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ROBERT MEARNS YERKES.

Reprinted from the MARK ANNIVERSARY VOLUME, Article XVIII, pp. 359-377, 1903

C. S. Sherring

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XVIII.

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I. PHOTOTAXIS AND PHOTOPATHY.

The motor reactions of organisms to light, so far as known at present, are of two kinds: phototactic and photopathic. In both *intensity* of the light, not the *direction* of the rays, is the determining factor. All those reactions in which the direction of movement is determined by an orientation of the organism which is brought about by the light are phototactic;* and all those reactions in which the movement, although due to the stimulation of light, is not definitely directed through the orientation of the organism are photopathic.†

Photo~~pathic~~tactic reactions are supposedly due to the fact that certain animals are forced by light so to orient themselves that symmetrical points on the surface of the body are equally stimulated. This, the so-called "orientation theory" of Loeb ('93, p. 86) and of Verworn ('99, p. 499 et seq.), accounts for those cases in which animals seek or avoid light. Evidently a bilaterally symmetrical organism receives equal stimulation on symmetrical points when the long axis of its body is parallel with the rays of light, the head being directed either toward or away from the source of light. When, as a result of orientation with the head toward the light, an animal moves toward the source of light the reaction is said to be positively phototactic; when the movement is away from the light it is negatively phototactic. These reactions may be either primary or secondary. They are primary when the animal moves in the axis of the rays, and secondary when, prevented from so doing, it moves at right angles to the axis, but at the same time into regions of increasing (positive secondary phototaxis) or diminishing (negative secondary phototaxis) intensity.

An organism which selects a particular intensity of light and confines its movements to the region illuminated with that intensity is photopathic.‡ The so-called "optimal intensity" is usually found by means of a phototactic reaction. Photopathic

* See Holt and Lee (:01) for the theory of phototactic reaction.

† It is to be noted that the terms phototaxis and photopathy are here given new meanings. Previously phototaxis has been applied to those reactions which were supposed to be determined by the *direction* of the rays of light, and photopathy to those due to differences in the *intensity* of the light.

‡ Strassburger ('78, p. 572) has described this kind of reaction for the swarm-spores of Ulothrix and Hæmatococcus.

reactions are in all probabilty frequent because of difference of sensitiveness to light in different regions of the body.*

II. STATEMENT OF PROBLEMS.

Davenport and Cannon ('97), Yerkes (:00), and Towel (:00) have shown that Daphnia is positively phototactic.

The experiments reported in this paper bear upon the following problems:

1. Does Daphnia react photopathically as well as phototactically? Is there any evidence of an "optimal intensity"?

2. Does the radiant heat accompanying light influence the movements of the animals?

3. Does heat, in the absence of light, have a directive influence upon the movements of Daphnia?

4. How does light in its effects upon Daphnia differ from heat? Are both effective only as they change the temperature of the organism?

III. EXPERIMENTS.

1. Tests for Photopathic Reactions.—*A.* METHOD.—As a means for discovering whether there is an "optimal intensity" of light for Daphnia an apparatus was devised which enabled the experimenter to observe, in a dark chamber, the movements of the animals in a glass dish the middle region of which was illuminated by a band of light which varied in intensity from zero at one end to as much as 20 candle-power at the other.

Figure A is a vertical section of the apparatus used for this work. It consisted of a cylindrical lens, *L*, 25 centimetres long, 10 centimetres wide, with a radius of curvature of 25 centimetres. One surface of the lens (Fig. B) was flat. This lens was fastened, for convenience of focussing, in a movable holder, *H*, and so placed that it focussed certain of the parallel rays proceeding from two 16-candle-power lamps (in some tests a 100-candle-power lamp was used), *C. B.*, in a line upon the bottom of a glass box, *T*, in which the Daphnia were placed. Just above the lens and in contact with its plane surface was a screen of black cardboard containing a triangular opening through which the rays reached the lens. This triangular opening permitted many rays to fall upon the lens at one end, and at the other none, as a result of which

* Parker and Arkin (:01, p. 156) call attention to the possibility of this kind of reaction in case of the earthworm.

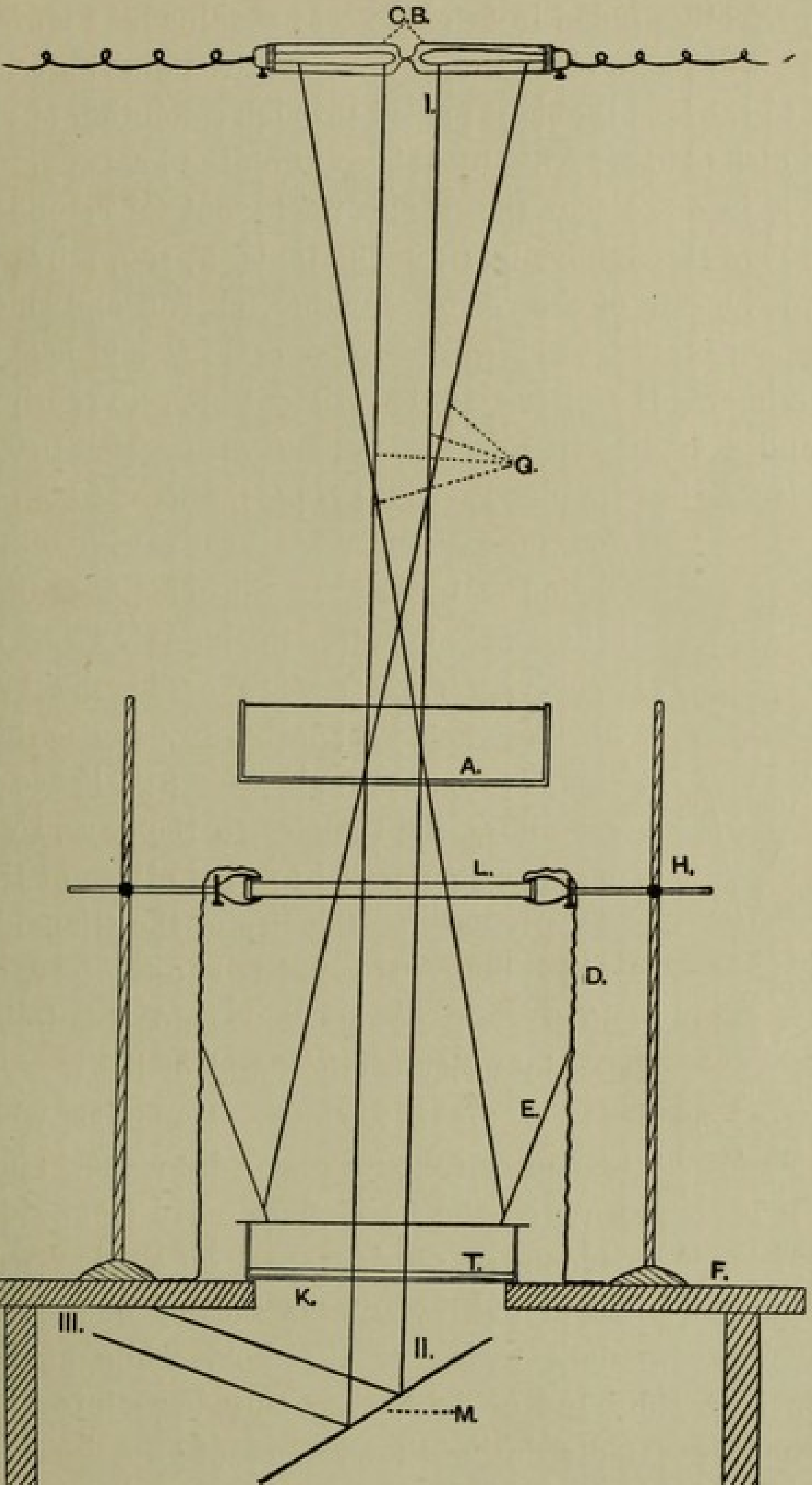

FIGURE A.—Apparatus for Giving a Band of Light Regularly Graded in Intensity.

C. B., two 16-candle-power electric lamps; *G*, rays of light; *I, II, III*, course of rays; *A*, a dish containing solution of alum 10 cm. deep; *H*, frame for lens, *L*; *E*, screens to cut off light from ends of glass box, *T*; *D*, cloth curtains to exclude light; *F*, table for apparatus; *K*, slit in table for passage of rays; *M*, mirror. Scale $\frac{1}{5}$.

a line of light perfectly graded in intensity was obtained. Figure B, an oblique side view of the lens, will make clear the form of the lens and its relation to the screen.

On its way to the lens the light passed through a solution of alum, 10 centimetres deep, in a glass dish, *A* (Fig. A). By this solution the heat-rays were cut off. From the box the rays, in order that the results might not be complicated by reflection, were allowed to pass through a slit, *K*, in the table, *F*, to a mirror, *M*, by which they were reflected to the side of the room. Further, all end and side light was shut off from the experiment-box by black cardboard screens, *E*, and heavy cloth curtains, *D*.

In the experiments the plate-glass experiment-box, 25 centimetres long, 5 centimetres broad, and 4 centimetres deep, was filled with water to a depth of .5 centimetre, and so placed that the band of light from the lens, which was 16 centimetres long and about 1 centimetre wide, illuminated the middle region of it, whereas the remainder of the box was dark. The Daphnia were, therefore, free to move either in the relatively dark regions or in the band of light. The smallest angle made by any ray with the bottom of the box, *T*, was approximately 81°, hence the animals moved almost at right angles to the rays, so long as their movements were parallel to the bottom of the box.

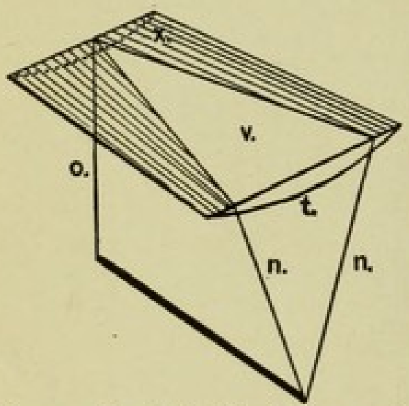

FIGURE B.—Cylindrical Lens and Screen with Triangular Opening.

X, horizontally placed screen of black cardboard resting upon the plane surface of the lens, with a triangular opening, *V*, beneath which is seen, at *t*, the curved outline of one end of the lens; *n*, *n* indicate the course of rays of light at the + end of the band of light; *o* indicates the course of the rays at the − end.

By varying the size of the triangular opening through which light was admitted to the lens, and by using lamps of different powers, it was possible to increase or diminish the intensity of the band of light.

B. OBSERVATIONS.—Daphnias when placed in the experiment-box wander into the band of light. Having entered the band they move from side to side in it, but seldom go outside; as soon as they reach the edge of the band and the anterior portion of the body comes into the dark region of the box, while at the same time the posterior portion is in the band of light, they turn back into the illuminated area. This reaction occurs repeatedly during the progress of an animal from one end of the box to the other. It is strikingly similar to the chemotactic reactions of Paramecium as described by Jennings ('97, p. 269).

Furthermore, the animals when once they have entered the band of light move very quickly to the region of greatest intensity of illumination, and remain there most of the time. It is to be remarked that the animals in moving from the lower to the higher intensity of light endeavor to orient themselves so that the long axis of the body is parallel with the rays of light. Because of the slight depth of the water in the box it was impossible for them to move far in a straight line when thus oriented without reaching the surface of the water or the bottom of the box. As a result of this condition the animals orient themselves with their heads toward the higher intensity region and swim upward at an angle of about 45° with the surface until they reach the surface; they then cease swimming and by reason of gravity sink toward the bottom of the box; in a few seconds they again swim upward. This is repeated, and thus the animal approaches, by a very indirect, zigzag path, the region of greatest illumination.

To the highest intensity (about 20 candle-power) which was obtainable with the apparatus from a 100-candle-power lamp, the Daphnia were uniformly positive in their phototaxis. And apparently when they had reached the + end of the band of light they were still trying to move on to a higher intensity. There is therefore no evidence from these experiments of an "optimal intensity."

As it seemed possible that a higher intensity might reveal the "optimal," further tests were made by simply placing a 100-candle-power lamp at one end of the glass experiment-box. Under these conditions the animals moved directly to the + end of the box. When no adiathermal screen was interposed between the lamp and the box the heat was so great as to kill them within a few seconds after they reached the point nearest to the lamp. But notwithstanding the fact that they were thus directed by the light into a region of exceedingly violent thermic stimulation the Daphnia never turned back. When a screen was used the animals after reaching the + end remained there, moving about in a very irregular jerky manner as if under the influence of a strong stimulus. They have been observed to move about in this way for as long as thirty minutes, within a few centimetres of a lamp whose light was almost too bright for the human eye to endure, without giving any signs of a tendency to become negative to the light. To all appearances the organisms are wholly unable to resist the directive influence of light, even though it lead them into intensities of stimulation far greater than those to which they are accustomed, or into the presence of positively harmful stimuli. In a previous paper (Yerkes, :00, p. 419) I have described the phenomenon of Daphnia being directed by light into harmful chemical solutions.

From these observations we learn that Daphnia is positively phototactic to light up to an intensity of 100 candle-power, and that there is no evidence of an "optimal intensity" between 0 and 100 candle-power.

2. **The Influence of Heat Accompanying Light.**—The following experiments were made to determine (1) whether the radiant heat which accompanies the light from a 16-candle-power incandescent lamp has any influence upon the motor reactions of

Daphnia; (2) whether the directive influence of light tends to diminish during the period for which an animal is subjected to it; (3) whether Daphnia shows any signs of fatigue in long-continued motor reaction to light and heat; and (4) whether, under conditions different from those of the previously described photopathic experiments, Daphnia exhibits any preference for a particular intensity of light.

A. METHOD.—The Daphnias to be observed were placed, one at a time, in a tin trough 60 centimetres long, 6 centimetres wide, and 8 centimetres deep, painted dead black inside and out to prevent reflection. The ends of the trough were glass, so that light from electric lamps could enter parallel to the long axis of the trough. A 16-candle-power lamp, in the circuit of which a key enabled the experimenter to turn the light on or off quickly, was placed 5 centimetres from each end of the trough. All side and all end rays, except those passing through the glass ends, were cut off by screens. At one end a glass vessel, having parallel vertical sides 15 centimetres square and 5 centimetres apart, filled with distilled water, was so placed as to interpose 5 centimetres of water between the lamp and the end of the trough in order that the heat-rays might not enter. At the opposite end of the trough both heat and light were permitted to enter.

The apparatus was set up in a dark room. The experiments consisted in placing a Daphnia at one end of the trough, turning on the light at the opposite end, and noting, with the aid of a stop-watch, the time taken by the animal to move from a line 5 centimetres distant from the end at which it started to the middle point of the trough, and, again, from there to a line 5 centimetres from the end nearer to the light. The first period mentioned may be designated as the time of migration for the "First Half" of the trip, the second as the time for the "Second Half," and the sum of the two as the time for the "Whole Trip." These expressions are used in the tables which follow. As soon as the animal had reached the light end the light was turned off at that end, and that at the other at once turned on. In the same way as for the first trip the time for the return trip was noted. This was repeated ten times in succession, thus giving records for ten trips toward the end of the trough at which the adiathermal screen was placed, and for ten toward the screenless end. In the tables the trips are marked "Water Screen," indicating those toward the screen, and "No Screen," those in the opposite direction. After an animal had made ten trips in each direction, the water screen was shifted to the other end of the trough and another series of ten trips in each direction recorded. This was done in order to eliminate any differences in the time of the trips toward the screen and those away from it which might arise because of slight intensity differences between the two lights or from other differences in the conditions of the halves of the trough.

The three columns of Table I marked "(Left) Water Screen" contain records of the times, in seconds, for ten trips toward the screened end of the trough when the screen was on the left of the experimenter as he faced the trough. The next three columns, marked "(Right) No Screen," contain results for the ten *return* trips of the same series. Likewise "(Left) No Screen" indicates that the screen had been transferred to the *right* end of the trough. The trips are numbered 1, 2, 3, etc., in the order in which they were made. From this description it appears that each animal used was permitted, under the directive influence of the light from a 16-candle-power lamp, to make 40 trips each 50 centimetres in length, in rapid succession. Half of these 40 trips were made under the influence of light accompanied by heat, the other half under the influence of light alone.

B. OBSERVATIONS.—Table I is a representative series of results gotten with Daphnia Number 1.

It is to be noted (1) *that the time of the trips rapidly decreases throughout the series; it being for the first two trips* 125 *and* 185 *seconds respectively, and for the last two* 58 *and* 57 *seconds;* (2) *that the time for the "First Half" is always considerably less than that for the "Second Half"; and* (3) *that the average time for all trips toward the Screened End* (*both the right and the left*), 74.9 *seconds, is practically the same as that for all trips toward the Unscreened End,* 73.3.

Similar series of results were gotten with four other animals, and in Table II the averages for the five are given. Each column in this case contains the averages for ten trips for each of the animals. The general averages at the bottom of the table are therefore for 50 trips under each of the four conditions, i.e., toward the left when the screen was on the left, toward the right when the screen was on the left, toward the left when the screen was on the right, and toward the right when the screen was on the right. In all 200 trips were made. Of these 100 were toward the water screen, and 100 away from it. At the bottom of Table II the average for each of these 100 trips is given.

In answer to the first question proposed at the beginning of this section, Does the heat accompanying light influence the movements of Daphnia? the experiments do not furnish a definite reply. From the general averages it appears that the time for the "Whole Trip" toward the Unscreened End (73.8 seconds) was 3.8 seconds less than for that toward the Screened End (77.6 seconds). One might conclude from this that the heat increased the rate of movement. But *examination of the individual averages shows that in two cases out of five the average time of movement toward the Unscreened End was longer than that toward the Screened.* For this reason, and also because of the slight difference of the general averages, we are forced to

TABLE I.

TIME (IN SECONDS) REQUIRED BY DAPHNIA NUMBER 1 TO SWIM 50 CM., WHEN INFLUENCED BY LIGHT ALONE AND WHEN INFLUENCED BY LIGHT ACCOMPANIED BY HEAT.

7 P.M., Dec. 11, 1901. Temperature of Water 20° C.

Number of Trip.	(Left) Water Screen.			Number of Trip.	(Right) No Screen.			Number of Trip.	(Left) No Screen.			Number of Trip.	(Right) Water Screen.		
	First Half.	Second Half.	Whole Trip.		First Half.	Second Half.	Whole Trip.		First Half.	Second Half.	Whole Trip.		First Half.	Second Half.	Whole Trip.
1	53	72	125	2	61	81	142	21	32	39	71	22	23	26	49
3	88	97	185	4	45	87	132	23	22	46	68	24	25	29	54
5	68	77	145	6	35	55	90	25	16	33	49	26	15	25	40
7	30	53	83	8	42	70	112	27	17	30	47	28	23	33	56
9	42	69	111	10	38	49	87	29	19	38	57	30	16	27	43
10	32	41	73	12	35	40	75	31	17	43	60	32	20	39	59
13	33	49	82	14	23	29	52	33	16	30	46	34	18	24	42
15	26	42	68	16	39	45	84	35	19	35	54	36	17	29	46
17	30	39	69	18	30	32	62	37	20	47	67	38	21	37	58
19	19	34	53	20	20	21	41	39	25	46	71	40	19	38	57
Average	42.1	57.3	99.4		36.8	50.9	87.7		20.3	38.7	59.0		19.7	30.7	50.4

Averages for all Trips (20) Toward Screened End. (Right and Left.)			Averages for all Trips (20) Toward Unscreened End. (Right and Left.)		
First Half.	Second Half.	Whole Trip.	First Half.	Second Half.	Whole Trip.
30.9	44.0	74.9	28.5	44.8	73.3

TABLE II.

THE AVERAGES FOR FIVE SERIES OF EXPERIMENTS LIKE THAT OF TABLE I. EACH COLUMN CONTAINS THE AVERAGES FOR TEN TRIPS MADE BY EACH OF FIVE DAPHNIA (NUMBERS 1 TO 5).

Number of Animal.	(Left) Water Screen.			(Right) No Screen.			(Left) No Screen.			(Right) Water Screen.		
	First Half.	Second Half.	Whole Trip.	First Half.	Second Half.	Whole Trip.	First Half.	Second Half.	Whole Trip.	First Half.	Second Half.	Whole Trip.
1	42.1	57.3	99.4	36.8	50.9	87.7	20.3	38.7	59.0	19.7	30.7	50.4
2	33.8	53.4	87.2	32.2	37.6	69.8	21.9	32.6	54.5	18.6	31.6	50.2
3	36.4	57.6	94.0	33.9	44.1	78.0	27.6	48.5	76.1	28.0	52.1	80.1
4	28.6	34.0	62.6	25 6	36.5	62.1	29.7	36.6	66.3	24.9	32.6	57.5
5	49.3	66.8	116.1	45.8	55.3	101.1	24.9	58.9	83.8	23.3	55.2	78.5
Gen. Aver.	38.0+	53.8	91.9−	34.9−	44.9−	79.7+	24.9−	43.1−	67.9+	22.9	40.4	63.3

Averages for all Trips (100) Toward Screened End. (Right and Left.)			Averages for all Trips (100) Toward Unscreened End. (Right and Left.)		
First Half.	Second Half.	Whole Trip.	First Half.	Second Half.	Whole Trip.
30.4	47.1	77.6	29.9	44.0	73.8

conclude that there is no decisive evidence of any influence upon the movements of Daphnia of the heat accompanying light.

To the second question, Does the directive influence of light tend to diminish during the experiments? we are able to answer, No; for throughout the period of observation the rate of movement, in each of the five animals, gradually increased. This was apparently due to an increase in sensitiveness to changes in the intensity of the light. As the experiments with an individual were continued there was a noticeable quickening in the orientation movements, and an increase in the rapidity of the swimming. From the evidence of the experiments it may be said that under the conditions with which we are dealing the sensitiveness of Daphnia to changes in light intensity and to the directive influence of light does not diminish but, on the contrary, increases.

In studies of Daphnia made by Davenport and Cannon ('97, p. 31), and by me (Yerkes, :00, pp. 407–414), the rate of movement was found to increase with the intensity of the light. Davenport and Cannon concluded that the difference was due almost entirely to difference in the precision of orientation. Although it is true that precision of orientation is the chief cause of the increase in rate, I find that the rapidity of the swimming movements also varies with the changes in the intensity of the light.

In view of the well-established fact that Daphnia moves more rapidly in strong than in weak light, how are the results of the experiments just described to be explained? In them, it will be remembered, the time for the "Second Half" of the trip toward the light was longer than that for the "First," when just the opposite was to be expected. It might be said that as the animals approached the light the intensity became too great for them, hence a hesitation which increased the time. This explanation is, moreover, supported by the fact that, whereas the path taken in the "First Half" of a trip was fairly straight, it became zigzag in the "Second Half."

But there is another fact to be considered. It should be remembered that when the animal in an experiment reached the end of the trough toward which it had been swimming, it was in a region of very strong light; then suddenly the light was turned off at that end, and turned on at the opposite end. This sudden and great change in the stimulus always caused the animal to start off toward the light at high speed. It seemed not improbable, therefore, that the shortness of the time for the "First Half" as compared with the "Second" might be due to this initial stimulus. For the purpose of settling this matter, observations were made in which the animals were started toward the light without the initial stimulus of the sudden change from strong to weak light. These experiments proved conclusively that the time for the

"First Half" was shorter than that for the "Second" only by reason of the initial stimulus. There was still some evidence, however, that the intense illumination of the end next the light somewhat retarded the animals in that they were forced by it to take a less regular course, and, although moving more rapidly if anything, because of the zigzag path followed they progressed, on the whole, more slowly.

In one instance an animal on its first trip swam to about the middle of the trough, then, ceasing to move toward the light, it swam about in circles. It looked as if the reaction was given to an "optimal intensity," and I at first thought that it was photopathic. Further experimenting showed that the animal would swim toward the end from which it had come, when the light was turned on there, but that toward the other end it would not swim farther than the spot already mentioned. Search for an explanation of the phenomenon revealed the presence of a number of bubbles (air?) at the bottom of the trough at the point beyond which the animal would not go, even when directed by strong light. The reaction therefore was not photopathic but chemotropic.

This single observation is of special interest and importance since Daphnias are usually so strongly positive in their phototaxis that they will pass through harmful chemical solutions, and even attempt to go through a drop of strong acid in their efforts to approach a light (Yerkes, :00, p. 419).

The question, Is there any evidence of fatigue? must also be answered in the negative. Although the animals in these experiments moved almost continuously for an hour, covering during that interval at least a distance of 2000 centimetres, if not 2500 centimetres, there was throughout an increase in the rate of movement, and no evidence whatever of fatigue.

The fourth question formulated has already been answered. There is no evidence of an "optimal intensity," and no clearly demonstrated photopathic reaction.

3. The Reactions of Daphnia to Radiant Heat.—Does radiant heat have any directive influence upon the movements of Daphnia? In the previously described experiments for testing the value, for the movements of the organism, of the heat accompanying light, there was little evidence of the influence of heat; but since light is itself an exceedingly strong directive agent, it may be that the effect of the heat was obscured by it. To determine in a more satisfactory and conclusive manner whether heat is a directive stimulus the following experiments were made.

A. Method.—Over a V-shaped glass trough 24 centimetres long, 2 centimetres wide, and 1.5 centimetres deep was swung a frame bearing five partitions, cut to fit the V shape of the trough. This frame could be raised above the trough or lowered so that the partition divided it into six equal portions. The trough was placed horizontally upon a table in a dark room. At 5 centimetres from one end of it was an electric heater, consisting of a metal frame which held coils of high-resistance wire. The heater presented to the end of the trough a radiating surface 10 centimetres square, and the heat from this surface could be felt by the hand at a distance of 40 centimetres.

The trough was filled with water to a depth of .5 centimetre, and the partitions lowered; then two Daphnia were placed in each of the spaces except those at the ends. In the accompanying Tables III, IV, and V the spaces are numbered 1 to 6, and the number of animals in each is indicated. When all was in readiness for an experiment the partitions were raised and the animals permitted to swim freely, or as the stimulus to be tested might direct them, for a period of three minutes. The partitions were then lowered, and an electric light turned on so that the positions of the animals could be recorded. This record having been made, the animals were again distributed as at the beginning of the experiment, i.e., two in each of spaces 2 to 5.*

It was necessary, in order that no undetected factors enter as directive influences, that check experiments be made just before each of the series of experiments to test the influence of heat. In these preliminary observations the conditions were, so far as determinable precisely the same as in case of the immediately following series, except for the absence of heat, the influence of which it was the purpose of the experiments to determine.†

B. Observations.—Table III is a record of the check series of ten observations preliminary to the experiments of Table IV. The vertical columns in the table give the number of animals in the various spaces at the end of each experiment. The result of the experiments is expressed by comparing the mean position of the animals at the beginning with the mean position at the end of the experiment; the difference of these means expresses the amount of movement toward either end (+ or −) in terms of spaces. At the beginning of an experiment, since the spaces 2, 3, 4, and 5 each contained two animals, the mean position as determined by the formula

$$\frac{\text{Product of space} \times \text{Number of animals}}{\text{Total number of animals}}$$

* All of the observations were made at night in a room from which light was excluded.

† As it seemed possible that heat might cause currents in the water of the trough which would change the positions of the animals, check experiments were made by placing a number of Daphnia in a glass tube, filled with water, one end of which was placed in snow, and the other over the electric heater. Under these conditions the animals collected near the snow end, although no movement of light particles of material suspended in the water could be detected.

was 3.5. After experiment 1 of Table III the mean position was 4, which indicates that there had been an average movement of half a space toward the end of the trough

TABLE III.

CHECK EXPERIMENTS IN DARKNESS. NO HEAT.

Period 3 min. Dec. 12, 1901, 7 P.M.

Spaces	1	2	3	4	5	6	
Location of Animals at Beginning of Each Experiment.	+End.	2	2	2	2	−End.	Average Movement.
Experiment 1	0	3	0	0	4	1	−0.500
" 2	0	2	1	2	0	3	−0.375
" 3	4	2	1	1	0	0	+1.375
" 4	1	1	0	3	1	2	−0.500
" 5	2	2	0	3	0	1	+0.500
" 6	1	2	1	2	0	2	0.000
" 7	1	3	0	2	0	2	+0.125
" 8	0	3	1	2	2	0	+0.125
" 9	3	2	1	1	1	0	+1.125
" 10	2	2	1	0	1	2	+0.250

Movement for series +.3125 (i.e., .3125 of a space toward the + end).

marked space 6. Since in the experiments heat was applied at the end next space 1, it will be convenient to designate that as the + end, and the opposite as the − end, in order that without confusion movement of the animals toward the heat may be designated as +, and away from it as − (see Table III). For this reason the movement in experiment 1, Table III, is expressed as −0.50 (i.e., the average movement of the eight Daphnia was a half-space toward the − end of the trough).

The check series of ten experiments in Table III resulted in six + movements, with an average for the series of +0.3125. There is therefore indication of a slight tendency toward the + end. This may have been due to undetected rays of light or to slight jarring of the trough. The movement is so slight, however, that it is not of great importance; a large number of observations would in all probability have resulted in an average of 0.

As soon as this check series was ended the heat was turned on and a similar series of experiments made to test the influence of heat upon the movements of the animals. At the beginning of the heat series the temperature of the water throughout the trough was about 21° C. At the end of the series it was 28° at the + end of the trough, and 25° at the − end.

Table IV gives the result of this test of the effect of radiant heat. The first experiment resulted in a marked movement toward the heated (+) end, but thereafter *every* experiment resulted in a movement in the opposite (−) direction. In experiment 1 it is almost certain that the heat had not yet had time to affect the water to a sufficient degree to influence the animals. The averages for the series is −0.475. This shows clearly that Daphnia is negatively thermotactic at a temperature of 28°. *It is noteworthy that all except the first experiment resulted in − movements.*

For the purpose of determining the relation of the amount of heat to the extent of the animals' migration, the trough was now removed to a distance of 20 centimetres from the heater (i.e., four times as far as in the experiments of Table IV). Table V contains the records for five check experiments, and ten heat experiments with the heater at this distance. For the check experiments the average movement was +0.65; for the heat experiments it was −0.15. If in this case, as in the previous series, we consider the + tendency, as indicated by the check series, which had to be overcome before there could be any − movement, it is clear that the influence of the heat should be expressed by 0.65, the positive tendency, plus 0.15, the negative result, or 0.80. In the previous series it would be 0.31 plus 0.475 or 0.785.

Examination of the experiments of Table V shows that a positive tendency gradually gave place to a negative. This would appear, in the light of the previous series, to be the result of the gradual increase in the temperature of the water, and especially of the increase in the difference of the temperatures of adjacent regions. At the end of the series of Table V there was only 1° difference in the temperatures of the end spaces, 1 and 6.

C. THERMOTAXIS.—Now, as to the evidence for the directive influence of heat, the experiments described prove conclusively that in the absence of light Daphnia moves away from the source of heat at a temperature of 28° or thereabouts. Is this merely a random wandering into regions of lower and more favorable temperatures, or is it a definitely directed movement similar to the phototactic reaction?

Loeb ('90, p. 43) proved that the larvæ of Porthesia *wander* into the warmer end of a dark box; and other investigators have demonstrated migration with reference to heat in the case of Myxomycetes, Protozoa, and certain larvæ of the Metazoa; but thus far no definitely directed movements in response to heat have been described.

In the first place it seems fairly certain that Daphnia, in the experiments of this paper, was affected by the heat-rays only as the temperature of the water changed; for at the beginning of the series there was no evidence of a directive influence, whereas just as soon as the temperature of the water began to rise at the + end the animals tended to migrate toward the − end.

As a matter of observation, the movements of Daphnia toward the − end were exceedingly irregular, being zigzag and indirect, and thus sharply contrasted with the usual photopathic movements. Notwithstanding this I believe that the two reactions are in principle the same; in both cases difference in intensity of stimulation

TABLE IV.

EXPERIMENTS TO TEST THE INFLUENCE OF HEAT UPON THE MOVEMENTS OF DAPHNIA.

Heated Surface 5 cm. from + End of Trough.
Temperature of Water at Beginning of Experiments 21° C. for all Regions of Trough.
Temperature of Water at End of Experiments 28° C. at + End of Trough, 25° C. at − End.
Period 3 min. Dec. 12, 1901, 7.45 P.M.

	Region of Highest Temperature.					Region of Lowest Temperature.	
Spaces	1	2	3	4	5	6	
Location of Animals at Beginning of Each Experiment.	+End.	2	2	2	2	−End.	Average Movement.
Experiment 1	3	1	2	1	1	0	+1.000
" 2	0	2	2	1	1	2	−0.375
" 3	0	0	1	2	3	2	−1.250
" 4	1	1	0	2	1	3	−0.750
" 5	0	1	1	2	3	1	−0.750
" 6	0	0	3	1	1	3	−1.250
" 7	1	1	1	2	2	1	−0.250
" 8	0	1	1	4	2	0	−0.375
" 9	1	1	1	2	2	1	−0.250
" 10	0	1	2	1	2	2	−0.750

Movement for series −.475 (i.e., .475 of a space toward the − end, away from heater).

TABLE V.

CHECK EXPERIMENTS.

Period 3 min. Dec. 13, 1901, 8 P.M.

Spaces	1	2	3	4	5	6	
Location of Animals at Beginning of Each Experiment.	+End.	2	2	2	2	−End.	Average Movement.
Experiment 1	0	2	2	0	4	0	−0.250
" 2	1	0	2	3	2	0	−0.125
" 3	3	1	3	1	0	0	+1.500
" 4	4	2	0	1	1	0	+1.375
" 5	3	2	0	1	1	1	+0.750
							Av. + .650

EXPERIMENTS TO TEST INFLUENCE OF HEAT WHEN HEATED SURFACE WAS 20 CM. FROM + END OF TROUGH.

Temperature of Water at Beginning of Experiments 22° C.
Temperature of Water at End of Experiments 26° C. at + End of Trough, 25° at − End.

	Region of Highest (+) Temperature.					Region of Lowest (−) Temperature.	
Experiment 1	2	1	1	0	3	1	0.000
" 2	2	1	1	2	2	0	+0.375
" 3	1	1	0	2	3	1	−0.500
" 4	1	1	2	3	0	1	+0.125
" 5	1	2	2	0	0	3	−0.125
" 6	2	0	0	2	1	3	−0.625
" 7	2	1	0	2	0	3	−0.250
" 8	3	1	2	0	2	0	+0.875
" 9	0	1	3	1	2	1	−0.375
" 10	0	2	1	0	2	3	−0.875

Movement for series −0.150.

for different regions of the body determines the direction of movement. I have therefore used the term thermotactic to refer to a motor reaction which is determined by difference in the degree of stimulation of different parts of the animal.

D. THE RELATION TO EACH OTHER OF HEAT AND LIGHT AS STIMULI.—These experiments have some bearing upon the theory that light stimulates an organism in essentially the same way as heat, that is, by altering the chemical processes of the tissues through changes in the temperature of the regions affected. Such a theory receives some support from the fact that the reactions of certain animals to light can be changed from positive to negative, or the reverse, by changing the temperature. Groom and Loeb ('90, pp. 166, 167) found that the nauplii of Balanus react differently to light at different temperatures; Loeb ('93, p. 91) has proved that Polygordius larvæ which are positively phototactic at 24° C. are negative at 29°; Massart ('91, p. 164) states that a flagellate, Chromulina, is positive at 20° C. and negative at 50°, and Strassburger ('78, p. 605) noticed that certain swarm-spores that were positive at 16° to 18° were negative at 40°.

Thus far in experiments with Daphnia I have been unable to change the sense, of the reaction to light by changing the temperature. Yet, if light affects the organism as does heat, one would expect that an organism which avoids high temperatures, as these experiments have shown that Daphnia does, would become negatively phototactic in the presence of strong light. But even light which is accompanied by sufficient heat to kill the animals is sought by Daphnia.. For this reason, and also because the reaction to light is exceedingly quick, whereas that to heat is slow, I feel justified in concluding that light acts upon Daphnia otherwise than does heat. It may well be, however, that the difference is one of degree rather than kind.

IV. SUMMARY.

1. Daphnia pulex is strongly positively phototactic to all intensities of light from 0 to 100 candle-power.

2. There is no evidence of preference for a certain intensity, the "optimal."

3. So far as the experiments described in this paper indicate, the heat accompanying the light from a 16-candle-power incandescent lamp does not have any noticeable influence upon the direction or rate of movement of Daphnia.

4. Subjection of Daphnia to 16-candle-power light for a period of one hour, during which interval the animal was kept in almost constant motion, showed a gradual increase in the rate of movement, and in the sensitiveness to changes in the intensity

of light throughout the period. There was no evidence of fatigue in animals that had moved at least 2000 centimetres in an hour.

5. Heat in the absence of light has a directive influence upon the movements of Daphnia. In a trough containing water of 28° C. at one end and 25° at the other they migrated toward the region of lowest temperature.

6. The movement is not direct, but irregularly wandering. It is, however, in all probability due to differences in the intensity of stimulation for different regions of the animal's body, and is therefore in principle the same as the photopathic reaction. Daphnia may therefore be said to be negatively thermotactic at a temperature of about 28° C.

7. The fact that in the case of Daphnia phototactic reactions cannot be changed from positive to negative or the reverse by changes in temperature indicates that light does not act upon the organism in the same way as does heat.

I am indebted to Prof. W. C. Sabine for the suggestion of the cylindrical lens as a means of obtaining a uniformly graded line of light, and to Professors E. L. Mark and G. H. Parker for assistance in the work.

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