THE ROLE OF RANDOM MOVEMENTS IN THE ORIENTATION OF *PORCELLIO SCABER* TO LIGHT

HARRY BEAL TORREY and GRACE P. HAYS
Reed College, Portland, Oregon

In his admirable paper on " The Selection of Random Movements as a Factor in Phototaxis," Holmes[1] has given great significance to random, that is, spontaneous, non-directive movements in the orientation of earthworms, blow fly larvae, and leeches, to light. As he carefully watched the movements of these organisms under the influence of light, it " soon developed that what seemed at first a forced orientation, the result of a direct reflex response, is not really such, but that the orientation which occurs and which is often quite definite is brought about in a more indirect manner by a mode of procedure which is in some respects similar to the method of trial and error followed by higher forms." The organism becomes oriented by following up those random movements which bring them away from the source of light.

While our experiments on the larvae of an undetermined species of blow fly and on a species of earthworm (*Allolobophora* sp.) materially lessen for us the importance of random movements as a factor in the orientation of these organisms to light, our conclusions are in complete accord with Holmes' view that the type of reaction he describes " differs from Jennings' ' motor reflex ' by which many of the so-called tropic reactions are produced in the Protozoa." This difference has little significance for Mast[2] who believes that " the only difference between the orienting reactions in the two classes of animals mentioned is that the unicellular forms studied by Jennings always turn toward a structurally defined side, while the metazoa investi-

[1] Journal of Comparative Neurology and Psychology, 1905, No. 15, p. 18.
[2] Light and the Behavior of Organisms, 1910, p. 51.

gated by Holmes are not thus limited in their direction of turning."

In thus minimizing a difference to which Holmes has explicitly called attention, Mast may have missed a cardinal point in Holmes' illuminating discussion. The direction of the random movements of the blow fly larvae as observed by Holmes is not predictable so far as it bears no definite relation to the source of light. The direction of the movements of *Euglena*, an organism in which the "motor reflex" plays an important part in its orientation to light, *is* predictable, since it *does* bear a definite relation to the source of light. In the one case, the orienting movements, made at random, are not controlled, as to direction, by the light; in the other case, the orienting movements are definitely controlled, as to direction, by the light. In the former, selection operates among so-called trial movements; in the latter, in so far as the movements are controlled or forced by an external agency, the method of trial is excluded. This difference, then, is of no little significance in an attempt to determine—as this paper is attempting to determine for certain organisms—the actual value of the orientation hypothesis that rests upon the assumption of trial movements.

2

The fact that some authors do not distinguish between random movements and directive movements forced by the environment has been a source of some confusion in the literature of animal behavior. Further confusion has centered about the conception of symmetrical stimulation repeatedly emphasized by Loeb and recently reaffirmed by Parker.[3] Investigators of the orienting reactions of non-symmetrical protozoa or symmetrical organisms such as rotifers and worm larvae that swim, like the protozoa, in spiral courses, have had difficulty in seeing the applicability of this conception to their material. That the conception is applicable, however, to the behavior of such organisms as *Euglena*, though not in the form apparently anticipated by some of its critics[4] a recent paper[5] has attempted to show. And its applicability to the orientation of earthworms and blow

[3]Journal of Animal Behavior, 1911, No. I, p. 461.
[4]Mast, 1910, p. 85.
[5]Torrey, Science, No. 38, p. 873.

fly larvae to light has been convincingly discussed by Parker in the paper just mentioned.

These conceptions of symmetrical stimulation and of forced directive movements have long characterized the tropism hypothesis, whatever other attributes it may be said to possess; and they appear to be quite inconsistent with the conception of orientation by the selection of trial reactions. There should be little danger of confusion, then, in designating as tropic reactions not only the very gradual turning movements that may or may not be connected with tonic contractions accompanying constant stimulation, but also the more abrupt and angular turning movements composed of a series of forced shock reactions, *all in the same general direction*, that we have repeatedly observed in the orientation of *Euglena* to light. Both extremes are, in fact, represented in the behavior of *Euglena*, which will be considered in another paper. Whether they also represent two different mechanisms of orientation is a question for the future to decide.[6] That they do not involve the selection of random movements there appears to be no doubt.

In the following account of the reactions of *Porcellio scaber*, it will be seen that although random movements are common they can readily be distinguished from the forced movements that occur in definite predictable directions in response to differential stimulation of symmetrically situated photoreceptors. But such phototropic movements not only exist; they are *large factors* in the orientation of *Porcellio* to light. This is true also for *Allolobophora* sp. and the larvae of an undetermined blow fly.

3

Porcellio scaber, a species of sow-bug, or wood louse, very common on the Pacific coast, is a typical symmetrical isopod with a pair of compound eyes set far apart in the head segment, and two pairs of antennae, of which the second antennae are conspicuous tactile organs, restlessly active during locomotion. The subequal walking appendages and the body in general are also sensitive to contact stimuli. Of other sense organs it is unnecessary now to speak.

[6] Since this was written, a paper by Dr. F. W. Bancroft, in the Journal for Experimental Zoology for November, 1913, appears definitely to have settled the question, for Euglena at least, in the affirmative.

During the day *Porcellio* is usually found under stones, logs, rubbish, in dark cellars, and various other sorts of cover from the light of the sun. Correlated with this habit is a definite negative phototropism.

In our first experiments, this phototropism was more or less masked by large individual differences in sensitiveness to light, and the apparent indifference of many individuals to light coming from incandescent bulbs placed directly in front of them. Later we discovered that the locomotion of many such indifferent individuals could be controlled with great definiteness by holding an incandescent bulb behind them, as they marched over a dead black table top, and moving it to one side or the other. Under these conditions—Mazda bulbs of both 25 w. and 60 w. were used—the organisms would move away from the light with the precision of a boat answering the helm. They could be guided in circles, in spirals, in courses that were directed, now to the right, now to the left, at the will of the experimenter.

That the eyes were the organs responsive to light was demonstrated by blinding them with a mixture of charcoal and glue. Individuals with the right eye blinded reacted to light from the left only; when the left eye was blinded light from the right was alone effective; when both eyes were blinded the individuals thus treated were indifferent to light from any direction.

4

Porcellio responds not only to changes in the direction of light. Exposure to light stimulates into activity animals that in darkness are quiescent; though sudden changes in intensity of illumination may produce inhibitory effects. Individuals vary considerably in their responses to these and all other types of stimulation. Marked differences may exist between individuals of the same size and apparently the same age; also between the reactions of the same individual at different times. Age differences are frequently connected with different reactions. Very young, unpigmented individuals are more responsive to directive stimulation than old. It is the rare exception for them to fail to respond, although adults are not uncommonly refractory. To sudden changes in intensity of light, however, old react at least as sensitively as young. In this connection the following case may be cited.

A female with a full brood pouch was placed in a Petri disk, round and round which she proceeded to move in the light of a 25 w. tungsten bulb. Many times when she was facing the light, the latter was turned off. Invariably she came at once to a dead stop Only occasionally when the light was turned off while she was facing *away* from it would she react similarly; being obviously less responsive in such cases. Sudden *increases* of intensity, (i.e., when the light was turned on) always produced definite inhibition of locomotion.

One of the brood of this female responded but rarely to sudden increases of intensity when facing the light, not at all to sudden decreases and never while going away from the light.

The fact that young are more readily directed in locomotion by light while they appear to be at least no more sensitive than adults to sudden changes in intensity of light. suggests the possibility of two mechanisms governing the two types of reaction. There is a wide variation in the responsiveness of adults to sudden changes in intensity, however. The problem presented here will be investigated further.

5

Though the eyes of *Porcellio* are sensitive to light, their power of forming images is approximately very small. Totally blind individuals avoid obstacles with the ease of normal individuals. When the second antennae of either are removed, however, they often bump squarely into obstructions, avoiding them only after contact through legs or body. The importance of the second antennae is emphasized by their constant activity during locomotion. when, by a rapid succession of tappings on the substratum, and wavings in the air, they explore the region immediately to the front. The usual random movements that are made by the anterior end of the earthworm and blow fly larvae are in *Porcellio* restricted to these mobile antennae. Since the head segment of *Porcellio* does not move perceptibly from side to side, it is only necessary to amputate the second antennae to eliminate what correspond to the usual random or trial movements in earthworm and blow fly larvae.

Such an operation was made in several cases. It was soon found, however, that, with or without the second antennae, *Porcellio* responded to photic stimulation under the conditions

of our experiments with unequivocal, definite, tropic reactions. So the operation was discontinued as useless. In later experiments on blow fly larvae and Allolobophora, the same definite tropic reactions were observed.

6

For the sake of clearness it should be pointed out not only that " random movements " and " trial movements " are expressions not always used in the same sense, but that apparently spontaneous random movememts may be controlled to some extent by the environment. The exploring movements of the second antennae of *Porcellio* are largely initiated and regulated by internal conditions; this is evident especially when environmental conditions remain constant. A slight change in the texture of the substratum, however, may produce marked changes in its behavior; in the absence of the antennae, contact differences may make themselves effective upon the path of locomotion through the legs or body. It is a truism that the behavior of an organism is a resultant of the responses to all simultaneously acting stimuli. A movement initiated from within, when the organism is exposed to various contact stimuli, may frequently be modified if not entirely inhibited by them. The same may be said of movements initiated from without.

It happens, therefore, that so-called " trial " movements in *Porcellio* and blow fly larvae and earthworms vary their character and intensity with circumstances. They may be so augmented by external stimuli as largely to obscure the tropic reactions which under other conditions are readily perceived. The source of the external stimulation may, however, be very inconspicuous. This was especially true in the case of a blow fly larvae that had been traveling away from the light in a direct course with very slight lateral movements of the anterior end. Suddenly the anterior half of the body was lifted and swung from side to side, up and down, in irregular movements of large amplitude that continued for several seconds. The cause of this change in behavior was finally discovered in a bit of filament from the paper substrate that had been picked up and was adhering to the anterior end. For the time, these vigorous " trial " movements, initiated probably by internal conditions but owing their conspicuous characters to contact stim-

uli, effectively masked the heliotropic movements so apparent under other conditions. Similar pronounced movements were frequently seen when a larva, crawling out over the edge of the glass plate on which it was being observed, would free the anterior third or half of its body. It would then wave this free portion about much in the manner of a leech. Dryness of the substratum may produce similar effects. Such behavior suggests the probability that even the small random or trial movements of the anterior end that ordinarily accompany locomotion are controlled—their amplitude, perhaps being determined—to some extent by contact stimuli.

7

It is possible then, to distinguish between random movements that have no connection with photic stimulation, and movements that Mast calls trials, but are conditioned by photic stimulation. For convenience in further analysis, it will be desirable to distinguish between two groups of reactions thus conditioned. In the one may be placed reactions to high intensities of light, such as direct sunlight; in the other, reactions to lower intensities. All of these reactions are regarded by Mast as trial movements similar to the avoiding or shock reactions of the lower organisms. The reactions of the second group—however we may view them as "trials"—do indeed resemble those reactions of such a form as *Euglena*, that are in the *same general direction* with reference to the source of light. The reactions of the first group, however, occur *either toward or away from* the source of light. They are non-directive with reference to the source of light.

This distinction is emphasized by our observations on earthworms and fly larvae. When light was allowed to fall from the side upon the extended anterior end of either of these forms, the first movement of the anterior end was for certain intensities of light *away from* the latter, whether directed toward or away from the light, when exposed.

8

To eliminate as far as possible all non-directive reactions from the behavior of *Porcellio* to light, in order to discover any directive, tropic movements of orientation that might be present, we adopted two very simple methods. The first consisted in

exposing sensitive individuals suddenly to lateral illumination. The individual to be observed was placed on a smooth dead black ground, in a dark room. When its orientation had been accurately determined by means of a 25 or 60 w. tungsten bulb a few inches behind it, away from which it was moving, or a distant light in the ceiling, another tungsten bulb of either 25 or 60 w. and at different distances varying between 20 and 40 cm., was suddenly turned on, so that its light should strike the animal from the side at an angle as near ninety degrees as possible. Sometimes at the instant the lateral light was turned on, all other lights were extinguished; at other times, they were not. In both cases, the direction, with reference to the lateral light, of the first movement of the organism out of its course was determined.

These experiments, simple as they were, gave results that were strikingly definite and convincing. *Almost invariably* the first movement was *away from* the lateral light. The reaction was sharper, on the whole, when light came from the side only. To the 60 w. light, at 40 cm., the response was more definite than to the 25 w. light at the same distance. But the reaction was unmistakably negative within the limits of variation of lighting and distance mentioned. A significant feature of the results was the ease with which they were obtained and the simplicity of means employed.

It must be remembered that all individuals are not equally sensitive to light. But the consistency with which many individuals turned *away* from the light, whether the latter was on one side or the other, left no room for doubt that the reaction was *forced in a definite direction.*

9

The second method of experimentation, equally simple, was determined by the fact that many individuals responded more readily to light coming from behind than from in front of them. The following series of observations taken one afternoon are not selected, but indicate the reactions of the first individuals tested.

The lamps used in these experiments gave a source of light 4 to 5 cm. in diameter. This fact it is important to keep in mind when considering the definiteness of the responses of *Porcellio* for the smaller angles of incidence recorded in the tables. For

instance, at 70 cm. from the organism the light used possessed an angular diameter of 4°; at 36 cm., 7°; at 50 cm., 6°; at 15 cm., 16°.

I. A 25 w. tungsten bulb gave the light at approximately 70 cm. from the animal. The latter was a medium-sized adult. Since the sexes respond similarly to light, no account was taken of sex in this and the following experiments. Having determined the orientation of the animal by means of a 60 w. bulb behind it, this bulb was turned off as the 25 w. light was flashed upon it, from in front, striking the eyes of the animal so as to make an acute angle with the axis of the body.

Trial 1, Light 35° to left ; response to right.
" 2, " 15° " " ; animal stopped, wavered, and turned to right.
" 3, " 70° " " ; animal stopped, then turned to right.
" 4, " 60° " " ; response to right.
" 5, " 10° " " ; animal stopped, moved forward, then to left (toward light).
" 6, " 5° " " ; same as 5.
" 7, " 3° " " ; same as 5.
" 8, " 5° " right; animal turned to left.

These trials show a tendency in the organism to turn away from the light, the direction in which the turn is made depending upon the position of the light and the angle at which it strikes the eyes; there is a stronger tendency to turn to the left than to the right, but this is overcome when the light from the left strikes the eyes at an angle with the body axis of 15° or more.

The same tendency to turn more readily to one side than to the other is seen in the next series; though here the organism turns more readily to the right.

II. Another individual. Lights as in Series I.

Trial 1, Light	10°	to	left,	36	cm.	distant.	Response to right.
" 2, "	35°	"	"	36	"	distant.	Response to right.
" 3, "	5°	"	right,	36	"	distant.	Response to right.
" 4, "	12°	"	"	36	"	distant.	Response to right.
" 5, "	5°	"	"	70	"	distant.	Response to right.
" 6, "	5°	"	left,	70	"	distant.	Response to right.
" 7, "	45°	"	right,	70	"	distant.	Response to left.
" 8, "	30°	"	"	70	"	distant.	Response to left.

As in the first series, the organism turns *away* from the light, either to the right or left, when light strikes it at an angle greater than a certain magnitude, in this case between 12° and 30°. When the light strikes it at an angle of 12° or less, the organism

turns *toward* the light in the definite turning movement that ultimately carries it *away* from the light.

The two series of trials just presented suggest a difference in the sensitiveness of the two eyes to light. Tests of each individual by means of a light shining upon it from behind, fully supported this view. The first individual was guided without fail to the left when the light came from behind at a small angle to the right; but the same individual did not respond with such definiteness to light coming from behind at a similar angle to the left. These statements will apply equally well to the second individual, if the directions are reversed.

III. Another individual, young, unpigmented. Lights as before.

Trial 1,	Light	25°	to right,	36 cm.	distant; response to left.
" 2,	"	3°	" left,	50 "	distant; response to right.
" 3,	"	3°	" "	50 "	distant; response to right.
" 4,	"	5°	" "	50 "	distant; response to right.
" 5,	"	5°	" right,	50 "	distant; response to right.
" 6,	"	5°	" "	50 "	distant; response to left.
" 7,	"	8°	" "	50 "	distant; wavered, then left.
" 8,	"	5°	" "	50 "	distant; wavered, then left.
" 9,	"	15°	" "	50 "	distant; response to left.
" 10,	"	5°	" "	50 "	distant; response to left.
" 11,	"	*en face*,		50 "	distant; toward light, then left
" 12,	"	5°	" "	35 "	distant; response to right.
" 13,	"	5°	" "	50 "	distant; response to left.
" 14,	"	10°	" left,	50 "	distant; response to right.
" 15,	"	8°	" right,	50 "	distant, response to left.
" 16,	"	10	" left,	50 "	distant; response to right.
" 17,	"	5°	" "	50 "	distant; stopped, then to left.
" 18,	"	10°	" "	50 "	distant; response to right
" 19,	"	*en face*,		50 "	distant; wavered, then to left.
" 20,	"	5°	to right,	50 "	distant; response to left.
" 21,	"	5°	" "	50 "	distant, wavered forward.

This series brings out the fact that although the individual responds to light as an approximately symmetrical animal, its reactions lose precision when the light rays fall upon it from the front at very small angles (e.g., five degrees or less) with the axis of the body.

The following record of another individual bears directly upon this point. Preliminary tests showed that this individual, almost symmetrically sensitive to light, responded toward the right a bit more readily than toward the left. A 60 w. Mazda lamp was used, about 15 cm. in front of the animal, a given number of degrees of arc to the right or left as the case might be.

Light	5°	to right;	5	trials.	Responses to right,		2;	left,	3.
"	5°	" left;	6	"	"	"	5	"	1.
"	10°	" right;	6	"	"	"	2	"	4.
"	10°	" left;	5	"	"	"	4	"	1.
"	15°	" right;	7	"	"	"	0	"	7.
"	15°	" left;	6	"	"	"	6	"	0.
"	20°	" right;	6	"	"	"	0	"	6.
"	20°	" left;	5	"	"	"	5	"	0.

It appears from these observations that while the initial locomotor response might be toward the light in a small percentage of cases, such responses occurred only when the rays of light made an angle of less than 15° on right or left with the body axis. This is not surprising when one remembers the large angular diameter of the source of light in this experiment. Beyond 15° the response was consistently away from the light. Further, in the few cases when the response was at first toward the light, the animal continued to turn toward the same side until it ultimately moved away from the light. These exceptional cases, then, only emphasized the negative phototropism of *Porcellio*.

SUMMARY

1. Reasons are given for considering every orienting reaction phototropic whose direction is predictable in that it bears a definite relation to the source of light. *Euglena viridis*, species of blow fly larvae and earthworms, and *Porcellio scaber* exhibit reactions of this type, which is not satisfactorily interpreted by the method of trial.

2. *Porcellio* is easily guided in any desired direction by changing the direction of light falling on it from behind.

3. The first locomotor movement made by *Porcellio*, when exposed suddenly to light striking it at an angle of 90° with the major axis, was *away from* the light.

4. The same pronounced negative reaction followed sudden exposure to light from the front at angles between 90° and 15°.

5. When exposed suddenly to light coming from the front at angles less than 15°, *Porcellio* moved with less consistency away from the light; but the reactions were, on the whole, markedly negative. This lack of consistency was referred partly to the relatively large angular diameter of the source of light, partly to demonstrable inequalities in the sensitiveness of the two eyes of certain individuals to light.