STUDIES ON REACTIONS TO STIMULI IN UNICELLULAR ORGANISMS. X. THE MOVEMENTS AND REACTIONS OF PIECES OF CILIATE INFUSORIA.[1]

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The present paper records an attempt to investigate by operative procedure the division of labor among the organs of locomotion of the ciliate body; to determine the part played by cilia of different position or structure in the usual movements and reactions. In many of the Ciliata the body is much differentiated, often bearing a number of different sorts of simple or compound cilia, variously distinguished as membranellæ, cirri, setæ, cilia proper, and the like. In such organisms as *Stylonychia* (Fig. 1) and *Stentor* these different structures have a characteristic distribution, and apparently differ markedly in function. Even in less differentiated infusoria a distinction between oral or peristomal cilia and body cilia can usually be made.

Observation of the behavior of these animals indicates that there is a division of labor among these cilia in the production of the usual movements. The organisms as they swim through the water follow a spiral course, usually swerving continually toward one side, but compensating the deviation thus caused by rotating on the long axis. The swerving is as a rule (though not invariably) toward the side away from the peristome or the oral cilia. The stroke of the oral cilia is of such a character as to tend to turn the body toward the side opposite to that on which they are situated, so that the swerving appears to be due to these cilia,—aided, as a rule, by the form of the body.

In reacting to most stimuli, these organisms turn toward a structurally defined side (see Jennings, 1900), and, as a rule, this is again the aboral side, or that opposite the oral or peristomal cilia. Observation indicates that this is due to the stroke of the oral cilia, or in some cases to a still smaller and more localized group of cilia. This has been set forth by a number of authors,—

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notably by Pearl (1900), in the case of *Colpidium*, and by Pütter (1900, p. 273), in *Stylonychia*. In *Colpidium*, according to the observations of Pearl, it is a group of cilia at the anterior end of the body which, invariably striking toward the oral side when the animal is stimulated by the electric current, cause the body to turn toward the aboral side. In *Stylonychia* it is the entire group of peristomal cilia that, striking toward the oral side, cause the body to turn toward the aboral side.[1] We can testify from our own observations that these relations seem clear. One naturally concludes, therefore, that the sidewise motion is determined by these peristomal or anterior cilia, and that if they were removed the motion would no longer occur. Massart (1901, p. 27), on the basis of Pearl's work, accepts the idea that the sidewise movement is caused by different cilia from the backward or forward motion,—aiding thus to distinguish between what Massart calls *phobism* (the backward movement in reaction) and *clinism* (the lateral movement).

The work here set forth was undertaken for the purpose of getting further light on this and related matters. If the anterior or oral cilia are removed by operation, will the organism no longer turn toward the aboral side when stimulated? And is the character of the spiral swimming modified by removal of such cilia? In general, does the removal of specific groups of cilia (with the accompanying alteration of the body form) have specific effects on the movements of the animal?

The behavior of pieces of infusoria has been studied by Verworn (1889) and Balbiani (1888).[2] The results of these investigators are of the greatest interest, but do not touch specifically the questions raised above. They found that pieces of ciliates move in general in the same manner as do the entire organisms. The reaction to stimuli by turning toward a certain structurally defined side, and the swerving toward a structurally defined side in the spiral course, in the uninjured animal, had not at that time been observed, so that these matters were, of course, not observed for the pieces. The questions proposed in this paper were therefore not touched by the experiments of Verworn and Balbiani.

[1] These are aided in the turning, according to Pütter, by the "running cilia."

[2] Balbiani's paper we have been unable to consult, so that we must depend upon the account of it given by Verworn.

In giving an account of the results of our experimentation, matters which were described by Verworn (1889) will not be dwelt upon, but the account will be confined to the points bearing on the questions raised above.

The operation of cutting the animals was done with a small knife, under the Braus-Drüner stereoscopic binocular, which has great advantages for such work. It was found best to cut the animals when resting against a clean glass surface. Most of the operations can be performed by the aid of some patience without great difficulty. In all cases the results set forth are drawn from experimentation and observation on a considerable number of specimens.

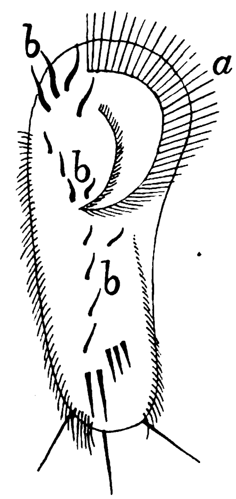

FIG. 1. *Stylonychia*, ventral surface, showing the distribution of locomotor organs (after Pütter, 1900).

1. *Stylonychia*.—Pütter (1900) gives a full account of the normal movements of this animal when uninjured, with a careful analysis of the action of the different cilia in producing the movements. For our purposes it is important to note the following different movements. (1) The animal runs forward on surfaces, chiefly or entirely by the aid of the "running cilia" *b*, Fig. 1. (2) When stimulated it jerks back a little, then turns to the right or aboral side. This turning appears to be due to the lateral stroke of the large peristomal cilia *a*. (3) The animal may also swim freely through the water; in doing so it swerves continually towards its right side, and revolves on its long axis from right over to left — the resulting path being a spiral. The swerving toward the right appears to be due to the lateral stroke of the peristomal cilia, and the revolution on the long axis might well be due to the same factor.

When *Stylonychia* was cut in two transversely just behind the mouth, so that the entire peristome remains with the anterior half, the pieces move as follows:

1. Anterior half, possessing peristome (Fig. 2, *a*).—After the first shock effects, the movement throughout is nearly like that

of the uninjured animal, but somewhat more rapid than usual. The piece runs forward on the bottom, turning to the right when stimulated. It differs from the entire animal in that it much more rarely jerks backward when stimulated, though it does this when the stimulus is powerful. When swimming through the water, it revolves to the right and swerves to the left, as in the entire animal. Since the anterior half possesses the peristome, the similarity of its movements to those of the uninjured animal was to be anticipated.

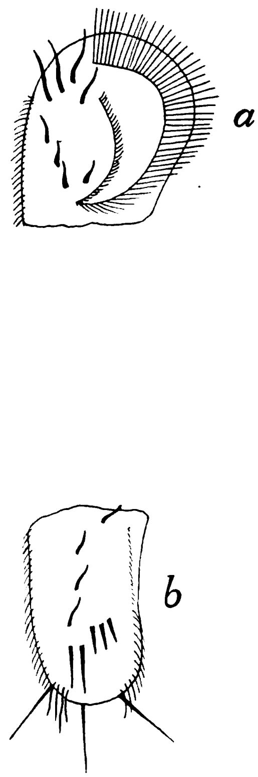

FIG. 2. Anterior (*a*) and posterior (*b*) halves of *Stylonychia*.

2. Posterior half, without peristome (Fig. 2, *b*).—Immediately after the operation the piece jerks rapidly backward, turning at the same time toward the right side. After a time it becomes quieter, and now it reacts essentially like the entire specimen, though it is somewhat less active. If stimulated with the glass hair at the posterior end its runs forward; stimulated at the anterior (cut) surface, it jerks backward and turns to the right. Chemical stimuli cause the same reactions. A little m/20 NaCl, or a weak solution of methylene blue was introduced with a capillary tube close to the piece; on coming in contact with the chemical the piece backs and turns to the right, just as is done by the entire animal.

Thus the presence of the peristomal cilia is not the determining factor for the invariable turning to the right as a response to stimuli.

3. Posterior one fifth. — The movements are somewhat less well coördinated than in the larger pieces. But after the shock effects have ceased, the piece creeps forward, *turning to the right*. It swims slowly through the water, swerving to the right and revolving to the left, as in the uninjured specimen.

4. Anterior one third. — This is very rapid in its movements, and circles almost continuously to the right. In the free water it revolves in the usual way. When stimulated, it turns to the right, but *does not jerk back*.

5. Middle one half. — This was obtained by cutting off the anterior and posterior fourths of the body. Its movements and reactions are essentially similar to those of the uninjured specimen.

6. Right and left halves. — These were obtained by splitting *Stylonychia* lengthwise. They move and react (after the shock effects have ceased) in nearly the normal manner. Thus, when stimulated mechanically or chemically, they jerk backward, and the right half turns toward its right (uninjured) side, while the left half likewise turns toward its right (injured) side.

A specimen was cut lengthwise in such a way that the left piece was a strip comprising about one third the body. This moved somewhat irregularly, but reacted in the same manner as the left one half just described — though it evidently bore no part of the peristome.

7. A small, left posterior corner, comprising less than one fourth the animal, reacted, after the effects of the shock had ceased, in the usual way — by backing and turning toward the right.

Thus, on the whole, pieces of *Stylonychia* from any part of the body, if amounting in size to as much as one fourth to one half of the animal, move and react essentially like the entire specimen. In very small or very irregular pieces the movements become irregular, as might be expected.

Similar results were obtained with *Oxytricha fallax*, and with a number of unidentified *Hypotricha*, though the smaller size makes most other species less favorable for such experimentation than is *Stylonychia*.

II. *Stentor cæruleus.* — In *Stentor* the oral (or adoral) cilia or membranellæ form nearly a circle at the broad anterior end of the body. *Stentor*, when free swimming, follows a spiral path, revolving from right over to left. It reacts to chemical and mechanical stimuli by backing a little, then turning toward the right aboral side. It is evident to observation that the adoral cilia play a large part in the turning; from their large size and their position at one end of the body it would be natural to conclude that the turning is due to them alone.

1. The entire anterior disk, with the adoral cilia and the mouth, was removed by a transverse cut near the anterior end (Fig. 3). The posterior portion (*b*, Fig. 3), having only the body cilia, swam through the water as usual, in a spiral, revolving from right over to left. The aboral side in *Stentor cæruleus* is usually curved in a very different manner from the oral side, so that it is possible to distinguish the two sides even when the disk is removed. The specimen deprived of the disk and anterior cilia reacted to mechanical and chemical stimuli by backing and turning toward the aboral side, just as does the uninjured specimen.

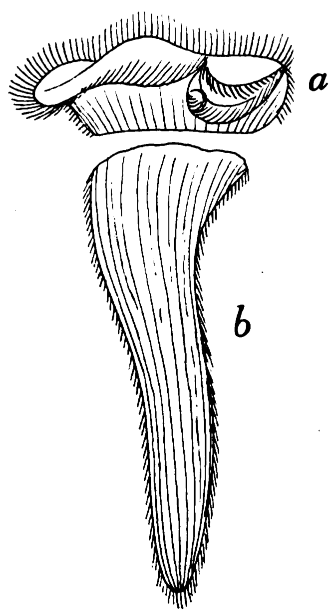

FIG. 3. *Stentor*, cut transversely just behind the disk.

After a time the specimen attached itself by the foot, and extended in the usual manner. Currents, due to the ciliary action, then passed backward toward the foot, or at times they were reversed, passing in the opposite direction. There was, however, no evident whirlpool formed, with a definite center, as in the uninjured specimen. The animal from which the disk had been removed, after becoming attached, reacted to mechanical stimuli by turning into a new position, and later by contracting, just as happens in the uninjured specimen. (On the behavior of *Stentor*, see Jennings, 1902.)

2. The disk portion (Fig. 3, *a*), bearing the adoral cilia and the mouth, also moved and reacted in the usual manner—revolving to the left as it swam, and responding to stimuli by backing and turning toward the aboral side.

3. Posterior one fourth—comprising about one half the slender "stalk" of *Stentor*.—This swims about, revolving to the

left. Whether on stimulation it turns toward a definite side could not be determined. After a time the small piece fixed itself by the foot and extended. The currents caused by the cilia were most of the time directed away from the attached end, being thus the reverse of the normal currents. At times, however, the current passed toward the foot.

When stimulated mechanically, the piece responded, like the entire *Stentor*, by bending into a new positiom, and later by contracting.

III. *Spirostomum ambiguum.* — Essentially the same results were obtained with this large infusorian as with *Stylonychia* and *Stentor.* Both the anterior half, bearing the adoral cilia, and the posterior half, without adoral cilia, move and react in much the same way as does the uninjured individual. They revolve to the left when swimming freely through the water, and turn toward the aboral side when stimulated. The anterior half moves more rapidly than does the posterior half, and when stimulated turns through a much greater angle than does the latter. The posterior half, if not strongly stimulated, frequently remains nearly quiet, or oscillates back and forth, as described in the third of these studies (Jennings, 1899). If stimulated mechanically or chemically, however, it backs and turns toward the aboral side.

A posterior one third of the body reacts in the same manner as the posterior one half.

A minute piece from the posterior end, less than half the length of the contractile vacuole, moved in the normal fashion, revolving to the left, and moving with the anterior (cut) end in front. The reactions to stimuli in such a small piece are very difficult to determine.

IV. *Paramecium caudatum.* — *Paramecium* is, of course, much less favorable for work of this character than are the infusoria of which an account is given above. This is due in part to the minute size and rapid movements of *Paramecium;* in part to the strong tendency for the cut pieces to disintegrate at once. But, with much patience, satisfactory anterior and posterior halves can be obtained.

1. Anterior half, bearing the oral groove and mouth (Fig. 4, *a*). This moves and reacts almost exactly as does the entire animal,—

revolving to the left, and turning toward the aboral side when stimulated mechanically or chemically.

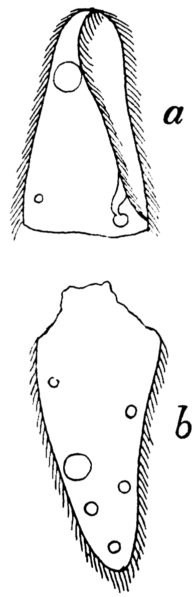

FIG. 4. Paramecium cut transversely. *a*, anterior half, with mouth and oral cilia. *b*, posterior half, without mouth or oral cilia.

2. Posterior half, without oral groove or mouth (Fig. 4, *b*). Much pains was taken to remove the entire oral groove and mouth, so that the posterior piece was usually a little less than one half the body. It was possible to distinguish the aboral side by the presence there of the contractile vacuole. The posterior half swims in a spiral, revolving, like the uninjured animal, to the left, and keeping the aboral side to the outside of the spiral. Its movements are slower than those of the anterior half, and it is much less sensitive, not reacting so readily to stimuli. The reaction to mechanical and chemical stimuli is by jerking backward and turning toward the aboral side, as in the uninjured individual. Thus the presence of the oral groove and oral cilia is not necessary in order that the usual movements and reactions may occur.

3. Middle third of *Paramecium* (anterior and posterior ends removed). — This behaves essentially like the anterior and posterior halves, or the entire animal.

SUMMARY AND CONCLUSIONS.

In all the Ciliata studied, including several of the Hypotricha (*Stylonychia*, *Oxytricha*, etc.), two of the Heterotricha (*Stentor* and *Spirostomum*), and one of the Holotricha (*Paramecium*), the movements and reactions of pieces of the organisms, if these are not too minute or too irregular in form, are essentially similar to those of the entire animal. The pieces swim in a spiral, swerving continually toward a certain side, just as do the entire organisms. They react to chemical and mechanical stimuli by backing and turning toward the same structurally defined side, as do the entire animals. This is true of pieces forming one fourth to one half the entire animal, whether taken from the anterior end, the posterior end, the right or left side, or the middle of the body. It is true, whether the piece does or does not bear any of the oral or other differentiated cilia.

These results establish the following facts:

1. The turning toward a structurally defined side after stimulation is not produced alone by the oral or peristomal or anterior cilia, or by any particular set of cilia, since it takes place in pieces of the body containing no specially differentiated cilia.

2. The swerving toward a certain side in the spiral swimming is not due alone to any special set of cilia, since it occurs in pieces from any part of the body.

3. The swerving toward a certain side is likewise not due to the geometrical form of the body (as to a groove on one side, such as we find in *Paramecium*), for it continues when the form of the piece is essentially altered (as by the removal of the oral groove in *Paramecium*).

4. The revolution on the long axis in a certain direction, while swimming, is not due to any special set of cilia, nor to any peculiarities of form of the body, since it occurs in pieces from all parts of the body.

5. From the foregoing paragraphs, 1–4, it must be concluded that the revolution on the long axis, the swerving toward a defined side in the spiral course, and the turning toward a structurally defined side when stimulated, are due to the method in which the cilia strike. This peculiar (one-sided) stroke is not limited to any particular set of cilia, but is shared by all the body cilia.

Division of labor is thus not marked, so far as these points are concerned, among the locomotor organs of these animals. As any portion of a crystal is organized like the entire crystal, so in the Ciliata any piece of the body, apparently, is organized so as to move and to react to stimuli in the same manner as does the entire animal.

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