the
part of the cortex (pallium) superadded to that primitively
associated with the olfactory apparatus.

In dealing with the functional problems the general somatic
sensations have received careful consideration and the results
obtained by Head and his collaborators have been incorporated.
Of special interest in this connection is the problem of the media-
tion of pain.   The questions here are many.   Are there special
afferent nerve fibers for pain only, or do some terminals of these
somatic fibers yield sensations of pain while other terminals of
the same fibers mediate different sensations, or can over-stimu-
lation of any of these fibers give rise to sensations of pain?   Our
author discusses these questions and concludes that there may
possibly be some special pain nerves, but also that " most sensory
nerves may upon occasion function as pain nerves."

The questions here put in connection with nerves mediating
pain, may be equally well asked with regard to the other
sensory nerves and they serve to raise the ghost of the doc-
trine of specific energies.   Although it is not much discussed,
and is usually criticized adversely, the doctrine of the specific
energies of nerves still casts its shadow over neurology.   The
rigid form of this doctrine, the form with which Helmholtz
worked, looks upon the sensory nerve fiber as an unbranched
thread running from its peripheral termination, where to be

sure it might be represented by a number of terminal filaments, by way of a ganglion to its center, there to mediate one kind of change the specific central response for that fiber. The structural picture on which this doctrine was based can no longer be accepted. We now know that the afferent neuron sends into the central system an axon which always branches and often forms connections remote from one another and plainly associated with diverse correlation centers, while the nerve fiber passing to the periphery from this same ganglion cell in many cases branches several times in its course, sends these branches to different peripheral localities and at the periphery may, in the skin at least, be connected with more than one type of sensory end organ. This calls for a reconsideration of the problem and it seems possible, therefore, to think of nerve impulses as having distinctive characters that determine which one of the many possible paths each type of impulse is to follow within the central system. Here is a field open for further study. In man the pathway for pain formed by central neurons in the spinal cord is represented both by a diffuse arrangement as in lower forms and also by a well marked tract. (Tractus spino-thalamicus lateralis). The recent observations of Head and Holmes make it probable that in the cell groups of the thalamus, where these fibers end, we have a center stimulation of which gives rise to our sensations of pain. It has been customary to associate changes in consciousness with the activity of the cortex only, but in view of these results we must now grant certain cell groups in the thalamus a like dignity.

The last chapters of the book treat of pleasure and pain (we need a better word antithetic to pleasure) and of the human cortex; its structure, functions and evolution. In the course of these chapters a new picture is given of the relation of the higher centers which increase in complexity from the bulb to the thalamus and from the thalamus to the cortex. In place of the usual notion of the impulses from complex higher centers acting on lower centers which are more or less indifferent or passive, our author points out that the incoming impulses set or adjust for discharge circuits of increasing complexity, as these impulses pass to higher and higher centers and as a consequence the return impulses from the cortex which release the final response, act by selecting one out of several circuits which are held ready

for action.   Thus the integration of the incoming impulses is continually in process at each level and impulses from above act in a large measure to release mechanisms partially prepared.

It has been one purpose of this review to show that Herrick's book is an introduction to a more significant neurology than is usually presented to us, for starting as it does with the reflex circuit as the unit of function and keeping the physiological relations in the foreground it illuminates the structural arrangements within the nervous system in a way that is both unusual and stimulating.