THE REACTIONS OF THE FLAGELLATE *PERANEMA*

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One figure

Peranema is a colorless, cigar shaped flagellate scarcely 0.05 mm. long and but little more than 0 01 mm. in diameter. A prominent contractile vacuole is found near the anterior end from which projects a heavy flagellum nearly as long as the body, Fig. 1. It is a hardy, sluggish creature, usually found in abundance in cultures rich in decaying organic matter. I have kept specimens in excellent condition for three weeks on a slide under a cover glass sealed air-tight with vaseline These flagellates ordinarily move in contact with solid objects or on the surface film, but sometimes they swim through the water very much like Euglena. I shall refer to the former method of locomotion as crawling. The rate of motion by either method is relatively slow, the crawling rate being only 1 3–2.6 mm. per minute and the swimming rate but very little more Owing to this very moderate rate of locomotion it is a simple matter to follow under high magnification every movement the animal makes.

In crawling, Peranema is frequently seen to continue for considerable distances in a fairly straight line It does not rotate as it does in swimming but proceeds with a given surface continuously in contact with the substratum to which it adheres with considerable tenacity, probably by means of secreted mucus. The flagellum extends straight forward and is rigid and motionless except for about one-sixth of the whole at the tip, which is bent at right angle so as to form a sort of hook, Fig. 1. This bent part of the flagellum vibrates rapidly, striking backward and forward in such a way that the free end describes a narrow ellipse. Thus the creature is literally drawn slowly and steadily along. This is the method of locomotion that is ordinarily seen but if the animals are strongly stimulated, as by the addition of a little iodin, marked wave-like contractions are seen to pass over the body from the posterior to the anterior end. That this wave-like contraction is at least at times functional in locomotion is shown by the fact that specimens with the flagellum removed, an operation which was repeatedly performed with a fine glass rod, are still capable of progressing, although much more slowly than before the operation. The activity of the flagellum is, however, alone sufficient to produce locomotion, for specimens are frequently seen moving quite actively and accurately in the direction of the flagellum when the body is bent at right angles to it, so that contractions in the body could not possibly function and still admit of movement in the direction of the flagellum. When iodin is added it not only induces marked contractions in the body but also much more vigorous action of the flagellum. Not only do the rate and the extent of vibration increase but a larger portion becomes active. Under such conditions the portion of the flagellum which vibrates increases from about one-sixth to more than one-half, the angle in it being much nearer the body. The combined effect of the increased activity in the flagellum and the contractions in the body causes the rate of locomotion to become almost double that ordinarily observed in crawling specimens.

If the iodin solution is strong enough the crawling specimens leave the substratum and swim freely through the water. I have never seen this method of locomotion under ordinary conditions; it must be very rare in nature. In swimming, the entire flagellum is active, having a motion somewhat like that of a snake except that it is not restricted to one plane but rotates continuously on its long axis so that it appears much like a cork-screw in motion. The body also rotates continuously when the animal swims, usually counter clockwise, like most of the free-swimming unicellular organisms, but the rotation of the flagellum is independent of this; it may often be seen when the body is stationary. As a matter of fact it is the rotation of the flagellum that causes the rotation of the body.

Reactions to Contact Stimuli.—The study of the reactions of Peranema was confined almost entirely to crawling specimens. As these animals move about they come in contact with objects, the tip of the flagellum usually striking the object first. Often when this happens there is no response. This is especially true when the object is small or when it consists of a mass of loosely compact granules or fibers, or when the flagellum strikes one side of the object. Under such conditions these creatures usually slide by or through the obstruction, their course being altered only in so far as the mechanical resistance requires. Ordinarily,

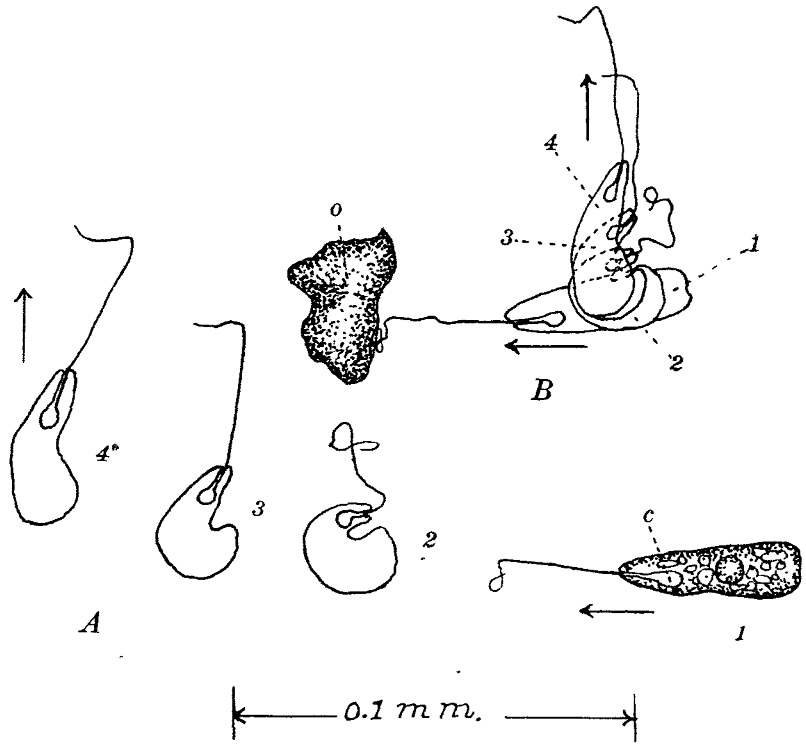

FIGURE 1. Camera drawings of specimens of Peranema representing the reaction to contact or chemical stimulation. A, Outline of four individuals selected from many suddenly killed in Worcester's fluid in different stages of the response. B, Outline of the same individuals superimposed to represent the relative positions of a specimen in different stages of the response; 0, solid object; 1, specimen crawling in the direction of the arrow, only the bent tip of the flagellum is active; c, contractile vacuole; 2, position taken immediately after stimulation; the flagellum is inactive, the turning of the anterior end being due to contraction on one side of the body; 3 and 4, later positions assumed, the body gradually straightens and the tip of the flagellum again becomes active. Note that the response results in a change in the direction of motion of approximately ninety degrees.

however, there is a definite response when the flagellum touches an object. The organism stops, the body bends sharply always toward the larger lip, throwing the anterior end with the flagellum, usually more or less curved and inactive, to one side through an angle of nearly 180 degrees, Fig. 1. Then the body gradually straightens again, the anterior end turning back somewhat toward its former position, the flagellum straightens, the tip becomes active and the creature proceeds on its new course, having changed its direction of locomotion approximately 90 degrees. In this way objects are avoided which frequently have been only slightly touched by the very tip of the flagellum. This bending reaction is not dependent upon the activity of the flagellum as maintained by Verworn (Allgemeine Physiologie, 1909, p. 451). It is entirely due to contraction of one side of the body. Moreover, I was unable to obtain any evidence indicating that the direction of motion in crawling specimens is changed in any other way. Neither the beating of the flagellum nor any thing connected with the wave-like contractions of the body functions in changing the course of this animal.

The fact that Peranema responds when only the tip of the flagellum is touched indicates that this structure is sensitive to contact. It does not, however, prove that it is, for it may be that the response is due to change in pressure on the anterior end of the body owing to the contact of the flagellum or to mechanical waves transmitted through it to the body. However this may be, the animal responds precisely the same when the body is touched with a glass rod, as was repeatedly done. Moreover, this response bears no relation to the location of the stimulus on the body; it is precisely the same no matter whether the posterior or the anterior end is touched, or any other point on the surface. There is no indication whatever of a differential response to localised stimulation. Peranema differs in this respect from most of the other unicellular forms that have been tested. When Lacrymaria or Stentor e. g., is stimulated on the posterior end it ordinarily does not respond the same as when it is stimulated on the anterior end. Thus the character of the response in these creatures depends in some measure upon the location of the stimulus, while in Peranema this is not true. But in this animal there may be local response to local stimulation. One often sees contraction of the tissue in the immediate region to which the stimulus is applied, and these contractions may spread over the body in wave-like form. Whether or not the direction and the character of the wave is dependent upon the location of the stimulus I am unable to say. At any rate the direction of motion is not changed by reactions of this nature, although the rate may be.

Thus we see that the reactions of Peranema which regulate the direction of motion are in the nature of trial movements. There is no indication of orientation and procedure directly toward or from objects or solutions, nothing in the nature of a tropism as defined by Loeb When the animal is stimulated, no matter how or where, it either moves more rapidly or stops, bends toward a given side and takes another course. If this relieves the stimulus it continues, if not it repeats the reaction until the stimulus does not again occur.

In this connection it is interesting to consider the reactions of specimens entangled in debris. The first response seen after a specimen gets into a fibrous mass which affords some obstruction is an increase in the activity of the flagellum. The tip does not only strike back and forth more vigorously but a larger portion becomes active. If this does not result in freeing the creature it responds by bending the body sharply, i.e., with the bending reaction, and starts in a different direction, after which, if still held fast, it may again lash the flagellum furiously and then again change its direction by bending the body. Thus it continues alternately trying the two different reactions until it becomes free. This indicates that we have here an adaptive change in the character of the response without any change in the environment such as Jennings discovered in Stentor; for it is hardly probable that these different responses can be accounted for by changes in the pressure of the tangle owing to variation in the activity of the flagellum or to the bending of the body.

Reactions to Chemicals.—My object in studying the responses of Peranema to chemicals was to ascertain if possible whether or not the flagellum is sensitive. In these observations colored substances were introduced under the cover-glass either in solution by means of a fine capillary pipet or as crystals by means of a fine glass rod. The reactions of the animals were then studied as they swam toward the colored substance which gradually spread out in the process of diffusion.

The responses to chemical stimuli consisted in all cases observed of sharp bending of the body and an abrupt change in the direction of motion just as in the reaction to mechanical stimuli.

However, in the case of iodin-green crystals introduced dry the animals ordinarily reacted as soon as the tip touched the colored solution; while in the case of methyl-green introduced in the same way they usually did not react until the body was entirely or nearly surrounded by the colored diffusion from the crystals; and in the case of methyl-blue introduced dry or chromic acid or iodin in solution they responded before the tip of the flagellum reached the colored diffusion. In these reactions there was no indication whatever of orientation in the direction of the lines of diffusion as demanded by Loeb's tropism theory. The animals in all cases crawled about in all directions and came in contact with the solution at all angles. Our evidence, however, leaves us in the dark as to the sensitiveness of the flagellum, for the creatures responded in one case before the tip of the flagellum reached the colored portion of the solution, showing clearly that chemical diffusion so weak that the color is invisible may be still strong enough to stimulate the animals. Thus the possibility of direct action on the body itself of chemical solutions too dilute to be visible was not excluded in any case.

Reactions to Light.—Specimens of Peranema under the microscope were at different times suddenly exposed to light varying in intensity from zero to direct sunlight and then suddenly shaded again. In the case of the lower intensities there was no indication of any response, but in direct sunlight it appeared at times as though the flash of illumination induced the typical bending reaction, especially in specimens which had been kept in light of low intensity for some days preceding the experiments. But at best these responses were so indefinite that if there really are any to light they can be of very little significance under natural environmental conditions. There is no evidence whatever of orientation in horizontal rays of light such as is found in Euglena and other similar organisms.

The several different methods of response observed in Peranema may be described somewhat as follows: (1) Increase in rate of locomotion; (2) Change from crawling to swimming and *vice versa;* (3) The becoming active of a greater portion of the flagellum than ordinarily takes part in the activity; (4) Augmentation in the wave-like bodily contractions; (5) Local response to local stimulation; (6) Bending of the body toward the larger lip.

SUMMARY

1. Peranema usually moves in contact with the substratum by means of a combination of wave-like contractions of the body and the flagellum, but it can move by the action of either alone The action of the flagellum is, however, ordinarily much more effective in locomotion than the wave-like contractions.

2. When very strongly stimulated, as by the addition of chemicals, it swims through the water free from the substratum much like Euglena. This is rarely seen under normal environmental conditions.

3. When crawling the flagellum projects straight forward; only the tip is active, and the organism usually moves on a straight course without rotation on the long axis. When swimming the entire flagellum beats in a rotary wave-like fashion, and the body rotates on its long axis and takes a spiral course.

4. Peranema does not orient. It responds to light very indefinitely if at all.

5. If the flagellum comes in contact with an object (tactile stimulation) the animal bends always toward the larger lip, then proceeds on a new course more or less nearly at right angles with the old. This same response can be induced by contact stimulation of any part of the body or by chemical stimulation.

6. There is sometimes local contraction at the point of stimulation but this does not appreciably influence the direction of motion.

7. If the body becomes lodged or entangled in debris while the animal is crawling, the tip of the flagellum gradually beats more and more vigorously and a larger part becomes active. If this does not free the animal it bends toward the larger lip so as to extend the flagellum in a different direction This then beats again as before, after which the body may bend again. Thus the bending of the body and the activity alternate until the animal becomes free or fatigued. This behavior seems to indicate that we have here different methods of response to the same stimulus.