# STUDIES ON REACTIONS TO STIMULI IN UNICELLULAR ORGANISMS. V.—ON THE MOVEMENTS AND MOTOR REFLEXES OF THE FLAGELLATA AND CILIATA.[1]

By HERBERT S. JENNINGS.

CONTENTS.



## I. Introduction.

IN the second of these Studies[2] I have described the mechanism of the motor reactions to external stimuli in the ciliate infusorian Paramecium caudatum. As there set forth, this animal has a fixed form of motor reaction to stimuli of all classes, which, expressed in general terms, is as follows: When unstimulated the animal swims with a certain structurally defined end (the "anterior") in front.

[1] Scientific Results of a Biological Survey of the Great Lakes, directed by Jacob Reighard, under the auspices of the U. S. Fish Commission, No. V. (Published by permission of the Hon. George M. Bowers, Commissioner of Fisheries.)

[2] Jennings: Studies, etc., II. On the Mechanism of the Motor Reactions of Paramecium, this journal, 1899, ii, pp. 311–341.

When stimulated motion takes place with another (the "posterior") structurally defined end in front, followed by turning toward one side which is structurally defined and invariable (the aboral in Paramecium), — finally succeeded by motion with the same end in front as at first. As thus expressed, the direction of motion after a stimulus has no relation to the nature or the position of the stimulating agent.

This method of reaction has a fundamental bearing on the interpretation of the life phenomena of these creatures, and the question is an important one as to how widespread such a style of reaction is among unicellular organisms. In the third of these Studies,[1] an account is given of the reaction methods of the ciliate infusoria Spirostomum ambiguum and Stentor polymorphus, in which it is shown that these animals react in essentially the same manner as Paramecium. Owing to the larger size of these animals, it was possible to localize the action of stimuli very precisely, so that, especially with Spirostomum, even more sharply defined results were obtained than with Paramecium. It was found (1) that Spirostomum reacts to both chemical and mechanical stimuli, *whether applied to the posterior end, the anterior end*, or the side, by swimming *backward* (followed by turning); (2) that the turning is always toward the *aboral* side, whether the stimulus occurs at the anterior end, the posterior end, *the oral side, or the aboral side.* All relation of the direction of motion to the localization of the stimulus seems thus excluded.

I have since made a study of the reactions of a considerable number of other Protozoa, representing various groups of the Flagellata and Ciliata, bringing out thus the more widely distributed reaction methods among these animals, as well as discovering for certain Protozoa modifications in important points of the general reaction method described in the two papers above referred to. The results of this study are given in the present paper.

It will be well to define sharply the main questions to which, in the study of a given Protozoön, answers are desired. These are as follows: —

1. Has the given Protozoön a fixed formula for motor reactions, similar to that of Paramecium?

2. After stimulation, does the organism always turn toward a certain structurally defined *side*, without regard to the nature or position of the stimulus?

3. After stimulation does the organism always move, before turn-

[1] JENNINGS: American naturalist, 1899, xxxiii, pp. 373-389.

ing, toward a certain structurally defined *end* (the "posterior") without regard to the nature or position of the stimulus?

These questions will serve as directives for the observations and experiments, which will not however be in any way limited by them. I give first a detailed account of the reaction methods of the different Protozoa studied, arranging them according to the groups to which the animals belong. This is followed by an analysis and summary of the observations, showing the variations in the motor reactions among the different Protozoa, and giving as far as possible the answers to the questions proposed above, as well as other general conclusions to be deduced from the facts presented.

## II. Flagellata.

The majority of the members of this group are very small and without striking differentiations of structure. It is therefore in most cases very difficult to determine whether the direction of motion after stimulation does or does not have any fixed relation to structural features of the animal's body. A study was made of the reactions of a few species, the results of which are presented herewith.

**Chilomonas paramecium Ehr.** — *Description.* — Chilomonas paramecium (Fig. 1) is a minute Flagellate which can always be procured in practically unlimited numbers by allowing aquatic vegetation to decay in water. In cultures of this sort Chilomonas is one of the first forms to appear: it is often present in such multitudes as to give the water a milky appearance. The great abundance in which it can be procured at any time make it a most favorable species for experimental studies on the Flagellata. The animal is of an irregularly oblong form, compressed sideways. One end (the "anterior") is usually broader than the other, and bears a shallow notch lying between two "lips." One of these lips (the "dorsal") is much larger and more prominent than the other, so that the anterior end presents the appearance of being obliquely truncate with a notch in the truncate border. From the notch, just beneath the larger lip, arise the two flagella, each of about the same length as the animal's body. The body is sometimes slightly curved, the concavity of the curve being on the so-called dorsal side. All these relations are shown in Fig. 1.

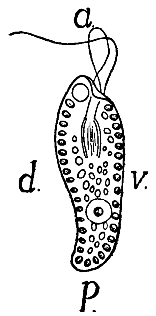


FIGURE 1. Chilomonas paramecium Ehr., right side, after Bütschli. *a*, anterior end; *p*, posterior end; *d*, dorsal side; *v*, ventral side.

*Movements.* — If a large number of specimens of Chilomonas are mounted and observed under the microscope, they will be seen at first to dart swiftly through the water, — so swiftly that the eye can with difficulty follow them. Some individuals soon come suddenly to rest: others follow, and after a time nearly all the animals are resting against the substratum, beginning movement again only when stimulated. When at rest, Chilomonas is attached by one of its flagella, which is thrown in a coil on the surface of the substratum, while the other may or may not retain a vibratory motion.

More exact observation of the movement brings out the following points. Chilomonas as it swims forward revolves on its long axis in such a way as to describe a path which is a spiral of some width. By introducing the animals into a gelatine solution, so as to compel them to move very slowly, it can be observed that the position of the body bears a constant relation to the axis of the spiral, the lower or smaller lip being always directed toward the outside of the spiral.

*Reactions to stimuli.* — (1) If to the quiet Chilomonas the faintest possible stimulus be given, as by gently agitating the water, or in any way loosing its hold on the glass, it merely resumes its usual motion, already described. In a certain sense this usual forward motion may then be considered (taking the resting individual as a starting point) as a reaction to the weakest possible stimulus. The motion seems then to be maintained without further stimulus, until the stimulus of contact with a solid (thigmotaxis) again induces the resting condition. The same facts, in accordance with which the usual motion of the animals may be conceived as (at first) a reaction to a weak stimulus, exist in the case of all the organisms studied, and will not be especially mentioned for each. It is usually very difficult to give the resting individual so weak a stimulus as to induce at first only the usual forward motion: as a rule the reaction takes the form to be described immediately.

(2) If now the swimming or resting Chilomonads be stimulated beyond this faintest degree, as by jarring the preparation strongly (mechanical stimulus), by letting the swimming animals come in contact with a diffusing chemical, or dropping them directly into a solution of some chemical (chemical stimulus), reaction takes place as follows. The animals dart swiftly *backward*, then *turn sideways toward the smaller lip*, then swim forward in the new path thus determined by the position of the smaller lip. At the moment of turning toward the smaller lip, the flagella, or at least one of them,

are turned toward the dorsal side, over the upper lip, as indicated in Fig. 2.

The point of essential importance here is of course the fact that the animals always turn when stimulated toward the smaller lip, without regard to the nature of the source of stimulus or its position. This is easily seen when the Chilomonads are examined in the thickened gelatine solution, in which all their motions are slow; it is much less easily made out in the animals swimming freely in water, though in all cases observed in which it was possible to determine under these conditions in which direction the animal turned, it was evident that this was toward the lower lip.

The method of reaction is very easily observed under the following conditions. A drop of water containing the animals is spread out in a thin layer on a slide and is left uncovered. The animals in this thin layer of water may then be watched with the high power of the microscope. As the water evaporates, the partial desiccation of the individuals near the edge of the drop acts as a stimulus; they dart backward, turn toward the smaller lip, swim forward, and repeat the operation indefinitely. At this time the layer of water has become so thin that the animals can swim in only one plane and are forced to lie upon one side; it is therefore at once apparent in which direction they turn, — in every case toward the smaller lip.

As in the case of Paramecium, the different parts of the reaction may be modified in intensity and duration by different conditions. Chilomonas usually swims backward only a short distance, but the distance thus travelled varies somewhat with the intensity of the stimulus, being greater with a powerful stimulus. As the animal swims backward it usually does not revolve at the same time on its long axis, though in the more extensive backward excursions it may do so. The amount through which the animal *turns* is very variable; with a faint stimulus there is a turn of but a few degrees toward the lower lip, while with a powerful stimulus, as when the animals are dropped directly into a strong chemical, or partially desiccated in the manner described, they may whirl about so as to describe a circle several times. When dropped into a weak solution of sodium chloride the entire reaction is repeated many times, — until finally the turning prevails over the other features, and the animals whirl about until they die.

When a Chilomonas swimming forward comes in contact with the edge of a drop of some diffusing chemical, as $\frac{1}{5}$ per cent sodium chloride, the reaction is given as above described, — the Chilomonas after reaction of course continuing to swim forward in a new direction. If this new direction, as frequently happens, again brings the animal against the edge of the drop, the reaction is repeated, and this repetition is continued until in accordance with the laws of chance, the animal's movement becomes so directed as not to carry it against the edge of the drop. These relations are identical with those described in the second of these Studies for Paramecium.

If a crystal of sodium chloride is placed against the edge of a cover-glass beneath which are large numbers of Chilomonads, as the diffusing salt passes under the cover-glass the following effects are observed. The Chilomonads affected all swim backward at once. Those whose anterior ends are directed away from the advancing salt solution, swimming backward, pass directly into the solution, and are killed. Those with anterior ends directed toward the crystal of sodium chloride, likewise swimming backward, move away from the diffusing chemical and therefore escape. Those with the body axis in intermediate directions, swimming backward, move obliquely with reference to the position of the advancing salt solution; some thus escape, while others are killed. The direction of motion bears no relation to the position of the source of stimulus, — the stimulated animals all swimming (at first) simply backward.

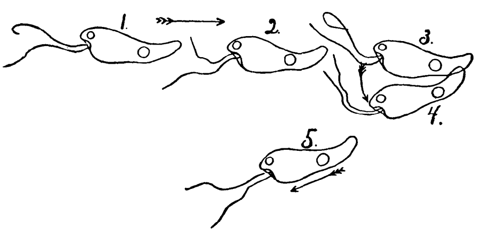


FIGURE 2. Motor reflex of Chilomonas. The arrows show the direction of movement, while the numbers show the successive positions taken.

The typical motor reflex in this animal may then be expressed as follows: Chilomonas when stimulated swims backward, turns toward its lower lip, then swims forward in the direction thus determined. The typical motor reflex of Chilomonas is shown in Fig. 2.

A comparison of the facts above given as to the movements of Chilomonas with those detailed in the second of these Studies for Paramecium reveals a complete agreement in all essential points between the motor reactions of the two, — the one a Flagellate, the other a Ciliate.

**Euglena viridis Ehr.** — *Description.* — The well-known form Euglena viridis (Fig. 3) is an elongated, somewhat fusiform creature, exceedingly flexible, and variable in shape. One end (the "posterior") is pointed; the other (the "anterior") is somewhat obliquely truncate, there being, as in Chilomonas, a larger and a smaller lip, with a notch between them. From this notch or mouth projects a single long flagellum. Just behind the larger lip and a little to the left of it lies a red eye-spot.

*Movements.* — When in undisturbed motion Euglena swims forward, revolving on its long axis and describing a slender spiral.

*Reactions to stimuli.* — When Euglena thus swimming is given a weak stimulus, as by its coming in contact with a drop of some weak chemical, or by a mechanical jar to the preparation, *it turns toward the larger lip*, then keeps on the course so laid out undisturbed. Euglena never swims backward under any circumstances, so far as observed. If the stimulus is a little stronger, the creature may stop for a moment before turning. If the stimulus is still stronger, the Euglena continues turning, so that it frequently revolves thus for a long time, toward the larger lip, without any forward motion at all. If the stimulus continues, the whirling Euglena gradually takes a spherical form, the motion ceases, and the creature proceeds to encyst itself. To any very strong stimulus the only response is the immediate assumption of a spherical form and prompt preparation for encystment. This occurs when the creatures are introduced into a chemical solution, as of NaCl, KI, etc., or when allowed to dry on the slide.

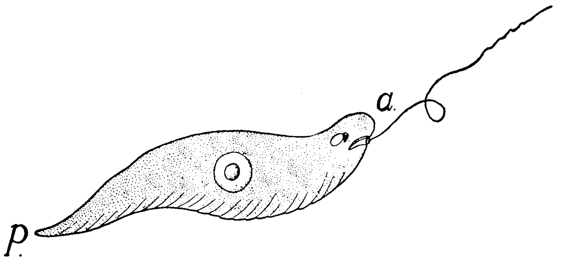


FIGURE 3. Euglena viridis Ehr., after Kent. *a*, anterior end; *p*, posterior end.

The motor reaction of Euglena consists then in simply turning toward the larger lip. Further reaction takes the form of preparation for encystment.

In this case then, as in those previously described, the direction of motion after a stimulus is determined by structural differentiations of the body, not by the position of the stimulating agent.

**Other Euglenidæ.** — Several other species of Euglena are common in fresh water; of these Euglena spirogyra and Euglena oxyuris were studied. These creatures are much more sluggish than Euglena viridis, moving only very slowly and lying quiet on the substratum for long periods; they seem much more vegetable than animal in their nature. In these creatures no definite motor reaction to a stimulus could be observed. When stimulated they either do not react at all, or simply assume the spherical form and make preparations for encystment.

In several species of Phacus and certain other green Flagellates no definite motor reaction plan could be made out; these organisms are worthy of further study in this connection.

In these Flagellata we have therefore a gradation in the complexity of the motor reaction to a stimulus. In Chilomonas we find all the features exhibited by Paramecium, — the swimming backward, turning toward one side, and again swimming forward; continued or severe stimulus causing repetitions of the reaction. In Euglena viridis the swimming backward is omitted, the creature merely turning toward one side when stimulated; continued or severe stimulus induces encystment. In Euglena spirogyra and E. oxyuris even the turning is omitted, there being little or no response to the stimulus but immediate preparation for encystment.

## III. Ciliata.

**A. Holotricha : Paramecium caudatum Ehr.** — An extended account of the motor reactions of this animal has been given in the first, second, and fourth[1] of these Studies.[2] For our present purpose the

[1] Jennings : This journal, 1899, ii, pp 355–379.

[2] The results given in section 3 of the fourth of my Studies (this Journal, 1899, ii, pp. 363–371) on the Relation of Chemotaxis to Chemical Composition in Paramecium require modification, owing to a chemical misinterpretation as to the factors which give solutions their characteristic properties. My discussion was based on the old ideas that the acid properties of solutions are due to the "acid radicals," the alkaline properties to the metal components. But modern chemistry has shown that the characteristic properties of acids are due to the hydrogen ions contained; of alkalies to the hydroxyl ions. This requires changes in my discussion and conclusions, and renders it probable that little or no significance is to be attached to the results as to the attractiveness of certain salts given in Table II, page 366 (*loc. cit.*) ; since, as was stated in that paper on page 369, they are inconstant. The only solutions classified as always attractive in my list on page 362 that are known not to contain hydrogen ions when pure are those of sodium and potassium fluoride, and of potassium permanganate. Tests of the samples of these substances used in my experiments have since shown that these, though

following statement of previous results is sufficient: Paramecium when stimulated swims backward, turns toward its own aboral side, and swims forward.

It is, perhaps, well to call attention again at this point to the fact that, taking the resting individual as the starting point, the usual straightforward motion may be considered as the simplest form of reaction to a very weak stimulus. Such a stimulus may most easily be given in the case of Paramecium by gently removing with a fine glass spicule the bit of material against which the animal is resting, or by a gentle rolling movement separating the Paramecium from this bit of material. Thereupon the animal resumes its forward course. This forward motion, however, continues long after the cessation of the external change which induced it, so that it may be proper to speak of the animal swimming forward in the normal manner as "unstimulated."

In addition to details previously given concerning the reactions of Paramecium, I wish to add here certain new results, which are of importance for interpreting the phenomena presented by the reactions of this and other unicellular organisms.

*Localized stimuli.* — (*a*) *Mechanical.* — With the new Braus-Drüner stereoscopic microscope of Zeiss, it is possible to apply localized stimuli to Paramecium, in the manner described in the third of these Studies (*loc. cit.*) for Spirostomum and Stentor. Under the Braus-Drüner microscope the Paramecia in a watch-glass are touched on various parts of the body with the tip of the finest capillary glass rod. By this means it is found that only the anterior end of the

procured as strictly chemically pure from a reliable firm, were contaminated with acid; after proper purification they were repellent throughout. All the solutions in which the Paramecia gather, therefore, contain hydrogen ions, and it is doubtless to these that the (apparently) attractive qualities are due, instead of to the anions as stated in the paper. On the other hand, my conclusion that the strong repellent power of other solutions is due to the metal components or kations rather than to the OH-ions seems justified, since of the thirty-six substances classified as having strong repellent powers, all contain such kations, while at most less than a dozen contain OH-ions. It is, however, not impossible that OH-ions are repellent also.

In my discussion and conclusions, therefore, wherever an effect was ascribed to the anions or acid radicals, it should be considered due rather to the hydrogen ions. Of the fourteen numbered paragraphs in which I have summed up my conclusions in this paper (*loc. cit.*, pp. 377–379), three — paragraphs 8, 9, and 11 — are to be modified in accordance with these facts. The other conclusions are not modified.

animal is markedly sensitive. When touched at the anterior end the Paramecium quickly gives the typical reaction previously described. But if any other part of the body is touched, the Paramecium does not react at all: it may be pushed out of its course, but does not of itself change its path in the least, in consequence of the touch.

It must be remembered, that owing to the minute size of Paramecium, it is impossible to give it a blow of any force; the creature is simply pushed aside by any object touching it, — just as a bubble of this size cannot be broken by touching it with a rod, in spite of its extreme delicacy. It is quite impossible to cut, bruise, or otherwise injure Paramecium in this way, so that the lack of reaction is doubtless due to the fact that the touch is too light to be perceived, except when it occurs at the sensitive anterior end.

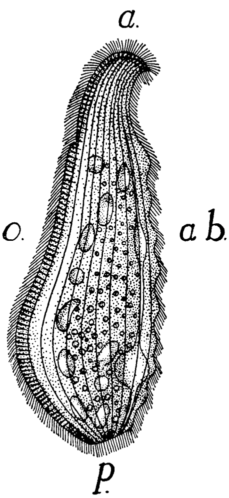

FIGURE 4. Loxophyllum meleagris O. F. M., after Bütschli. *a*, anterior end; *p*, posterior end; *o*, oral side; *a b*, aboral side.

(*b*) *Localized chemical stimuli.* — For determining the effects of localized chemical stimuli, a capillary glass rod was coated with the chemical to be tested and held near the animals, at one end or one side. The chemical then diffuses, and the effect when it reaches the animal can be noted. It is convenient to use as a stimulus some colored chemical, so that its diffusion can be seen; methyl green serves well for this purpose.

Holding the glass rod thus coated with methyl green *behind* a number of Paramecia, all of which are resting with their anterior ends placed against a solid (thigmotaxis), it is found that as soon as the diffusing chemical reaches the animals, coming of course first in contact with their posterior ends, they at once *swim backward*, — therefore into the densest part of the solution, where they are killed.

If the methyl green is held in front of them, so that it first comes in contact with the anterior end, the Paramecia likewise swim backward, — therefore *away* from the densest part of the solution, so that they escape.

If a bit of the methyl green or a crystal of sodium chloride is placed in the midst of a group of Paramecia that are oriented in no particular direction, each individual begins to swim backward when the diffusing chemical reaches it. Some thus swim toward the centre of diffusion of the chemical, others away from it, others obliquely, — exactly as described for Chilomonas.

It does not follow, however, from the above experiments that when Paramecium swims backward into a chemical solution which first touches its posterior end, this reaction is due to a stimulus at the posterior end. It is possible that when the diffusing chemical approaches the Paramecium from the rear, no reaction is caused *till the solution reaches the anterior* end. It is impossible to determine by observation whether this is true or not, even with a colored substance like methyl green, as the Paramecia usually begin to react before the color can be seen to have reached them at all. The possibility remains then that in Paramecia all motor reactions may be due to a stimulus at the anterior end, — the rest of the body not being sufficiently sensitive to receive a stimulus at all.

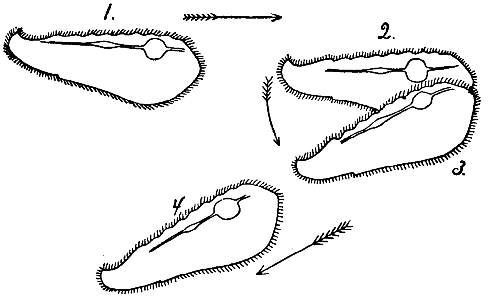


FIGURE 5. Motor reflex of Loxophyllum meleagris. The arrows give the direction of motion; the numbers show the successive positions occupied.

**Loxophyllum meleagris O. F. M.** — *Description.* — Loxophyllum meleagris (Fig. 4) is of a flattened leaf-like form, about three times as long as broad, the anterior end tapering to a point, the posterior end broad. One border (the oral or ventral) is extremely thin; the other (aboral or dorsal) thicker and bearing a series of papillæ. The anterior end usually curves toward the aboral side.

*Movements.* — This animal usually glides along the substratum, lying on one side, — after the manner of the Hypotricha. Like the Hypotricha, it may also at times leave the bottom and swim freely through the water: at such times it revolves on its long axis from left to right. The gliding motion is the usual one, however.

This gliding motion is either straight ahead or in a gentle curve toward the aboral side, — the latter being evidently due to the curvature of the anterior part of the body. The straight forward movement seems to occur in individuals in which the curving of the anterior end is not marked.

*Motor reactions.* — When Loxophyllum comes in contact with an obstacle of any sort, it turns toward the thin *oral side.* If stimulated in other ways, as by a mechanical shock, or by a chemical stimulus, it may swim backward a short distance, then turn toward the oral side. The reaction of Loxophyllum is represented in Fig. 5.

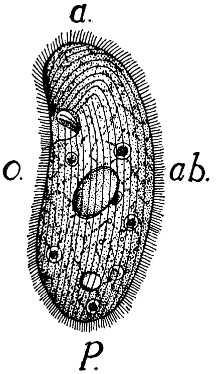


FIGURE 6. Colpidium colpoda Ehr., after Schewiakoff, from Bütschli. *a*, anterior end; *p*, posterior end; *o*, oral side; *a b*, aboral side.

It will be noticed that in this case the path of the unstimulated animal takes (frequently) the form of a curve toward the aboral side, while a stimulus causes always a sudden turn toward the opposite, or oral side.

**Colpidium colpoda Ehr.** — *Description.* — Colpidium colpoda (Fig. 6) is somewhat kidney shaped, narrower at the anterior end, two or three times as long as broad, and curved toward the side on which the mouth lies (the oral side).

*Movements.* — In Colpidium we find the same phenomenon in the direction of the normal movement as in Loxophyllum, but more pronounced. The animal swims in a strong curve forming the arc of a circle, with the oral side toward the centre of the circle. This is most evident when the animal is following a plane surface, keeping one side against the surface, as it frequently does. When swimming freely through the water it likewise swerves continually toward the oral side, at the same time revolving slowly on its long axis, so that its path takes the form of a wide spiral. The curving of the path toward the oral side seems clearly a consequence of the curved form of the body.

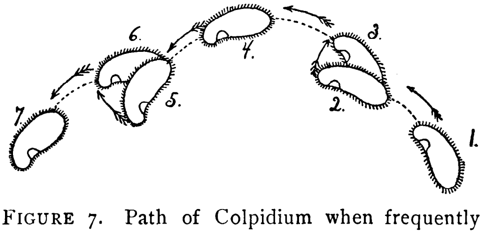


FIGURE 7. Path of Colpidium when frequently stimulated. The arrows show the direction of motion; the numbers give the successive positions taken.

*Motor reactions.* — When stimulated in any way, Colpidium turns toward its aboral side. This may be observed in the usual course of the animal as it glides along a surface. As above stated, its undisturbed path is a curve toward the oral side, but as it at short intervals comes in contact with an obstacle or is otherwise stimulated, it gives a short jerk toward the aboral side. Its path therefore usually takes the form shown in Fig. 7.

The reaction is made more evident by using some direct means of stimulating the animals. If a drop of some chemical, as a weak solution of NaCl, is introduced beneath the cover-glass of a preparation of Colpidia, the latter always turn toward the aboral side when they come against the edge of the drop: this is true whether the animals are gliding along a surface or swimming freely through the water. The backward swimming, so noticeable as a part of the reaction in many forms, is nearly omitted here; if the stimulus is strong there is a sudden stoppage before the turning, with at times a slight backward jerk.

If the animals are dropped directly into a solution of a chemical which acts as a stimulus, they begin at once to whirl about, turning continuously toward the aboral side.

Putting all together, the movements and reactions of Colpidium are then as follows: the unstimulated animal swims in a curve which follows the curve of the animal's body, turning therefore continually toward the oral side; at any effective stimulus the animal alters its course by turning toward the aboral side (at times jerking a little backward at the same instant).

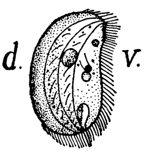


FIGURE 8. Microthorax sulcatus Eng., after Engelmann. *d*, dorsal edge; *v*, ventral edge; *a*, anterior end; *p*, posterior end.

**Microthorax sulcatus Eng.** — *Description.* — Microthorax (Fig. 8) is very small, and somewhat lens shaped, one surface flattened, the other convex and bearing three longitudinal grooves. The anterior end has a blunt point curved toward the ventral edge, the posterior end is rounded. The "dorsal" edge is strongly convex, the ventral edge nearly straight.

*Movements.* — Microthorax usually creeps or swims on the substratum, lying either on the flat surface or the convex surface; perhaps rather more commonly on the flat surface. The path is not a straight one, but forms a curve, the animal continually turning toward its more convex edge (dorsal). When swimming freely through the water Microthorax revolves continually on its long axis; at the same time it swerves toward the convex edge, so that the path becomes a spiral one.

*Motor reactions.* — When Microthorax meets an obstruction or comes in contact with water containing some effective chemical in solution, or is otherwise stimulated, it turns with a sudden jerk *toward the convex (dorsal) edge*, then goes forward again. The sudden turn may or may not be accompanied by a backward jerk. Microthorax never turns toward its straight (ventral) edge.

**Dileptus anser O. F. M.** — *Description.* — Dileptus anser (Fig. 9) is lanceolate in form, pointed at the posterior end, and extending at the anterior end into a long, somewhat trunk-like portion. On one side (the oral) lies the mouth; along the opposite side (the aboral) is a row of contractile vacuoles. The anterior trunk-like portion is slightly curved in such a way that the convexity of the curve lies on the oral side, — the tip being thus directed toward the aboral side.

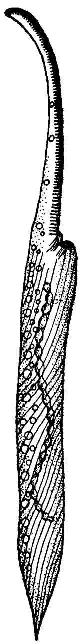

FIGURE 9. Dileptus anser O. F. M., after Wrzesniowski, from Bütschli. *a*, anterior end; *p*, posterior end; *o*, oral side; *a b*, aboral side.

*Movements.* — When swimming freely through the water the animal revolves on its long axis in such a way that it describes nearly the surface of a cone, the posterior end forming the apex, while the convex curve of the anterior process (oral side) looks always toward the outside of the cone. In other words, the anterior end swerves continually toward the oral side, the continued revolution carrying the animal forward in a spiral course.

Dileptus may also contract and extend and twist itself about in very irregular ways, though so far as observed the oral side may always be seen to look toward the outside of the irregular curves formed.

*Motor reactions.* — When Dileptus in its forward course strikes against an obstruction or comes in contact with the edge of a drop of some chemical solution, it swims backward, then turns toward the oral side, — toward the convex curve of the proboscis-like anterior region, — then swims forward over the new path so determined.

Rarely the animal becomes so twisted that the convex curve or oral side of the proboscis comes to lie nearly in a line with the aboral side of the remainder of the body. In such a case it is toward the oral side of the proboscis that the animal turns, without regard to the posterior part of the body.

*Localized stimuli.* — (*a*) *Mechanical stimuli.* — Dileptus is of such a size that the effects of localized stimuli may be tried, in the manner above described for Paramecium. Touching the anterior end with the spicule of glass, it is found to be exceedingly sensitive, the reaction described above being given at the slightest touch. If the posterior part of the body is touched, usually no reaction is given, showing that, as in Paramecium, this part of the body is very little sensitive as compared with the anterior end. By a strong stimulus, however, the animals may be made to react by touching the posterior end, but *they then swim forward*, instead of giving the typical reflex above described. While it seems to be only a small part of the anterior end that is especially sensitive, a sufficiently strong stimulus on any part of the anterior half of the body causes the animal to swim backward, while a strong stimulus applied to any point back of the middle of the body causes Dileptus to swim forward.

Thus in Dileptus the reaction to a mechanical stimulus varies with the position of the stimulus, — a stimulus in front causing backward motion, a stimulus behind causing forward motion. These results thus differ from those previously obtained for Spirostomum (see Studies, etc., III, *loc. cit.*); in Spirostomum an effective stimulus at any point of the body caused a contraction followed by swimming *backward.*

In Dileptus we have therefore a reaction with relation to the localization of the stimulus. But strangely enough this reaction with reference to the localization of the stimulus occurs, as will be shown, (1) only in relation to backward and forward motion, not in relation to movement sideways; (2) it occurs also only in the case of mechanical stimuli, there being no sign of it in the case of chemical stimuli.

(1) As to the first point, we have now to consider the results when the stimulus is applied on one side. If the animal is stimulated on the anterior half of the body, it swims backward, turns to the oral side, and swims forward. If the stimulus is a light one, the backward motion is for only a fraction of the animal's length, when turning takes place. Now, if the animal is stimulated on the oral side, it persistently turns toward that side. The stimulus may be repeated, the animal receiving a series of slight taps; it then turns continually *toward* the rod which is giving the stimuli. If on the other hand a series of stimuli is given in the same way on the aboral side, the animal continually turns *away* from the stimulating agent. There is not the slightest indication of reaction with reference to the localization of the stimulus so far as the direction of turning is concerned. Dileptus when stimulated always turns toward the oral side if it turns at all.

(2) As to the second point, we may proceed to an account of the effects of

(*b*) *Localized chemical stimuli.* — If a crystal of NaCl or a capillary glass rod coated with methyl green is held in front of a resting Dileptus, there is for a moment no response. Then as the diffusing chemical reaches the animal, it darts backward, thus escaping from the advancing flood without injury.

If the chemical is placed some distance behind the Dileptus, as the diffusing chemical reaches it the animal *darts backward*, as before, thus approaching and entering the dense solution, where it may be killed. If the chemical solution comes from one side, the same reaction is given, — the direction of motion being then neither toward nor away from that from which the solution is coming. If the animals are dropped directly into a weak chemical solution, the reaction is likewise the same.

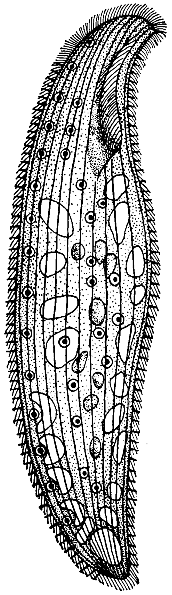


FIGURE 10. Loxodes rostrum O. F. M., after Bütschli. *a*, anterior end; *p*, posterior end; *o*, oral side; *a b*, aboral side.

There is thus no sign in the reaction to a chemical of any relation to the localization of the stimulus. It seems probable that no reaction occurs until the diffusing chemical has reached the sensitive anterior end of the animal; then the typical reflex is given without relation to the direction from which the chemical came.

**Loxodes rostrum O. F. M.**—*Description.*— Loxodes rostrum (Fig. 10) is a very large infusorian, of a flattened elongated form, the anterior end pointed and curved toward the oral side; the posterior end likewise pointed or sometimes blunt. One of the sides is convex, the other deeply furrowed. The mouth lies on one edge (the oral), not far from the anterior end. Owing to its large size and the slowness of its motion, Loxodes is an especially favorable form for observing the effects of localized stimuli.

*Movements.* — Loxodes moves very slowly, at times creeping along the substratum on one side, at times swimming freely through the water. In the former case the path is nearly or quite straight; in the latter case the animal revolves and the path is a spiral, the aboral edge lying to the outside of the spiral.

*Motor reactions.* — When Loxodes strikes with its anterior end against an obstruction, or thrusts it suddenly into a solution of some chemical, it swims slowly backward and turns to the aboral side.

*Localized stimuli.* — (*a*) *Chemical.* — If a crystal of sodium chloride is dropped near the anterior end of Loxodes, it swims backward (thus away), turns to the aboral side, and swims forward. If the salt is dropped near the posterior end, the Loxodes, when the diffusing solution reaches it, swims backward, as before. It thus approaches and enters the densest part of the solution, where it may be plasmolyzed and killed.

(*b*) *Mechanical stimuli.* — Touched on the anterior part of the body with the glass rod, Loxodes gives the complete typical reaction. Touched on the posterior part, it swims forward. Touched on the aboral side, the animal turns persistently *toward* the stimulating agent; on the oral side, it turns *away* from the stimulating agent. Thus it always turns toward the aboral side.

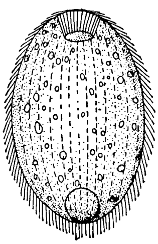

FIGURE 11. Prorodon niveus Ehr., modified from Ehrenberg.

The facts as to the reactions of Loxodes are thus precisely parallel to those of Dileptus. The animal reacts with reference to the localization of mechanical stimuli so far as backward and forward motion is concerned, but not so far as movement sideways is concerned. In the case of chemical stimuli there is no relation to the localization of the stimulus.

**Prorodon.** — In all of the Protozoa thus far discussed, there is a more or less striking asymmetry in the form of the body, and this asymmetry is directly correlated with the method of reaction, so that the direction in which the animal turns after receiving a stimulus may be expressed in terms of the animal's structure. But there are a number of infusoria in which no such asymmetry is to be observed, the animals presenting apparently a complete radial symmetry. Such is the case for example with Trachelomonas among the Flagellata: such also is nearly or quite the case with Coleps hirtus and with the various species of Prorodon (Fig. 11) among the Ciliata. The reactions of a number of such forms were studied with care, but in most cases it was impossible to tell whether the animal does or does not turn after stimulation always toward the same side, — the different sides not being distinguishable.

Finally a large species of Prorodon was secured which presented the elements necessary for a solution of the problem.

*Description.* — Prorodon (outlines of a certain species of which are shown in Fig. 11) is oval in form, with the pharyngeal tube at the anterior end, so that it is not possible to structurally distinguish different sides. It is therefore of course impossible to tell, from the structure alone, whether the animal after stimulation always turns toward a definite side or not. But here the food vacuoles come to the rescue. The animals contained numerous food vacuoles of different size and color, and these occupied definite positions within the body. The movement of the food vacuoles was so slow as not to be apparent except upon long observation. By fixing upon one of these vacuoles, occupying a definite position near one side of the animal's body, it was possible to determine in every case the direction of movement of the animal with reference to the position of this vacuole. Upon doing this, it is found that Prorodon, like the other infusoria, always turns toward the same side.

*Movements.* — The motion of the unstimulated Prorodon is straight forward, at the same time revolving on the long axis to the left.

*Motor reactions.* — When stimulated it first swims backward, — sometimes a very little, sometimes a long distance. Then it turns. One specimen whose movements were studied contained near one side a large brown food vacuole, — the other food vacuoles being much smaller and less deeply colored. In every case this animal turned after stimulation toward a point in its body surface lying about fifty degrees to the right of the position of this large brown vacuole. In other words, if a plane is passed through this vacuole and the longitudinal axis of the Prorodon, and another plane cutting the first at an angle of about fifty degrees is likewise passed through the long axis, the animal always turned after stimulation in this second plane. Moreover, it always turns in the same direction in this plane, — in a direction definable as follows: when the brown food vacuole lies in the *upper* surface the direction of turning is somewhere in the right half of the animal; if the vacuole is below, the turning is to the left. Similar results were obtained by a study of other individuals.

It thus appears that the radially symmetrical Prorodon likewise always turns toward a definite side. Though anatomically symmetrical, it is physiologically unsymmetrical.

**B. Heterotricha: Stentor polymorphus Müller.** — An account of the reactions of this animal was given in the third of these Studies (*loc. cit.*). The reaction to a stimulus is essentially as follows: the animal contracts, swims backward, turns to the right, and swims forward.

**Spirostomum ambiguum Ehr.** — The reactions of Spirostomum were likewise described in the third of these Studies. When stimulated, the animal contracts, swims backward, turns toward the aboral side, then swims forward.

In the case of localized stimuli, the Spirostoma previously described (*loc. cit.*) reacted in the same manner whatever the part of the body stimulated. Stimuli at the anterior end, at the posterior end, or on one side, caused the characteristic reflex, including the swimming backward. In view of the different results obtained for Dileptus anser, Loxodes rostrum, and the Hypotricha, as detailed in this paper, I have been at some pains to re-examine the reactions of Spirostomum. I can confirm the results previously given, from experiments on specimens from several cultures. As noted in the previous account, the posterior end is slightly less sensitive than the anterior end, and the percentage of cases giving the typical reaction was slightly less in the case of stimuli at the posterior end, as compared with the results of stimulation at the anterior end. In specimens from some cultures the difference in reaction to stimuli at the two ends was greater, but in the majority of cases a mechanical stimulus at the posterior end caused the animals to contract and swim backward, exactly as does the same stimulus at the anterior end or the side.

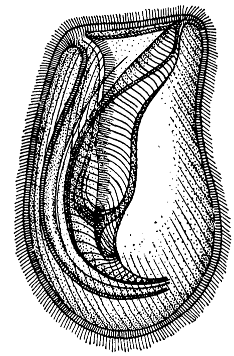

FIGURE 12. Bursaria truncatella O. F. M., after Schuberg, from Bütschli, ventral view. *a*, anterior end; *p*, posterior end; *r*, right side; *l*, left side.

To what is this difference between Spirostomum on the one hand and Dileptus, Loxodes, and the Hypotricha on the other, in regard to reactions to localized mechanical stimuli due? Spirostomum is a very long slender form, and the posterior part seems relatively much more sensitive than in the other cases; it seems probable that to this greater sensitiveness of the posterior end is due the production of the typical reflex when the posterior part is stimulated. Spirostomum differs from most of the others in that it always contracts strongly before responding with the motor reaction; possibly this contraction and the typical motor reflex with its backward swimming are closely bound up together, so that whatever causes the former must cause the latter also.

**Bursaria truncatella O. F. M.** — This very large Ciliate has proved much less favorable for experimental work than was expected, owing to its extreme delicacy. To the slightest unfavorable influences or mechanical injuries it succumbs quickly, passing first into a pathological condition, then rapidly going to pieces.

*Description.* — Bursaria (Fig. 12) is ovate, truncate anteriorly, broader and rounded posteriorly. The oral side is flattened, with a very deep groove passing far into the substance of the body; the aboral side is strongly convex.

*Movements.* — The animal usually swims forward, revolving to the left. At times it jerks back a little (probably as a response to a slight stimulus); at the same time the revolution may partly or completely stop. At times it swims forward for some time without revolving; at such times the path is in some individuals a straight line, in others a regular curve. The direction of the curve probably depends (as in Colpidium and Loxophyllum) on the form of the animal's body. In almost all cases observed the path was a gentle curve to the right (the oral side being considered as ventral). In one or two cases of individuals which had been kept for a long time and were possibly in a pathological condition, the forward path was a curve to the left.

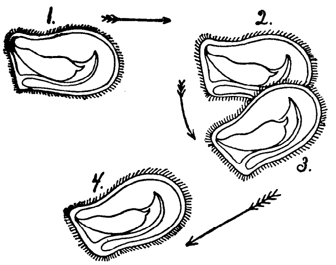


FIGURE 13. Motor reaction of Bursaria truncatella. The arrows show the direction of motion throughout the reaction, while the numbers indicate the successive positions occupied.

*Motor reactions.* — Bursaria is excessively sensitive to external influences: at any stimulus it swims backward more or less, then turns to the right, and swims forward. The turning to the *right* as a response to a stimulus is invariable whether the regular course is a straight line, a curve to the right, or a curve to the left. Bursaria confined under a supported cover-glass can detect the difference in the water as it nears the edge of the cover-glass nearly a millimetre from the edge. It then turns, always to the right, — even though its right side already lies next to the edge of the water, so that it is compelled to turn in this direction more than 180° to avoid the edge, while to the left it would have had to turn through but a small angle.

The reaction of Bursaria is represented in Fig. 13.

**C. Hypotricha: Oxytricha fallax Stein.** — *Description.* — Like most of the Hypotricha, Oxytricha (Fig. 14) has a strongly dorso-ventrally flattened body, the dorsal surface being convex, the ventral surface plane. The cilia and cirri serving for locomotion are confined to the ventral surface. The mouth is situated on the ventral surface a very little in front of the centre, from it a row of large cilia, the adoral zone, passes forward and to the left as far as the left corner of the anterior margin; thence it passes along this margin to the right corner. The posterior portion of the animal is distinctly broader than the anterior portion. Anterior and posterior ends, right and left sides, and dorsal and ventral surfaces are thus strongly marked and easily distinguishable.

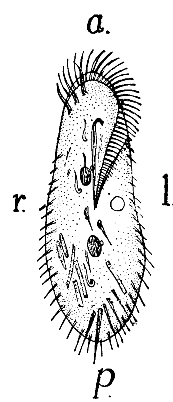


FIGURE 14. Oxytricha fallax Stein, after Kent, ventral view. *a*, anterior end; *p*, posterior end; *r*, right side; *l*, left side.

*Movements.* — Oxytricha usually runs along the substratum with ventral side applied to it, by means of the ventral cirri. When running along a plane surface, the path followed is in some individuals a straight line, in others a curve to the right, in others a curve to the left. Whether the path is a straight line or a curve, and in the latter case the direction of curvature probably depends partly or entirely upon the form of the given individual; some specimens in which the body was curved distinctly to the left followed a path that was likewise curved to the left. For a given individual traversing a plane surface the direction of the curvature was constant, so far as observed, although the degree of curvature of the path varies in one and the same animal.

Individuals running about on an irregular surface amid detritus, algæ, etc., may follow the substratum in any direction it takes them, running around the surface of spherical or irregular masses, or following a filamentous alga as it curls to the right or left, or up and down. The direction of movement seems determined by the form of the substratum on which the animals are moving.

Besides this usual motion along the substratum, Oxytricha may swim freely through the water, at the same time revolving on its long axis.

*Motor reactions.* — (*a*) *Mechanical stimuli.* — As Oxytricha runs along the substratum it frequently comes in contact with small obstructions; it thereupon jerks slightly backward and *turns to the right* (that is, toward its own right side), then again pursues a forward course. Similarly if some moving infusorian strikes in its course against the Oxytricha, the latter jerks back and turns to the right. If the preparation containing the moving animals is jarred, they all jerk backward, turn to the right, and move forward. As Oxytricha moves along the substratum it will frequently be seen thus to jerk back and turn a little to the right, there being probably invisible sources of stimuli affecting the animal. The turning to the right after such a jerk backward is invariable, whether the original path was a straight line, a curve to the right, or a curve to the left. In long continued observation of many individuals I have never yet seen one turn otherwise than to the right after a stimulus. The typical motor reflex of Oxytricha is shown in Fig. 15.

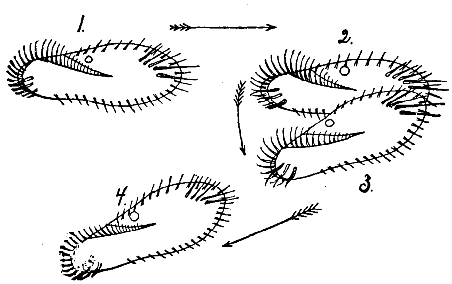


FIGURE 15. Motor reflex of Oxytricha fallax, viewing the animal from the ventral side. The arrows give the direction of motion; the numbers show the successive positions occupied.

(*b*) *Chemical stimuli.* — If a weak solution of some chemical, as sodium chloride, is allowed to run beneath the edge of the cover-glass, so that there is a sharply defined boundary between the edge of the drop and the water containing the infusoria, many of the latter will in their course come against the edge of the drop. They thereupon turn to the right. This turning to the right occurs both when the animals strike with the anterior end squarely against the edge of the drop, and when they come against it obliquely. Cases were observed in which the Oxytricha simply grazed the edge of the drop with its right side; it nevertheless after jerking backward turned to the right. In such a case, if the forward course again leads the animal against the edge, it turns to the right again. It is evident that continued turning to the right will soon bring the animal completely around, so that it will be headed in the opposite direction.

Animals swimming freely through the water and at the same time revolving on the long axis, likewise turn to the right when they come in contact with the edge of a drop of some chemical in solution. If they are dropped directly into a solution of sodium chloride they jerk backward, turn to the right, and so continue for a long time, — the whole effect being that of a jerky whirling toward the right. Dropped into 6 per cent solution of sodium hypochlorite, they all whirled steadily and smoothly to the right. Some other chemicals cause the animals to swim backward a considerable distance before turning to the right; doubtless variations in the effects of chemicals similar to those described in the fourth of these Studies (*loc. cit.*) for Paramecium might be worked out for Oxytricha.

*Localized stimuli.* — (*a*) *Mechanical.* — Touching various points on the surface of the body with the capillary glass rod, the anterior end is found to be much more sensitive than the rest of the body. The slightest touch at the anterior end — apparently even a touch to one of the cirri of this region — causes a strong reaction. The posterior part of the body is much less sensitive; the tip of the glass rod may even be thrust so violently against it as to leave a visible mark, without any strong reaction being caused. The animal reacts indeed, but quietly as compared with the violent movement when the anterior end is touched.

Touched at the sensitive anterior end Oxytricha reacts by darting backward, turning to the right, and swimming forward again (typical motor reflex).

Touched on the posterior half of the body, usually no reaction is caused. If a strong blow is given with the tip of the capillary glass rod sufficient to make a visible mark, the animal responds by *running forward.*

Touched on the left side, the animal jerks back a little, then turns to the right (away from the stimulating agent).

Touched on the right side, Oxytricha jerks back a little and turns to the right, as before, — therefore toward the stimulating agent. The rod may give repeated quick taps on the right side; the animal turns persistently to the right, as if following the rod. If touched repeatedly on the left side, it of course turns as persistently away from the rod.

Thus Oxytricha, like Dileptus and Loxodes, reacts with reference to the localization of the stimulus so far as backward and forward motion is concerned, but not so far as motion sideways is concerned: it turns toward a structurally defined side, without regard to the place of stimulation.

(*b*) *Localized chemical stimuli.* — As already shown, Oxytricha responds to a chemical stimulus which first affects the anterior end or the side by backing a little, turning to the right, then swimming forward, — without regard to which side it is that first comes in contact with the chemical. There remains to be described the reaction to a chemical stimulus coming from behind. If a crystal of sodium chloride or a rod coated with methyl green is placed behind the resting Oxytricha, there is for a moment no response; then as the diffusing chemical reaches the animal, the latter at once swims backward. It thus passes into the densest part of the solution and may be killed. Usually after swimming some distance backward, this motion is exchanged for a whirling motion to the right. If the chemical is placed in front of Oxytricha, it darts backward, as before, — thus away from the diffusing chemical. If the animals are introduced directly into the chemical, they fall at once to swimming backward, which usually gives place soon to a whirling to the right.

The direction of motion after a chemical stimulus has thus in Oxytricha no evident relation to the localization of the stimulus.

**Hypotricha in general.** — Without determining the species, the reactions of a considerable number of other Hypotricha (using this group as limited by Bütschli) were examined. All agree in the main features of structure with Oxytricha, and the method of reaction was practically identical in all. At any stimulus, except a mechanical stimulus confined to the posterior half of the body, all the species examined jerk backward more or less, turn to the right, then go forward again. No exception to this turning to the right after a stimulus was seen in any case.

As shown by the foregoing description of Oxytricha and other Hypotricha, the infusoria of this group present in their reactions certain features which give much complication to their locomotion as a whole. (1) In following an irregular substratum, such as a crooked alga filament, the animals may turn to the right or left or up or down, — the direction being determined solely by the form of the surface on which they are moving. This may be a mechanical result of the method of locomotion. As is well known these animals use a number of large cilia or cirri on the ventral side like legs for creeping. In following an alga bent to the left, for example, on coming to the bend the cirri on the right side would on being pushed forward find nothing to rest upon; the left cirri on the contrary would find a point of support, and thus pulling alone on the body, would necessarily turn it to the left. (2) In the same species some of the unstimulated individuals follow a straight path; others a path which curves to the left; others a path which curves to the right. Since, so far as observed, the path of a given individual is always curved in the same direction, it seems probable that the curve of the path is due to the form of the body; but the fact that the degree of curvature in the path of a single individual varies indicates the possibility of the presence of other factors in determining the direction of movement.

In spite of this greater complication in the movements of the Hypotricha as compared with other infusoria, it is in this group that the reaction to a stimulus by turning in a definite direction (to the right) without regard to the position of the source of stimulation, is peculiarly striking and easily observed. This is of course owing to the fact that the Hypotricha do not revolve as they move through the water, as is done by most other infusoria, but run along the bottom with the ventral side below. There is thus no difficulty in determining the direction in which the animals turn after stimulation, and this is invariably toward the right side.

**Other Infusoria.** — The foregoing discussion contains an account of the reactions of representatives of the chief groups of the infusoria, with the exception of the Peritricha. The members of this group are nearly all fixed forms, and hence not fitted for determination of the questions raised in this paper. It is true that such forms as Vorticella frequently break from their stalks and swim freely through the water. But the movement seems less well coördinated than in the other infusoria, and to almost every stimulus these creatures respond by sharply contracting the body and folding the adoral cilia inward, at the same time of course ceasing to move. I have not as yet therefore succeeded in determining with certainty any such regularity in their motor reactions as was observed in other infusoria. In addition to the species whose reactions are above described, I have studied many other species which did not, for one reason or another, give clear results, and which were therefore not included in my account. It is of course possible that a complete analysis of the reactions of some of these forms may give results differing in principle from those here detailed; in other words it is possible that essentially different laws of reaction may obtain as between different infusoria. But from the considerable number of representatives of different groups whose reactions were worked out and above described, it is believed more probable that the general principles of the motor reaction methods for the entire group have been obtained. No attempt has been made in the present paper to give an exhaustive account of the reactions of any of the organisms studied; rather were their reactions examined with a view to the answering of certain definite questions, stated in the introduction.

We will now proceed to an analysis of the observations above recorded and a discussion of the conclusions to be drawn in regard to the nature of the motor reactions of these creatures.

## IV. Analysis of the Observations, Summary, and Conclusions.

(1) The first of the questions proposed in the introduction was, Has the given Protozoön a fixed formula for motor reactions, similar to that of Paramecium?

This question has now been answered for representatives of the main groups of Flagellata and Ciliata, — including a Flagellate with two flagella (Chilomonas), others with a single flagellum (Euglenidæ), representatives among the Ciliata of the Holotricha (Paramecium, Loxophyllum, Colpidium, Microthorax, Dileptus, Loxodes, and Prorodon), of the Heterotricha (Stentor, Spirostomum, and Bursaria), and of the Hypotricha (Oxytricha and others). In all these species a fixed and definite type of motor reflex was shown to occur, though with much variation in details. In general, when one of these organisms is affected by a decided stimulus, the motor reflex takes the form of a swimming toward one end (structurally defined), turning toward one side (structurally defined), then swimming again with the same end in front as before stimulation. This question is then to be answered in the affirmative, — under the limitations given in the following paragraphs.

In the details of the reflex there is much variation. This may be brought out by noting the difference in behavior when each organism comes, for example, against the edge of a drop of a weak solution of some chemical, as sodium chloride. The lowest motor reaction is shown perhaps by Euglena viridis, which simply turns toward a definite side (the larger lip): if stimulation continues, it takes the spherical form and prepares to encyst. There is here no swimming backward and no contraction. A still lower condition is found in Euglena spirogyra and E. oxyuris, in which there is no motor reaction at all, the organisms simply remaining quiet and beginning the process of encystment at any evident stimulus. Most of the organisms studied gave the typical motor reflex above characterized. In others

(Spirostomum and Stentor), a strong contraction of the body is an additional feature of the reaction.

(2) The second question proposed was, After stimulation does the organism always turn toward a certain structurally defined *side*, without regard to the nature or position of the stimulus?

This question is answered for all the organisms studied in the affirmative. In any given organism the side toward which the creature turns after a stimulus is invariable, and has no relation to the localization of the stimulus.

The side toward which the animals turn is variously defined. In very closely related forms, as in the different Hypotricha (Bütschli), common structural features define the direction toward which the animals turn (in this case, toward the right side). In more distantly related species it is not possible to name any single structural peculiarity by which the direction of turning can be defined. Thus Chilomonas turns toward its lower or smaller lip, Euglena toward its upper or larger lip. Paramecium, Colpidium, Loxodes, and Spirostomum turn toward the aboral side; Loxophyllum and Dileptus toward the oral side. Microthorax turns toward its "dorsal" edge; Stentor, Bursaria, and the Hypotricha toward the right side. Prorodon turns toward one side which is invariable, but not structurally marked. There is of course such great variation in the structure and form of these animals that the same term (as "right" or "aboral") may have very different significations with respect to the general form in different species, so that there is no especial reason for expecting uniformity in this matter. The direction of turning in a given case depends on the structural and functional peculiarities of the locomotor organs, taken in connection with the geometrical form of the body on which they act.

The relation of the direction in which the animals turn after stimulation to the usual direction of locomotion is likewise variable. Most of these organisms, as they swim forward unstimulated, swerve toward one side or the other, — so that a spiral course results, if they at the same time revolve on the long axis. This side toward which the creature swerves may or may not be the same as the side toward which it turns after stimulation. In Chilomonas, Paramecium, Microthorax, Dileptus, Stentor, Spirostomum, and Bursaria they are the same; in Loxophyllum and Colpidium the animals swerve in ordinary locomotion toward one side (owing to the form of their bodies), while after stimulation they turn toward the opposite side. The

Hypotricha may swerve from a straight line either to the right or to the left, but after stimulation the turn is always to the right.

(3) Before taking up the third question proposed in the introduction, it will be well to state briefly the facts brought out in regard to the comparative sensitiveness of different parts of the body. As shown by localizing mechanical stimuli, *the anterior end is much the most sensitive part of the body.* This was demonstrated for Paramecium, Dileptus, Loxodes, Stentor, Oxytricha, and in a less marked degree for Spirostomum; it is probably true for the others also.

(4) The third question proposed in the introduction was, After stimulation does the organism always move, before turning, toward a certain structurally defined *end* (the "posterior") without regard to the nature or position of the stimulus?

This question is answered, in the general form above stated, in the *negative.* Yet the conditions and limitations of this negative are such that an analysis of the observations is necessary for an appreciation of its signification.

(*a*) As pointed out in the accounts of Chilomonas and Paramecium, the usual *forward* motion of all the organisms above described may be considered a reaction to a stimulus, if the resting condition be taken as a starting point — inasmuch as the beginning of this motion is due to an external change. The resting individual may be induced to resume the forward motion by any very gentle movements such as will separate it from the object against which it is resting, without giving it a stimulus of a pronounced character. It then requires another stimulus to induce again the resting condition.

(*b*) Some forms, as Euglena viridis, do not swim backward at all even when strongly stimulated, — the typical motor reflex consisting merely of the turning toward a definite side.

(*c*) For other organisms, the following facts are brought out by the experiments with localized stimuli: —

In Dileptus, Loxodes and Oxytricha, the end toward which the animal moves after a mechanical stimulus depends upon the localization of the stimulus; to such a stimulus at the anterior end the animals react by swimming backward, while if the stimulus is at the posterior end they swim forward.

For chemical stimuli, on the other hand, in the same infusoria, as well as in others, the *absence* of any such dependence of the direction of motion on the position of the stimulating agent was demonstrated.

Since the experiments with localized mechanical stimuli clearly demonstrate that the organisms just named have the power to distinguish stimuli upon the posterior part of the body from those on the anterior part, and to vary their reaction accordingly, the question arises as to why this power is not exercised in the case of chemical stimuli. The fact that the organisms swim backward when stimulated by a chemical substance diffusing from the rear has cost the lives of many infusoria in these experiments. This perverse and useless method of reaction has been demonstrated to occur in Chilomonas, Paramecium, Loxodes, Dileptus, Spirostomum, Oxytricha, and other Hypotricha.

The explanation of this lack of appropriate reaction in the case of chemical stimuli is probably as follows: As stated above, it is proven in many cases that the anterior end is much more sensitive than the remainder of the body, — the latter being comparatively impercipient. Thus a light touch with the glass rod, that would at the anterior end induce a strong reaction in Paramecium, Loxodes, Dileptus, Stentor, or Oxytricha, produces in these same organisms when applied to the posterior part of the body no reaction at all. Now, suppose a chemical substance diffusing somewhere in the rear of one of these infusoria. As the very dilute solution first reaches the posterior end, it is too weak to act as a stimulus upon this comparatively unsensitive part. The animal therefore remains quiet, and the chemical continues to diffuse, until, coming from the rear, it reaches the sensitive anterior end. Thereupon a strong reaction is induced, which, resulting from a stimulus applied at the anterior end, takes the form of swimming backward, etc., rather than forward. The animal may thus enter the destructive solution and be killed by it.

Spirostomum ambiguum presents an exception to the general rule, in so far that even mechanical stimuli applied to the posterior end usually induce the swimming backward, exactly as when applied to the anterior end. The greater relative sensitiveness of the posterior end of Spirostomum and its habit of contracting strongly at any stimulus seem to be connected with this fact. (See the account of Spirostomum above.)

To unlocalized stimuli — that is, stimuli applied to the entire surface of the animal at once, as when they are dropped into some chemical solution or when the vessel containing them is strongly jarred — all the organisms respond by swimming first *backward*. In such a case it is perhaps only the anterior end that actually receives a stimulus.

In a recent paper[1] I have attempted to set forth the bearing of the results gained by a study of the motor reactions of Paramecium on the psychology of that animal. The investigations recorded in the present paper require a modification of one of the statements therein made, — if not for Paramecium, at least for other infusoria. This is the statement that the direction of motion in the motor reaction has no relation to the localization of the source of stimulus. This statement was based on the reactions of Paramecium and other infusoria to localized chemical stimuli, and the reactions of Spirostomum to localized mechanical stimuli. These phenomena taken alone seem to justify the statement for Paramecium and Spirostomum, yet the facts obtained by a study of other infusoria show that the statement cannot be generalized for this group of animals. We have in the infusoria a remarkable transitional stage toward a real perception of the localization of the stimulus, — reaction with regard to such localization so far as motion along the body axis is concerned; a blind reflex without regard to the localization of the stimulus, so far as motion sideways is concerned.

(5) On the whole, the investigation has shown that the motor reaction plan of the infusoria studied is essentially the same as that previously described for Paramecium. Until it is clearly shown that some members of these groups react in a manner essentially different from that which I have described, we may assume provisionally that this manner of reaction is characteristic for the Flagellata and Ciliata in general. We may therefore extend provisionally the chief general conclusions drawn from a study of the movements of Paramecium to the Flagellata and Ciliata as a whole. The more important of these conclusions may be stated briefly as follows: —

1. The motor reactions to stimuli in the Flagellata and Ciliata take the form of a reflex of definite character, the usual features of which are that the animal moves backward some distance, turns toward a structurally defined side, then moves forward.

2. Different kinds of stimuli do not produce correspondingly different kinds of reaction, but this motor reflex is produced by chemical stimuli of all sorts, by fluids active through their osmotic pressure, by heat, by cold, and by mechanical shock; in fact, by all agents capable of causing a motor reaction. Chemotaxis, tonotaxis, thermotaxis, etc., are therefore not essentially different forms of

[1] JENNINGS: American journal of psychology, 1899, x, p. 503.

activity: they are due to the same reflex, merely induced by different agents.

3. The direction of motion throughout this reflex has to only a very limited degree a relation to the localization of the stimulus. The direction of turning has absolutely no relation to such localization, being determined by structural differentiations. Whether motion shall take place backward or forward along the body axis is however to a certain extent determined by the localization of the stimulus.

4. The general effect of this reflex is to take the organism out of the sphere of influence of the agent causing the reaction, and to prevent it from re-entering.

5. Chemotaxis is by no means a passive motion due to attraction or repulsion of the protoplasmic substance by other substances, but is an active movement due to the production of this motor reflex by the chemical agent in question. The organisms leave certain areas vacant ("negative chemotaxis") as a result of the fact that the influences at work in these areas cause this motor reflex. They gather in certain areas ("positive chemotaxis") when the conditions within these areas are *not* such as to cause the motor reflex, while the surrounding influences do cause it. There is then no such thing as direct attraction or repulsion shown by these animals. Corresponding statements may be made for thermotaxis, tonotaxis, etc.

6. The motor reflex through which these reactions are produced is of the same order as the motor reflexes of higher animals, so that there is no reason for holding the reactions of these unicellular organisms to be of an intrinsically different nature from those of higher forms.

7. The behavior of these organisms shows them to occupy an extremely low place in the psychological scale, most of their activities being due to a single reflex.

8. There is evidently no immediate analogy between the reaction movements of these unicellular organisms and the growth movements of higher forms ("tropisms"), so that the phenomena shown by the former do not justify the drawing of direct conclusions concerning the latter.

These conclusions, as well as others of a less general nature, have been developed in detail by the author in previous papers,[1] so that it is not necessary to dwell upon them here.

[1] See, in addition to the papers previously cited, a lecture by the author on "The Behavior of Unicellular Organisms," in the Woods Holl Biological Lectures for 1899.

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