The Journal of
Comparative Neurology and Psychology

Volume XIV 1904 Number 6

THE BEHAVIOR OF PARAMECIUM. ADDITIONAL FEATURES AND GENERAL RELATIONS.

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With 17 figures in the text.

CONTENTS.

Since Paramecium is usually taken as a type for the study of unicellular animals, it is desirable to have its reactions to stimuli as fully known as possible. In attempting to put together the results of numerous investigations made during the last fifteen years on the behavior of this animal, I have found that there are still a number of reactions which have not been described, or have been described incorrectly, and that certain general relations running through the behavior have never been brought out. The present paper attempts to fill, so far as possible, these gaps in our knowledge, supplementing and unifying previous accounts of the behavior of Paramecium. The writer tries to point out omissions or errors in his own previous work with the same impartiality as in the works of others.

The chief subjects dealt with are, in the first place, what we may call the *action system* of Paramecium; in the second place, the fundamental character of the stimulations to which the animal responds. In the third place an account is given of certain imperfectly or incorrectly known reactions, with particular reference to their relation to the "action system" of Paramecium. The chief reactions thus taken up are "rheotaxis," "geotaxis" and "electrotaxis."

Methods.—A word should be said here as to certain methods of work. Throughout the following paper accounts are given of the direction of the *effective* beat of the cilia. This was determined in every case by mingling finely ground India ink with the water containing the Paramecia, thus observing the direction of the currents caused by the cilia. By using such a method one is not reduced to conjecture as to the really effective direction of the ciliary beat, as has been the case in certain papers on this subject, but this effective direction is determined immediately by observation. I have supplemented this method by observing the cilia of animals partly confined in a gelatin solution, in the usual way, and of animals partly stupefied with chloretone. These methods gave especially good results when combined with the use of India ink, to show the currents. Owing to its fineness, blackness, and absolute lack of chemical action, I have found the use of India ink (or Chinese ink) much preferable to that of carmine or indigo. The ink is procured in sticks and rubbed up with water in the usual way.

I. THE ACTION SYSTEM.

By the behavior of an organism we mean essentially the regulation, by means of movement, of its relations to environmental conditions. The characteristic complex of movements by which the relations of Paramecium to its environment are determined may be called the "action system" of the organism. Most animals have certain peculiar methods of action, depending largely upon their structure—upon what VON UEXKÜLL (1903, p. 269) calls the "biologische Bauplan"—by which most of their behavior is brought about. These characteristic ways of acting are usually few in number and form a unified system, providing a definite reaction combination for any stimulus. The reaction systems of different animals vary as much as do their structures. Thus many different agents acting on a given animal may produce the same set of movements, while on the other hand the same agent acting on organisms of different "action systems" produces in each case different movements. The method of reaction then depends as much on the action system of the organism in question, as upon the physical or chemical action of the stimulus. The usual relation between the two factors may be expressed as follows: The action system supplies a limited number of methods of action, the character of the stimulus (including its localization) determines which of these methods shall be set in operation.

In dealing with the action system of Paramecium, we have to consider, first, the usual movements and the environmental relations which they induce; second, the typical modifications of these movements (the reaction types), under the influence of stimulation.

1 *The Usual Movements; Spiral Swimming.*—As is well known, Paramecium continually swerves toward the aboral side and revolves on its long axis as it swims through the water, so that its course is a spiral one (Fig. 3). The revolution, so far

as I have observed, is always *over to the left,* when the anterior end is directed away from the observer. That is, the upper surface is continually passing to the observer's left (the lower surface of course to his right).[1] Before using the stereoscopic binocular I supposed that the revolution was sometimes over to the right, sometimes over to the left (JENNINGS, 1899, p. 316). But observation of thousands of cases since this instrument was used has never shown a single exception to the revolution over to the left. I have repeatedly known observers working with the usual monocular microscope to assert that part of the Paramecia in a given culture were revolving over to the right, but on examination with the stereoscopic binocular they invariably became convinced that there was no exception to the revolution over to the left. The appearances shown by the monocular microscope are very deceptive in such phenomena, and I do not believe that observations with it even by practiced observers are reliable on this particular point.

The revolution is still over to the left when the animals are swimming backward. This is contrary to the statement made in the second of my "Studies" (JENNINGS, 1899, p. 316), when I was working with the monocular microscope. But the binocular leaves no doubt upon this point. When the forward movement is reversed, the direction of rotation is *not* reversed.

The oral groove of Paramecium always passes, if the oral side is down and the anterior end away from the observer, from the right behind to the left in front (as represented in BÜTSCHLI, 1889, Pl. 63, Fig. 1 *a*). Many observers have reported Paramecia in which the direction of the groove is "reversed," running from the middle obliquely to the right instead of to the left.

[1] There is no general agreement as to the designation of the direction of a spiral. The above method seems most convenient for free swimming organisms, since it gives the results of immediate observation, and other methods of designation usually have to be translated, for practical purposes, into this one. If we used the method of designation proposed by NÆGELI (1860), the spiral of Paramecium rises from south to west. If we designate the direction of rotation by the method used in spiral cleavage, imagining a small observer situated in the long axis of Paramecium with head toward the anterior end (KOFOID, 1894, p. 180), then we must say that the rotation is to the right.

But the monocular is deceptive on that point. An investigator who was certain that in a particular culture many of the individuals were thus "reversed" made at my request a careful examination of a large number, after killing them with an excellent fixing solution. Not a single reversed specimen was found. If such exist, they are certainly extremely rare.

The obliquity of the oral groove—from right behind to left in front—appears to be the opposite of that which would assist the revolution over to the left. If the groove should act like the groove of a screw, moving along a solid ridge, the animal would revolve over to the right instead of over to the left. It is of course known that the revolution on the long axis is independent of the groove, since when the animal is cut in two in such a way that no part of the groove remains on the posterior half, this half nevertheless continues to revolve on its long axis when moving forward (JENNINGS and JAMIESON, 1902). The significance of the direction of the oral groove is probably to be sought in its relation to the stream of water which it leads to the mouth.

The width of the spiral path of Paramecium varies much. The spiral is narrowest when the animal is progressing most rapidly, through water which presents no stimuli; its width is then equal to about one-half the length of the animal. Usually the spiral is wider than this; the length of the animal is perhaps a fair measure of the average width. In many cases, as after stimulation, the width is much greater; it may be several times the length of the animal. Paramecium as a rule makes one turn of the spiral, reaching a corresponding phase or position, in about four times its length; but this relation is also variable.

The spiral motion is compounded of three factors: (1) the forward movement; (2) the swerving toward the aboral side; (3) the revolution on the long axis. Each of these factors depends on certain peculiarities in the stroke of the cilia. The forward motion is due of course to the fact that the cilia strike in a general way backward. The revolution on the long axis is due to the fact that the stroke is not directly backward, but is oblique. This obliqueness in the stroke of the cilia is easily rendered evident by mounting the animals in water containing a large quantity of India ink in suspension, as described above. After the violence of the movement has subsided, specimens may be studied that are restrained by coming in contact with a solid, or by swimming into a crevice. In such specimens, still revolving on the long axis, it may be seen that the particles of India ink on the upper surface of the animal pass backward and, when the anterior end is directed away from the observer, to the observer's right. That is, on the right side of the animal the particles pass toward the oral groove, on the left side away from the oral groove (Fig. 1). This

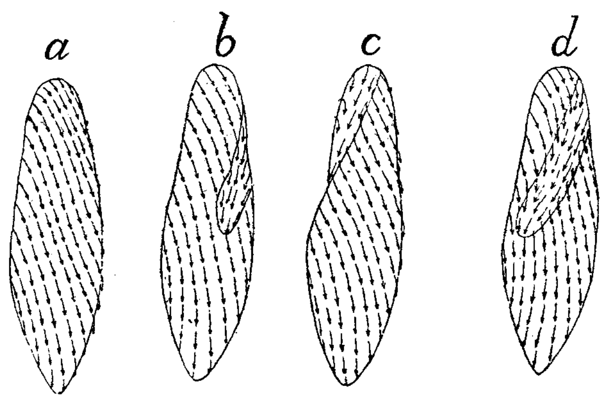


Fig. 1. Diagrams showing the direction of the water currents caused by the cilia, in different positions of the animal. *a*, aboral surface; *b*, right side; *c*, left side; *d*, oral surface.

movement is indicated in a transverse section of the animal by Fig. 6, *a*. It is evident that the ciliary motion thus indicated would turn the animal in the opposite direction from the currents—that is, over to the left. In the oral groove the cilia strike more nearly directly backward, with but a slight obliqueness that is opposite that of the body cilia. This is shown by the fact that a current runs within the groove from its anterior to its posterior end (Fig. 1, *b*, *c*, *d*).

The swerving toward the aboral side is due, in the normal swimming, largely to the more powerful stroke of the cilia in the oral groove. It may be increased, under stimulation, by a change in the beat of the body cilia of the anterior end at the left side of the oral groove, by which they strike toward the oral groove instead of away from it. On the number and strength of action of the cilia showing the changed beat depends the amount of swerving toward the aboral side.

All the three factors in the spiral course may vary more or less independently of each other, and on the amount of such variations depends the width of the spiral, the number of turns in a given distance, and the like. The effects of stimuli consist largely, as we shall see, in changing the proportional parts played by these various factors—decreasing or stopping one, increasing another, etc.

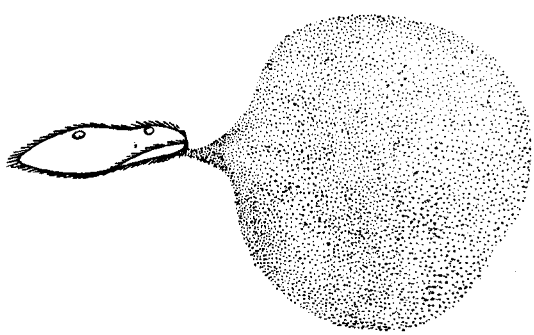


Fig. 2. A Paramecium swims toward an area containing India ink; before it reaches the boundary of the area a cone of the ink is drawn out by the action of the oral cilia, reaching the anterior end and oral side.

Owing to the stronger and more direct backward beat of the oral cilia, in swimming forward a current of water is caused to pass from in front in the form of a cone to the oral side and mouth. This is rendered evident when a cloud of India ink is added to the water containing many Paramecia. The cloud has for a time a definite boundary surface. When the Paramecia swim toward this surface, the latter may be seen to extend out in the form of a cone, to meet the advancing animal (Fig. 2). As soon as this black cone comes in contact with the anterior end of the Paramecium, the latter stops and turns in another direction—this occurring some distance from the gen-

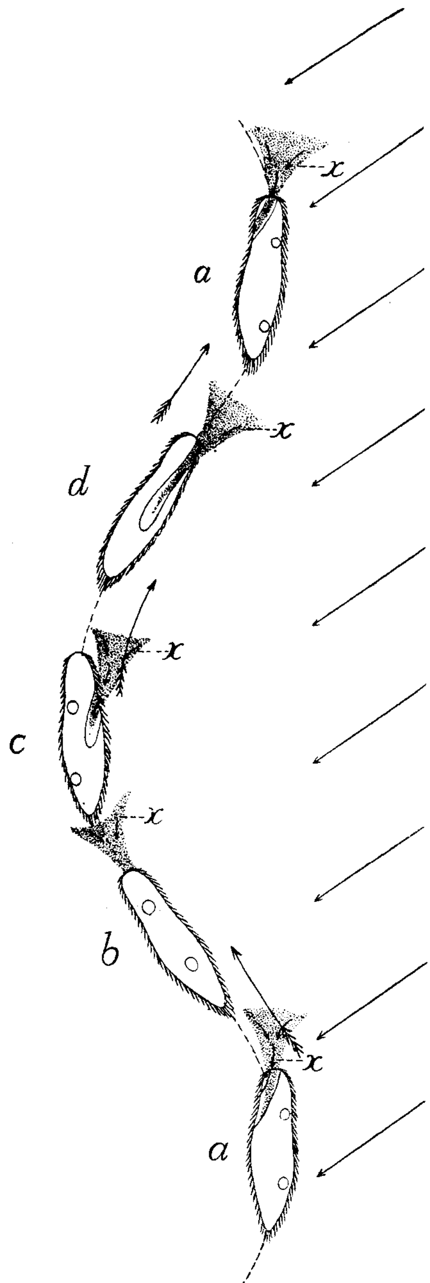


Fig. 3. Spiral course of Paramecium, showing how the animal is subjected through this method of swimming to many changes in its relation to the environment. The arrows at the right indicate some agent (light, gravitation, a water current or the like) acting from a definite direction: the relation of the animal to this agent is continually changing; at *b* the body is nearly transverse, at *d* nearly parallel to the arrows. The dotted areas *x* show the currents of water carried to the anterior end by the movements of the oral cilia.

eral boundary surface of the cloud. This explains the observation often made that Paramecia and other infusoria react and turn away seemingly some distance before reaching the agent causing the reaction. Thus, on approaching a bubble or the free surface of the water, infusoria often react and turn away when still separated by a marked interval from the air surface. A little of the water next to the air has been drawn out to meet the animal, which then reacts to any modification the water may have undergone by contact with the air.

Thus in its forward course the animal is continually receiving "samples" of the water in front of it, and reacting to these samples. In its spiral path Paramecium becomes pointed successively in many different directions, so that it "samples" the water from many directions (Fig. 3). When the spiral is very narrow, the animal swimming rapidly forward, these samples all come from near the axis of the spiral and therefore show little variation. But in most cases the direction from which they come is continually changing. Thus we may say that Paramecium, through its spiral course, is continually "trying" the water in various directions. Or, to express the same thing in a more objective way, through the spiral course the most sensitive portion of the organism is subjected successively to water coming from many different regions.

In another way the spiral course subjects the organism to varied experiences. Suppose that a force which acts in straight lines from a definite direction is operating on the swimming organism from one side; for example, light, or the electric current, or gravity, or a current of water. By its spiral course the organism is brought successively into different relations with this agent (Fig. 3). In one phase of the spiral, as at *d*, it swings more nearly into parallelism with the lines of action of the agent; in another it is becoming more nearly transverse, as at *b*. In the case of light the anterior end is becoming more illuminated in one phase, less in another; in other words, the anterior end is subjected to continual variations in the intensity of illumination. With gravity, or a water current, the swinging is assisted in one phase of the spiral, resisted in another, so that the animal is subjected to continual variations in the resistance it meets. These changes give opportunity for directive or regulative stimulation. It is only when the axis of the spiral course is in the lines of force—in other words, when the organism is "oriented"—that such changes cease. These relations will be brought out in detail later in describing the reactions to certain stimuli.

Altogether, we see that the "action system" of Paramecium contains elements of such a nature as to subject the animal to the greatest possible number of changes in the environment, thus giving it opportunity to react to all such changes.

2. Modification of the Movements under Stimulation; Reaction Types.—In the behavior of Paramecium under the action of stimuli we may recognize a certain number of distinct reaction types. (1) The chief one of these is that which I have in former papers called the "motor reflex" or "motor reaction," and which I shall call here, for reasons given later, the "avoiding reaction." The others are (2) the movement forward from the resting condition; (3) the coming to rest of a moving individual; (4) certain features of the reaction to the electric current; (5) local contractions of the body, and possibly (6) the discharge of trichocysts. The list of reaction types thus rises to a considerable number, but the last three named play almost no part in the regulation of the relations of Paramecium to its environment under natural conditions. We shall deal *in extenso* here only with the most important reaction type—the "avoiding reaction."

3. The Avoiding Reaction.—Through this reaction type occur most of the marked reactions of Paramecium that have often been spoken of as "tropisms" or "taxes;" in other words, the reactions to stronger stimuli of all sorts. The avoiding reaction consists, when well marked, of the following: the animal swims backward, turns toward the aboral side, then resumes the forward motion. I have called this in former papers the "motor reaction" or the "motor reflex." But the former is a general term, properly used for any movement that takes place as a response to a stimulus, and hence not fitted for characterizing a special reaction type. To the second, objection has been raised on the ground that the word *reflex* should be used only when a nerve cell is concerned; there are perhaps other and better grounds for leaving open the question whether the movement in this reaction is in the nature of a reflex or not. For these reasons I have sought for a simple expression which shall bring out the essential character of the reaction without prejudice to its nature in other respects. The most general effect of this reaction is to remove the reacting organism from the source of stimulation and direct it elsewhere; it may, therefore, be appropriately called the "avoiding reaction." By this reaction, as I have shown in previous papers, Paramecium responds to heat, cold, mechanical stimuli, chemicals of all sorts, osmotic stimuli—in fact, to stronger stimuli of almost all classes.

The avoiding reaction is brought about through certain modifications of the three factors in the spiral swimming. The first phase of the reaction is a slowing, suspension or reversal of the forward component in the spiral course. In a very pronounced reaction, caused by a powerful stimulus, the forward course is reversed, while the revolution on the long axis and the swerving toward the aboral side continue as before. The animal therefore swims spirally backward for a distance (Fig. 4). When the stimulus is weaker, the forward course is merely suspended for a moment—the revolution and swerving toward the aboral side continuing. Finally, in some cases the forward course is merely made slower. The backward swimming or stoppage is brought about by a reversal of the forward component in the stroke of the cilia. In a pronounced reaction all the cilia are reversed (Fig. 4); in a less marked reaction the body cilia are reversed while the oral cilia are not (Fig. 5). In the latter case the effect on the currents in the water, as shown by the movements of particles of India ink, is

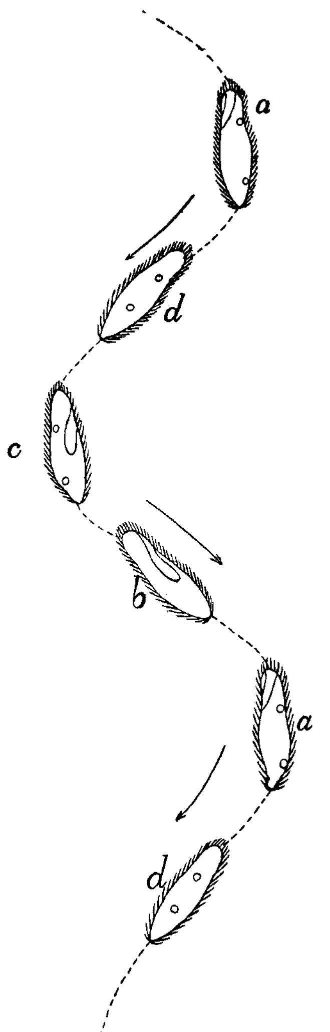


Fig. 4. Backwa rd spiral cours of Paramecium in reacting to a stimulus. *d*, *c*, *b*, *a*, successive positions occupied. The turning is to the left, in the same direction as in Fig. 3.

peculiar. The currents pass forward everywhere, save in the oral groove, where they pass backward. Since the animal at the same time revolves on its long axis, the particles in a given region close to the Paramecium at first dart forward, then later backward, depending on whether the body surface or the oral groove is directed toward the region in question.

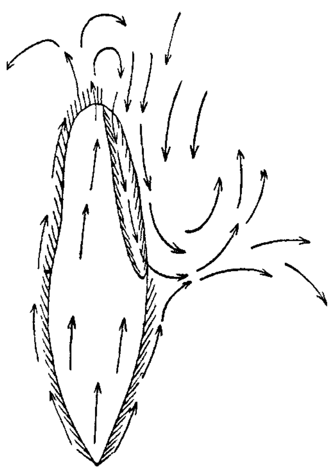
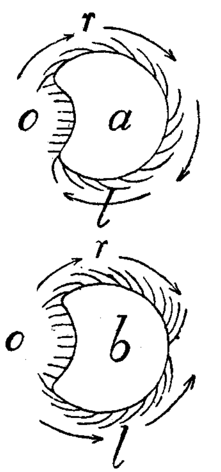


Fig. 5. Currents in the reaction to a weak stimulus, or near the end of a reaction to a strong stimulus. The animal moves backward: the body cilia are reversed, the oral cilia are not. The arrows show the direction of the water currents.

The second feature in the avoiding reaction is the increased turning toward the aboral side. This is due to two changes in the stroke of the cilia. The first and less important is the fact, mentioned above, that after a stimulus of not very great intensity the body cilia are reversed, while the oral cilia continue to beat backward. This of necessity turns the anterior end toward the aboral side. The second and more important factor is a change in the stroke in the body cilia of the left side, in the anterior portion of the animal. In the ordinary swimming, as we have seen, the cilia of the right side strike toward the oral groove (Fig. 1, *b*), those of the left side away from the oral groove (Fig. 1, *c*). But in the avoiding reaction, both while the swimming backward continues and after it has ceased, the cilia of both right and left sides strike toward the oral side. This of course drives the body of the animal toward the aboral side. The difference between the stroke of the cilia in the usual course, and in the avoiding reaction is shown in sectional views in Fig. 6.

Thus the cilia to the left of the oral groove play a most important part in the avoiding reaction, reacting by a reversal of the direction of the usual stroke—at least by a reversal of the transverse or oblique component of the stroke. They thus play a part similar to the large cilia at the left of the peristome in the Hypotricha, and to the cilia which WALLENGREN (1902) designates as the "*Drehungswimpern*" in Opalina. It is to their reversal that the most characteristic features of the reaction are due.



The change in the stroke of these cilia of the left side explains the third feature of the avoiding reaction; namely, the modification of the revolution on the long axis. The turning toward the aboral side in the reaction involves an increase in the swerving found in the normal swimming, in proportion to the rate of revolution. The change in the stroke of the cilia of the left side causes, as we have seen, the increased swerving; it likewise causes a decrease or stoppage in the revolution on the long axis. In the usual swimming, the cilia of both right and left sides tend to turn the body over to the left (Fig. 6, *a*); in the

Fig. 6. Diagram of cross sections of Paramecium (viewed from the anterior end), showing the obliquity of the ciliary stroke. *a*, condition in the usual forward progression: the body cilia all strike toward the right side; *b*, condition while turning toward the aboral side, in reacting to a stimulus: the cilia of the left side have changed the direction of their stroke; *l*, left side; *r*, right side; *o*, oral groove. The arrows show the direction in which the cilia tend to turn the body.

avoiding reaction the cilia of the left side tend to turn the body to the right, those of the right side to turn it to the left (Fig. 6, *b*). Thus the cilia of the two sides oppose each other so far as revolution is concerned, but co-operate in causing the body to swerve toward the aboral side.

The effectiveness of the change of beat of the cilia of the left side varies much, apparently as a result of the fact that the number of cilia having the changed stroke varies. On this point it is exceedingly difficult to determine numerical or precise quantitative relations. But if the stimulus is weak, apparently only a few of the cilia at the anterior tip of the left side change their direction of stroke; with a stronger stimulus the number is greater. It is possible further that the amount of change in the stroke of individual cilia is variable; from some of my observations I believe this probable. But whatever the nature of the variation, the following results are produced. If the effective beat of these left cilia is only slightly changed, the anterior end then describes but a small circle, as in Fig. 8, *a*. As the effective beat of these cilia changes farther, the swerving becomes stronger and the revolution slower, so that the anterior end swings in a larger circle (Fig. 8, *b*). Finally all the cilia beat toward the oral side; the revolution on the long axis has then entirely ceased, while the swerving toward the aboral side is very rapid. As a result the anterior end describes the circumference of a circle, in the radii of which lies the long axis of the body (Fig. 9). Thus the swerving toward the aboral side varies inversely as the rate of revolution on the long axis. In the unstimulated swimming the revolution is rapid and the swerving slight; in the strongest reaction the revolution is zero and the swerving is strong, while between these two extremes an indefinite number of gradations exist. The change in the forward stroke of the cilia seems more nearly independent of the two interconnected sets of changes just described. The rapid forward swimming may be combined with the minimum of swerving and the maximum of rotation; the animal then shoots rapidly forward. On the other hand, the forward swimming may either entirely cease, or be converted into a backward movement, in combination with the same minimum of swerving and maximum of rotation. In the former case the animal merely rotates rapidly on its long axis, neither advancing nor retrograding; in the latter case it shoots rapidly backward. But whenever the swerving toward the aboral side becomes largely increased, the longitudinal motion seems to decrease; this is probably a necessary consequence of the fact that the effective stroke of many of the cilia is in this case lateral, so that only a comparatively weak component is left for movement along the long axis. While swerving strongly, however, the longitudinal motion may be either forward, or zero, or backward.

As our analysis thus far shows, it is quite inadequate to conceive the cilia as having merely forward and backward strokes —"expansive" and "contractile" phases. The effective stroke may be nearly straight backward or forward; or obliquely backward or forward, with various grades of obliqueness; or transverse. Furthermore, the cilia of different parts of the body may vary independently in their effective stroke. Thus, we have above distinguished the following conditions:

1. All the cilia strike almost directly backward (forward course, Fig. 3).
2. All the cilia strike almost directly forward (backward course, Fig. 4).
3. All the cilia strike obliquely backward and to the right, save the oral cilia, which strike nearly directly backward (forward course, with much swerving toward aboral side).
4. All the cilia strike obliquely forward and to the right, save the oral cilia, which strike nearly directly forward (backward course with much swerving).
5. All the cilia strike transversely to the right (rotation on the long axis, without progression or retrogression.)
6. The cilia of the right side strike obliquely to the right and backward; the cilia of the left side strike obliquely to the left and backward (forward course, swerving to the aboral side, without rotation).
7. The cilia of the right side strike obliquely to the right and forward; the cilia of the the left side strike obliquely to the left and forward (backward course, swerving to the aboral side).
8. All cilia strike obliquely forward, save those in the oral groove, which strike backward (backward course after a weak stimulus, or after the effect of a strong stimulus has nearly expired, Fig. 5).

It must be added that the extent of body surface on which the cilia show any of the characteristic strokes mentioned is exceedingly variable. Often, for example, the body cilia of only the anterior tip, or the anterior half, show the transverse stroke, while posterior to this they do not. Farther, the cilia of the posterior half of the body frequently cease beating effectively, showing only a slight quivering, while the anterior cilia are still very active. As a result of a long study of the ciliary movements, one retains the impression that almost any combination of forward, reversed, oblique or transverse strokes is possible among the different areas of the body, and that those mentioned above are only typical combinations, produced under more or less definite conditions. As a rule a combination is produced such as brings about a well ordered movement of some sort, but under certain conditions the movements of the cilia are such as to produce only a disordered quivering or jerking, without movement in any definite direction. This is sometimes the case for example when the animal is immersed in a strong chemical. Under some conditions a similar result is produced also, as we shall see later, by the electric current.

What are the conditions on which depends the direction of the effective stroke of the cilia in any given region of the body? The question is a very difficult one. According to the tropism theory, the direction of the effective stroke of the cilia—that is, whether the "contraction phase" or "expansion phase" was the effective one in producing movement—depended on the direct action of stimuli on the part of the body bearing the cilia in question. Certain agents impinging on any given region of the body caused the "contraction" or backward stroke to be more effective; others had the opposite effect. But we now know that this conception was far too schematic. As a result of a stimulus applied to a single definite region of the body, certain cilia beat effectively in one way, others in a different manner, and the first effect is soon followed by a second one, equally complicated. Thus, a touch at the anterior end with a glass rod, or a chemical acting on the surface, (1) produces reversal of the stroke of the cilia over the entire body; (2) then a return of the oral cilia to the backward stroke, the others remaining reversed; (3) then causes the body cilia of the left side to strike toward the oral groove (whereas before they struck in the opposite direction), while the forward stroke of the body cilia becomes converted into a backward one. There is a co-ordinated system of movements, producible in many ways, a system that is variable in many respects, yet as a rule varies in such a way as to retain throughout its co-ordination.

The change in the stroke of the cilia is correlated in many cases with certain other phenomena. Paramecium still retains to a very slight degree the power of contraction that is so marked in many other ciliates. The anterior end especially

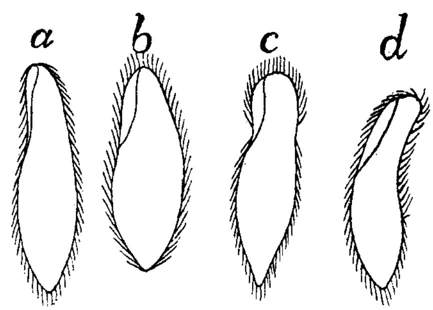


Fig. 7. Relation of reversal of the ciliary stroke to contraction. *a*, usual condition: over the entire surface of the slender body the cilia strike backward; *b*, the body is contracted, becoming short and thick: all the cilia are reversed; *c*, anterior end alone contracted, and cilia reversed in this region alone; *d*, contraction on the aboral side, curving the body: cilia reversed in the contracted region.

may be shortened and thickened, or narrowed and lengthened, or bent to one side, to an appreciable degree. These movements are hardly to be observed in specimens swimming freely through the water. But if the movements are impeded and the animals partly flattened out between the slide and cover, partial contractions are very evident. It is then to be observed that whenever contraction takes place, the cilia of the contracted region become partly or entirely reversed (Fig. 7, *b*), beating no longer forward, but backward or transversely. At times the whole body contracts, becoming shorter and thicker; at the same time it begins to swim backward. The moment the more slender form is restored, the animal begins to swim forward. Frequently only the anterior half or anterior tip is contracted (Fig. 7, *c*); then the cilia are reversed in this region alone. Again, one often sees the aboral side contract strongly, so that the animal curves toward this side. At the same time the cilia are reversed on this side, while they continue to strike as usual on the oral side; the animal then of course turns toward the aboral side (Fig. 7, *d*). Is this coincidence of the reversal of ciliary movement with contraction to be considered a necessary relation, so that whenever contraction occurs, the cilia must be reversed? STATKEWITSCH (1903) shows that the same relation exists in the reaction to induction shocks, so that the generalization seems very probable.

4. The Avoiding Reaction as a Factor in Behavior.—Let us now leave the detailed physiology of the avoiding reaction, and consider it as a factor in behavior; that is, its effect on the relation of Paramecium to the environment. We may, for the sake of a vivid realization, put the conditions in the form of a problem, with a slightly subjective tinge. The Paramecium has been swimming forward without stimulation; on reaching a certain region it is stimulated. What is to be done in order to avoid or escape the stimulation?

The first feature of the reaction—the swimming backward or stopping—of course either removes the animal from the region where it is stimulated, or prevents it from entering farther. This reaction is, logically if we may so express it, an absolutely correct one. Since the animal was not stimulated till a certain point is reached, then *was* stimulated, in order to avoid the stimulation it is sound practice to retrace the course; in other words, to restore the condition which did not stimulate. With the swimming backward the direction of the water currents is likewise reversed, so that no more of the water from the stimulating region is brought to the mouth.

The next problem is, in what direction shall the Paramecium now swim forward so as to avoid further stimulation? To determine this, it would be well if a trial could be made of the different conditions immediately in advance. This is exactly what the Paramecium does. It begins to turn toward the aboral side, at the same time continuing to revolve slowly on the long axis. In this way the anterior end swings about in a circle and is pointed successively in many different directions (Fig. 8). From each direction a little water is brought to the anterior end and mouth by the oral cilia. Thus the Paramecium is given opportunity to "try" the water in many different directions. When the water coming from a certain one of these directions does not show the conditions which acted as a stimulus, the ani-

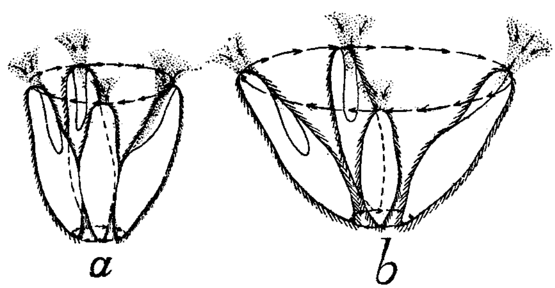


Fig. 8. Diagrams of the way in which Paramecium swings its anterior end about in a circle, in reacting to stimuli. *a*, reaction to weak stimulus; *b*, reaction to a stronger stimulus. From each different direction a current of water is brought to the anterior end. (The forward or backward component of the motion is omitted from the diagram).

mal may move forward in that direction, since now there is no further cause for reaction. If the original stimulus was weak, the anterior end is swung about in a small circle, "trying" the water from a number of directions varying only a little from the original one (Fig. 8, *a*). If the stimulus was very strong, after swimming backward a long distance the animal swings its anterior end about a larger circle, a circle of which the longitudinal axis forms one of the radii; thus directions are "tried" which diverge as much as possible from the original one (Fig. 9). If in any of these "trials" the stimulus is again strongly received, the animal may repeat the whole reaction from the beginning—retracing its course anew, and beginning a new set of "trials."

With a very powerful stimulus, such as a strong chemical, this reaction makes the impression of being violent and disordered, as indeed may the reactions of a human being under similar conditions. But with a moderate stimulus the reaction may be very delicate. This may be illustrated by the behavior of Paramecia within an area of water containing carbon dioxide. Part of the reaction under these conditions was described

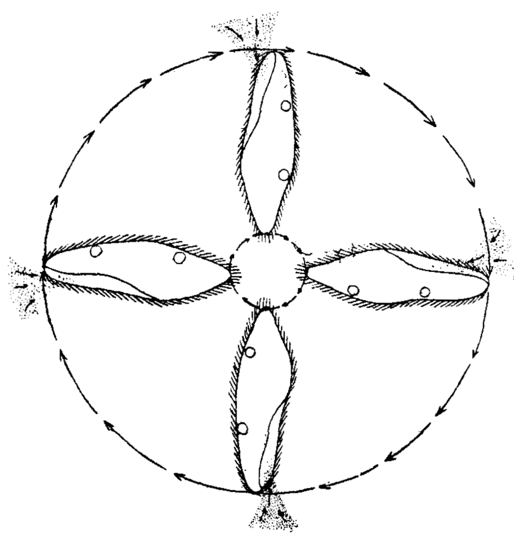


Fig. 9. Diagram of the swinging of the anterior end about a large circle, in reacting to a strong stimulus. The revolution on the long axis has entirely ceased.

in one of my earlier paper (JENNINGS, 1899, p. 331), though without a full appreciation of its real significance. The Paramecium, swimming slowly within the area of carbon dioxide, comes near to the edge of the area, where it receives water containing none of the gas in solution. This change acts as a very mild stimulus; the organism merely stops and swings its anterior end gently toward the aboral side, "trying" a new direction. If the water now received is still without the carbon dioxide, the Paramecium swings its anterior end still farther, at the same time continuing to revolve on the long axis, which changes the direction of swinging. As soon as the water it receives contains carbon dioxide, it swims ahead, changing its course only when it again receives water without the gas in solution. The reaction under such conditions is a very delicate one, keeping the animal in close touch with the environmental conditions. The behavior does not impress one as a definite "reflex"; the Paramecium is seen merely to change its course a little after trying several slightly differing directions.

The behavior of Paramecium in swinging its anterior end about in a circle is essentially similar to the "feeling about," "searching," or "trial" of a higher organism. We know, of course, no more of subjective qualities in any organism outside the self than we do in Paramecium. If we describe the "feeling about" or "searching" of any higher animal in a purely objective way, we shall find that the description takes essentially the same form as for Paramecium. Under certain conditions the organism performs certain movements, which subject it to certain environmental changes. As long as the conditions remain of essentially the same character, it continues these movements. As soon as these movements induce conditions differing in a certain way, the movements stop. This description fits equally well the movements of a cat trying to escape from a cage (see THORNDIKE, 1898), of a dog searching for a bone, and of Paramecium reacting to carbon dioxide. In its method the behavior seems fundamentally similar throughout.

The behavior of Paramecia under such "repellent" stimuli follows then, perhaps, as effective a general formula as could be devised. When stimulated it performs movements which take it away from the source of stimulus, and direct it successively in many ways, until the stimulation ceases. Reaction of this character is essentially that of "trial and error" as we find it in higher animals. From this standpoint the behavior may be summed up as follows: When there is "error" the organism "tries" various directions or methods of action till one is found in which the "error" ceases. These relations have been brought out by the author for lower organisms in general in a previous paper (JENNINGS, 1904, *b*).

We must ask here the question whether the reaction method of Paramecium above described should or should not be called a *reflex*—a term which I have applied to it in previous papers. The question which interests us here is not whether an act performed without the intervention of a nervous system may properly be called a reflex; it may be strongly doubted whether the anatomical structure of organisms forms a proper basis for classification of types of behavior. But does the reaction method described fall in the concept of a reflex, judged merely as a type of behavior?

A reflex is commonly described as a fixed and invariable method of response to a definite stimulus. It is rare, however, that such definitions are found to be rigidly maintainable for given instances; the excellent discussion of HOBHOUSE (1901) shows how the reflex concept must be modified and its limits effaced, till it flows easily into other behavior types, before it can be applied to the phenomena actually found in animal behavior. Such a process of softening down is certainly necessary before we can make the reflex concept apply to the avoiding reaction of Paramecium. This reaction is composed of three factors, which may vary more or less independently of one another, in such a way that an absolutely unlimited number of combinations may result, all fitting the common reaction type. The possible variations may be expressed as follows: If the Paramecium be taken as a center about which a sphere is described, with a radius several times the length of the animal, then as a result of the avoiding reaction the Paramecium may traverse the peripheral surface of this sphere at *any point*, moving at the time either backward or forward. In other words, the reaction may carry it in any one of the unlimited number of directions leading from its position as a center. While the direction of turning is absolutely defined by the structure of the animal, yet the combination of this turning with the revolution on the long axis permits the animal to reach any conceivable position with relation to the enviroment. In other words, Paramecium, in spite of its curious limitations as to method of movement, is as free to vary its relations to the environment in response to a stimulus as an organism of its form and structure *could* conceivably be.

Again, the reaction at times keeps the organism in the closest possible touch with the environment, continuing as long as certain conditions continue, increasing in effectiveness as the conditions causing it increase in intensity, and ceasing when the conditions causing it cease, maintaining the organism throughout in certain relations with the source of stimulation. Altogether, I believe that the following admission must be made. If we consider the reaction of Paramecium a reflex, it is because we are convinced beforehand that such an organism *can* show only reflexes. If the actions of Paramecium did belong to some higher type of behavior, there could be little objective evidence of this, beyond what we already have.

In Paramecium the reaction has not been shown to be modifiable by previous experience, so that from this criterion the behavior retains the characteristics of a reflex. But in a close relative, Stentor, such modification by experience has been demonstrated (JENNINGS, 1902), so that it may be presumed that technical difficulties alone have thus far prevented our observing it in Paramecium.

The effectiveness of the method of reacting by "trial and error" that we have described above for Paramecium depends upon the power of discrimination of the reacting organism. By "discrimination" of stimuli we mean, in an objective study of behavior, that the organism reacts differently to the different stimuli in question. In this sense Paramecium discriminates acids from alkalies and salts, and these again from sugar. Furthermore, it discriminates different strengths of solution, reacting differently, for example, with relation to weak and to strong acids. On the other hand, it does not effectively discriminate different acid substances, save in so far as one is stronger than another. Thus it swims into weak carbonic acid, which is harmless, and likewise into weak sulphuric acid and copper sulphate, which kill it. It does not markedly discriminate a ten per cent sugar solution from water, hence it swims readily into sucl a sugar solution and is killed by the osmotic action.[1] Thus in re-

[1] Details as to the facts cited are given in my previous papers on Paramecium here we are concerned only with the interpretation of these facts.

gard to powerful acid substances and to sugar solution it makes what we would call in ourselves a "mistake." In higher animals we recognize that the power of accurate discrimination is one of the "higher" powers, becoming more secure as development progresses. We cannot, therefore, be surprised that it should not be perfect in so low an organism, nor that such organisms, through lack of discrimination of injurious and non-injurious agents, often react in a way that leads to their destruction. Any organism reacting by the method of "trial and error" is subject to the possibility of destruction in some of the "trials."

This method of "trial and error," based on the "avoiding reaction" above described, plays a large part in the behavior of Paramecium. Through it are produced the "negative" reactions to agents of all sorts, as well as the collections formed in certain chemicals, in regions of optimum temperature, and the like. On the other hand, there exist certain reactions in which the final relation to the environment is brought about in a more direct way—notably "positive thigmotaxis" and certain features of the reaction to the electric current. These reactions will be taken up later.

II. Nature of Stimulation.

Just what is the nature of the stimulation which produces this reaction by "trial and error" in Paramecium? An examination of the facts shows that as a general rule the effective stimuli consist of some *change* in the conditions, or, what is the same thing to the organism, of some change in the relation of the organism to the conditions. Change is the essential feature in producing the chief reactions of Paramecium.

This statement requires of course some qualification in detail. A change may be nearly instantaneous, while the consequent reaction of the animal of course requires time, and must, therefore, continue for a certain period after the change has been completed. If the animal is suddenly subjected to a one-fourth per cent solution of common salt, it continues to react for a short time after the instant of the change, though if the conditions now remain constant, it soon ceases to react. The length of time the reaction may continue after the change is completed varies with different agents, becoming longer as the agent is more powerful. The phenomena may be expressed in the following somewhat indefinite way: the animal reacts to the change as long as *its effect as a change* continues. In the limiting case of a stimulus so powerful as to be destructive, the reaction may continue for a considerable period, till death intervenes. In such cases we have then a continued reaction to a condition that remains constant for some time. But with destructive agents, the action of the agent seems progressive, so that there is really a continual change in the relation of the organism to the agent, till the progressive series of changes ends in death. Whatever the explanation in these rare cases of destructive conditions, change is elsewhere the fundamental feature of the stimuli producing the chief reactions in *Paramecium.* This is the result which stands out clearly from all my work on stimulation in Paramecium.

A change from one condition to another produces a reaction when neither the preceding nor the following condition, acting continuously, produces any such effect. Thus, Paramecia may live and behave normally in water at 20° or at 30°, yet a change from one to the other, or a very much less marked change, produces the avoiding reaction. Paramecia may live without reaction in tap water or in water containing one-tenth per cent sodium chloride, but the change from the former to the latter produces the avoiding reaction. This relation could be illustrated by innumerable cases, taken from my earlier papers on Paramecium.

In all cases of course a *certain amount* of change is required in order to produce reaction; in other words, there is a certain necessary threshold of stimulation. Since the change itself is the real cause of the reaction, it is probable that the amount of change necessary will bear some definite relation to the intensity of action of the agent in question before the change. In other words, it is probable that the reactions are subject to WEBER's law, as they are known to be in bacteria (PFEFFER, 1904, p. 625). The corresponding quantitative relations have not been worked out for Paramecium.

The fact that change is the essential feature in causing reaction is of course correlated with the fact that organisms become acclimatized, so far as reaction is concerned, to a certain strength of stimulus. To say that the organism becomes thus acclimatized is indeed little more than to say that it reacts only to changes.

The change which produces stimulation may be a direct alteration in the environment, as when a chemical is brought near a specimen, or when it is touched at the anterior end with a glass rod, or when the temperature is raised or lowered from without. But under natural conditions the change is more usually produced by the movements of the animal itself. In its rapid swimming the animal passes from one region to another, the conditions in one region changing to those in the next, and thus causing reaction. Further, as we have seen, the spiral course gives opportunity for frequent changes to act upon the organism; the anterior end is pointed successively in many directions, receiving "samples" of water from each direction. The greater the swerving in the spiral course the greater the opportunity for frequent changes to affect the animal. The avoiding reaction, with its swerving in many directions, may indeed be looked upon as a method of subjecting the organism successively to many changes.

It is, however, not mere change *per se* that causes the reaction, but change of a certain kind or in a certain direction. Of two opposite changes, one usually produces the reaction, while the other does not. Paramecium reacts when it passes out of a weak acid, not when it passes in; it reacts when it passes into an alkali, not when it passes out. A Paramecium at 28° reacts at passing to a higher temperature, not at passing to a lower one; a Paramecium at 20° shows the opposite relations. The direction of change which produces the avoiding reaction may be briefly characterized as that leading *away from the optimum*, while change leading toward the optimum produces none. It is thus clear that in most cases the actual determining factor in the reactions is the direction of movement of the animal, not the mere orientation, as has sometimes been held. The significance of these relations in connection with the theory of general "pain reactions" I have considered elsewhere (JENNINGS, 1904, *b*). Here we may point out, as a relation of some interest, that in Paramecium it is an injurious or negative stimulus that primarily induces motor reactions. This is not at all in agreement with the theory sometimes set forth, that the effect of such stimuli is to cause a cessation of activity.

In no case, so far as I am aware, has it been shown that the reaction in Paramecium is due to the difference in intensity of a graduated stimulus on the two sides or ends of the animal, as is assumed by the orthodox tropism theory. In most cases it has been demonstrated that the determining features of the reaction are not of this character.

I have above illustrated the fact that in reactions to chemicals and in temperature reactions, it is a change that causes the response; details are given in my previous papers. In the reactions to changes in osmotic pressure, a very marked change to a higher pressure is required to produce reaction; the opposite change, even to distilled water, is without effect. In the reaction to mechanical stimulation, sudden contact of the anterior end with a solid produces the reaction, though continuous contact is of no effect. Paramecium is not, so far as known, sensitive to light. But in other infusoria the writer has recently shown (JENNINGS, 1904) that it is the change in light intensity, at the sensitive anterior end, that induces reaction. The reaction occurs when the change is due to an actual alteration in the source of light, or when it is due to a movement of the organism. Orientation is produced through the fact that in the spiral course the anterior end of an unoriented organism is repeatedly subjected to changes in illumination. To these changes it reacts, by the method of "trial and error," above described, till it comes into a position where such changes no longer occur; such a position is found only when the animal is oriented. The reactions to light are particularly instructive for the part played by the spiral course, with its swerving from side to side, in causing changes in the intensity of the stimulus, and hence in determining the reactions. While in Paramecium there is no reaction to light, certain other reactions are produced in the manner just set forth. These reactions we shall analyse in the next section of this paper.

III. Reactions to Certain Stimuli, with Special Reference to the Part Played by the "Action System."

A. Reactions Produced through the "Avoiding Reaction."

1. Reactions to Water Currents; Rheotaxis.—Under rheotaxis is usually understood the orientation of the organism in line with a water current, and movement with or against the current. I have come across a reference to such a reaction to water currents in Paramecium only in two papers dealing primarily with reactions to the electric current—namely the papers of Dale (1901) and Statkewitsch (1903, *a*). Dale says: "It is sufficient to watch the behavior of Paramecium in water contained in a tall jar in which convection currents have been produced, in order to be convinced of its tendency to swim with a stream of water" (Dale, *l. c.*, p. 354). He attempts to use this tendency to swim with the current in explaining the movement to the cathode in the reaction to electricity, but has no farther observations on rheotaxis itself. Statkewitsch (1903, *a*, pp. 102-104) likewise observed that Paramecia swim with currents caused by the absorption of water by porous substances, but showed that this has nothing to do with the movement to the cathode, since the latter occurs in the same way, whatever the direction of the water currents.

I have carefully examined the reaction of Paramecium to water currents under various conditions. The reaction varies with different individuals, and it is difficult to arrange the conditions in such a way as to make the reaction a very precise one. But in all my experiments a large majority of the animals showed the opposite relation to the direction of the current from that mentioned by Dale and Statkewitsch. They turned the anterior end up stream and moved against the current. There were usually a number of individuals, however, that showed the opposite relation, and I can well believe that in some cultures the majority may conduct themselves in this manner, and that this was the case with the Paramecia observed by the authors named. But certainly as a rule most of the organisms swim against the current, not with it. The phenomena may best be observed by placing Paramecia in a tube which is narrowed in the middle and open at both ends. Only the central part of the tube is filled with water, the two ends containing only air. Over the two ends are fitted rubber caps, such as are used for medicine droppers (Fig. 10). By compressing

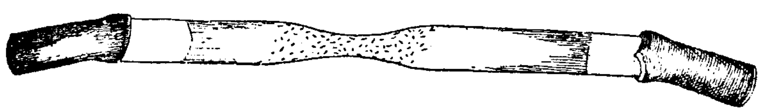


Fig. 10. Tube for study of the reaction to water currents. See text.

one of these caps the water is forced through the narrow part of the tube with any desired velocity, and is always under complete control. With a certain velocity of current most of the animals are seen to become oriented and to swim against the current. The tube must not be too narrow, since in this case many of the individuals strike against the side of the tube, and then no longer respond well to the current, the contact reaction interfering with "rheotaxis" as well as with many other reactions. In any case, many individuals show no orientation or are oriented in the opposite direction, yet the phenomenon is sufficiently general to show clearly that we have here a real reaction of the organism.

How is this reaction to water currents brought about? If we direct a fine current of water for a moment upon a Paramecium that is swimming quietly, we find that it gives the "avoiding reaction" in a not very pronounced form. That is, it stops, or begins to progress more slowly, and swerves more strongly toward the aboral side, appearing thus to swing from side to side, the anterior end really describing circles of considerable size, as in Fig. 8, *b*. The effect of this current on the animal is of course to change in some way the resistance it meets in swimming, or the pressure of the water upon it. Such an environmental change produces, then, like many other changes, the avoiding reaction, with its "trial" of different directions. The same result is produced by setting the water in motion in other ways, as by causing the vessel containing the animals to vibrate back and forth.

If now we produce a more extensive current, and allow it to continue, as in the experiment shown in Fig. 10, we find the same result produced. The animals at first pause, then swing the anterior end about in a circle, thus "trying" many different directions. They then swim forward in one of these directions. The reaction is then repeated, and this occurs as a rule several times, until they have come into a position with anterior end directed up the stream. The reaction then ceases; the animals swim forward in the usual spiral manner. They have become oriented by the method of "trial and error," the "trials" continuing till the position of orientation was reached.

We have seen that the original cause of the reaction was a change in the environment—the movement of the water—causing a change in the resistance or pressure the Paramecium meets. But why does the reaction continue till orientation is reached, then cease? Consideration of the relation of the current to the spiral course followed by the animal shows that this is exactly what we should expect from all that we know of the behavior of the animal and the cause of the present reaction. Consider a specimen that is swimming transversely or obliquely to the current, as in Fig. 11. In its spiral course it swings the anterior end first against the current, to the point *a*, then with the current to the point *b*. In the swing toward *a* the movement is resisted by the current; in the swing toward *b* it is aided by the current.[1] Its relation to the current thus changes during each turn of the spiral; in one phase the movement is "easier" from being aided, in the next more difficult, from be-

[1] The upward and downward movement of the swing may be neglected for our present purpose.

ing resisted. As we know, exactly such changes act as stimuli, and the animal reacts, as we have seen, in the usual way. It swings its anterior end about in a circle, so that the body axis occupies successively many positions, and continues or repeats this reaction as long as it is subjected to the changes mentioned But when it comes into a position such that its relation to the current remains constant, it no longer reacts, for to constant conditions, unless destructive, Paramecium soon becomes acclimatized. Such a position is found only when the axis of the spiral path coincides with the direction of the cur-

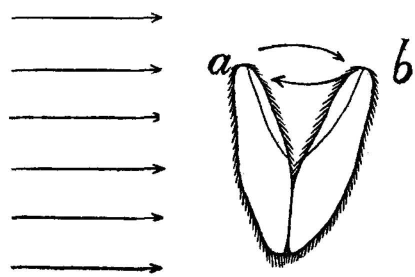


Fig. 11. Diagram to illustrate the cause of the reaction to currents of water. The straight arrows indicate the direction of the current. The swinging of the unoriented Paramecium in its spiral course from the position *b* to *a* is resisted by the current, while the movement from *a* to *b* is assisted. (The same diagram illustrates the conditions in the reaction of gravity, if the straight arrows represent the direction of gravity).

rent. In this position the animal of course still swims in a spiral, the anterior end describing circles about the axis of the spiral. But in every phase of the path the axis of the body forms the same angle with the axis of the spiral, and hence with the direction of the water current, so that its relation to the current remains constant, and there is no farther cause for reaction. Orientation has been attained through the "method of trial and error."

But why do the majority of the animals become oriented with anterior ends against the current? Our description thus far accounts for the position of the body axis, but not for the more usual direction of the anterior end. We know that as a rule when Paramecium is subjected to changes of opposite character, such as may be called plus and minus, it reacts to one of these changes, but not to the opposite one (above, p. 466). In its spiral course the unoriented organism is subjected, under the action of a water current, to plus and minus changes in resistance. As a rule it is the minus change that induces the reaction, while the plus does not. This is perhaps intelligible, from the fact that *Paramecium* normally receives some resistance in its swinging toward the aboral side, so that when the pressure of the current comes from the oral side, *driving* the animal toward the aboral side, the change from the usual condition is a very marked one. Therefore, whenever the Paramecium swings from *a* to *b*, Fig. 11, a reaction is induced, causing strong swerving toward the aboral side. This is effective in the next phase of the spiral, causing the animal to swing far in the direction *b*—*a* (since the aboral side is now toward *a*); thus the animal becomes more nearly oriented. Since this movement from *b* to *a* involves only a plus change, it causes no reaction; the ordinary spiral swimming is resumed, so that in the next phase the animal swerves only a short distance toward *b*. But this involves the minus change, inducing reaction again; so in the next phase of the spiral the animal swings still farther in the direction *b*—*a*, and is now nearly oriented. This process continues, the animal swinging far in the direction *b*—*a* and only slightly in the direction *a*—*b*, until the axis of its path coincides with the direction of the current; then the plus and minus changes cease, and there is no cause for further reaction. The general principle on which the orientation depends is this: whenever moving in a certain direction causes increased swerving, this increased swerving must show itself chiefly in the succeeding phase of the spiral, thus causing the animal to swerve farther than usual in the opposite direction.

In cases where it is the plus change which induces the reaction, the organism must, in the way just described, finally come into orientation with anterior end directed down stream. If both plus and minus changes induce reaction, then the animals become oriented in either direction, the essential point being only that the axis of the spiral coincides with the current direction. This condition is apparently found in a number of specimens in any given culture.

2. *Reaction to Gravity; Geotaxis.*—The general features of the reaction of Paramecium to gravity have been described by JENSEN (1893). JENSEN further proposed a theory to account for the reactions; but at the time his work was done, the "action system"—the general complex of structural relations, movements and reactions, by which most of the behavior is brought about—was not known. JENSEN'S theory could therefore take no account of this system, and I believe that in view of the known facts and of those which I shall bring forth in the present account, it can be no longer maintained. My present purpose is to describe the method by which the reaction to gravity occurs, and to show the relation of this to other reactions and to the "action system" of Paramecium.

The gross facts are as follows: When Paramecia are placed in a vertical tube, fairly free from other sources of stimuli, they swim upward, to the upper end of the tube. Control experiments show that gravity is the real directive influence. But usually some individuals in any culture show the opposite effect, swimming downward, while others do not become oriented at all. In certain cultures the majority of the individuals swim downward, or are indifferent. The reaction to gravity is easily overcome or modified by the action of other agents (SOSNOWSKI, 1899, MOORE, 1903).

JENSEN'S theory to account for the reaction to gravity was as follows: The cause of the reaction is the difference in pressure upon the two sides or ends of the animal; the lower end or side is in a region of greater pressure than the upper. The greater pressure acts as a stimulus to cause the cilia on the lower side of the body to beat more strongly. As a result, the anterior end must be turned in the opposite direction (that is, upward), until it points in the direction of least pressure. The two sides are now similarly affected by the pressure, so that there is no cause for further turning. JENSEN'S theory is thus an application of the typical tropism schema to the reaction to gravity, the difference in pressure on two sides or ends of the animal being the determining factor.

Does the unoriented animal react as JENSEN supposed, by turning *directly* toward the side of least pressure? This question is not to be answered from *a priori* considerations; only actual observations of the movements of the animal in becoming oriented can give us a reliable answer. With the BRAUS-DRÜNER stereoscopic binocular such observations can be made without great difficulty. The best plan of experimentation that I have found for giving many opportunities to observe the animals at the time orientation takes place is as follows. The animals are placed in a long U-tube (Fig. 12). The two open ends are covered with rubber caps, and the tube is at first placed with free ends upward. The Paramecia collect at the free ends. Now the tube is inverted; the clouds of Paramecia at the two ends move upward, toward the cross piece of the U which is now above (Fig. 12). Arriving here, most of them do not cease swimming, but move across the cross piece of the ∩ and even start obliquely downward. Here the reaction occurs; they turn around and swim upward again. At this point (x, Fig. 12) one has at any instant a large number of specimens in the process of becoming oriented with anterior ends upward. The binocular is now brought to bear upon this region, and the method of reaction is evident. The spiral course becomes wide, the animals swerve strongly toward the aboral side, so that the anterior end is moving about in a circle; the Paramecia appear to oscillate irregularly back and forth. In other words, they are reacting in the usual "trial and error" way—"trying" successively many different positions. This is continued till they have gradually worked around into a posi-

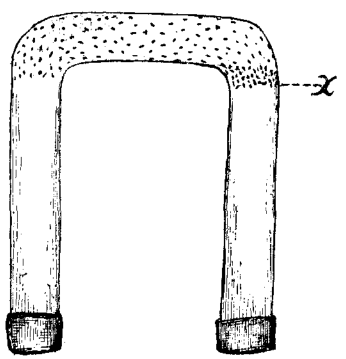


Fig. 12. Tube for study of the reaction to graviy. x, place where the change of direction of movement occurs.

tion with anterior end upward. The strong swerving then ceases; the animals swim upward in the usual spiral path.

Thus, observation shows that the reaction is not brought about in accordance with the tropism schema, as was supposed by JENSEN. The animal does not turn *directly* into orientation, as that theory requires, but the turning is throughout toward the aboral side, and the orientation is attained by the "method of trial and error."

What is the cause of the reaction? JENSEN's theory that it is the difference in pressure on the two sides of the animal loses whatever plausibility it may have had, when the nature of the reaction itself is known. As we have seen, the turning in the reaction is not due to differential action on upper and lower sides, but to swerving toward a side that is structurally defined —the aboral side—whatever the position of the latter with reference to gravity. Thus the difference in pressure certainly does not act in the direct way supposed by JENSEN.

Furthermore, as we have seen above (p. 467), in no other reactions of Paramecium is the difference in intensity of a graduated stimulus on the two sides or ends of the animal known to be the determining factor in the reaction.

On many other grounds it is highly improbable that this difference in pressure is the effective agent. The difference in pressure between the two sides is so excessively minute in proportion to the total pressure acting on the animal, that it is almost inconceivable that this difference should be perceived. The infusorians are of course under atmospheric pressure; this is equal to the pressure of a little more than 10,000 millimeters of water. As JENSEN shows, the difference in pressure between the two sides of certain of the infusoria which show the reaction to gravity is only that of 0.01 mm. of water. Hence the difference in pressure between the two sides of the organism is only $\frac{1}{1,000,000}$ of the pressure acting everywhere on the surface. Furthermore, JENSEN showed that the reaction still occurs when the atmospheric pressure is more than doubled; the effective difference in pressure would then be less than $\frac{1}{2,000,000}$ the general pressure. When we consider the large threshold differential required for the perception of differences in pressure in known cases—for example, about $\frac{1}{10}$ in man—we can hardly believe that a differential of $\frac{1}{2,000,000}$ is perceptible by infusoria. JENSEN did not calculate this threshold differential, but said in general that the great sensitiveness here shown agreed well with the great sensitiveness to chemical, thermal and other stimuli. But the great sensitiveness assumed to exist for chemcals and heat was based on the theory that the reaction was due to the difference in intensity of the agent in question on the two sides or ends of the animals. This I have shown in previous papers not to be the cause of the reactions in question; they are due to changes in intensity brought about by the movements of the Paramecia from one region to another. The degree of sensitiveness required is therefore much less than would be necessary on JENSEN's theory, and does not approach remotely such a minuteness of threshold differential as JENSEN's view requires for the reaction to pressure.

Further, JENSEN assumes that the reaction is brought about when there is a difference of a similar order of magnitude to that above mentioned, between the anterior and posterior ends of Paramecium. Now, we know that the anterior end is much more sensitive than the posterior; this has been shown precisely for mechanical pressure. A Paramecium touched with a glass hair at the anterior end reacts violently, while the same touch or a stronger one on the posterior half of the body produces no reaction. Thus it may be considered practically certain than an increase of pressure on the posterior end such as JENSEN's theory assumes to be the effective agent would cause no reaction whatever; any reaction to the existing pressure which might occur would be due to that at the anterior end.

JENSEN makes one attempt to differentiate experimentally between the direction of gravity and the direction of decrease of pressure, and to show that the Paramecia follow the latter instead of the former. He placed Paramecia in a tube inclined to the perpendicular, and observed that, while often the Paramecia first swim vertically upward against the inclined wall, then turn away, and again swim vertically up till they strike it, etc., in other cases they swim obliquely upward along the wall. From this latter fact he concluded that they swim in the direction of decrease of pressure, instead of in the direction of action of gravity. It is difficult to imagine from what data or by what process of reasoning this conclusion was reached. The decrease in pressure of course takes place in an inclined tube in the same direction as in a perpendicular one, and coincides in both cases with the direction of gravity. JENSEN's experiment was not of the least value in differentiating the two directions; indeed, so long as the pressure is due to gravity the two directions in question must coincide. If, therefore, the observations mentioned speak in the least against the view that the organisms tends to move in the lines of the direction of gravity (which, as DAVENPORT, 1897, p. 123, has shown, they do not), then they speak equally against the view that the movement is in the direction of decrease of pressure.

What then is the effective stimulus in the reaction to gravity? In the other reactions of Paramecium we have found that the effective stimulus is due to some change in the conditions, or, what amounts to the same thing, in the relation of the organism to the conditions. In the reactions to gravity exactly the conditions are present for the production of such changes, and the reaction is of precisely the character that might be expected from such changes as occur. The conditions are quite parallel to those found in the reactions to water currents. The changes in question are brought about through the fact that Paramecium swims in a spiral, swinging successively in many directions. In an unoriented specimen the upward phase of the swerving is resisted by gravity, making the motion more difficult; the downward phase is assisted, making the motion easier. The effect of these repeated changes in resistance or the ease of swimming is similar to the effect of repeated streams of water directed on a quiet animal. The result of such environmental changes is, as we know, to produce the "avoiding reaction," and this is what we see in the reaction to gravity.

The animal swerves farther toward the aboral side, and this, with the revolution on the long axis, causes it to occupy successively many different positions. When as a result of these repeated "trials" it comes into such a position that the changes causing the reaction no longer occur, the reaction ceases. Such a position is found only when the axis of the spiral course coincides with the direction of gravity. It this position the body of the animal, maintaining a constant angle with the axis of the spiral, maintains also a constant angle with the direction of gravity; changes in the relation of its swerving to the direction of gravity, therefore, no longer occur. To constant conditions Paramecium quickly becomes acclimated, so now reaction no longer takes place.

Whether the anterior end is directed upward or downward depends upon whether the plus or minus change in resistance induces the reaction. If the minus change—the change from the greater resistance of the upward swing to the less resistance of the downward swing—is the effective stimulus, then the animal will become oriented with the anterior end upward, for every time it swerves downward the reaction is induced, causing it to "try" many new positions, while when it swerves upward no reaction is induced, and it retains the position reached. This is apparently the usual condition of affairs. On the other hand, if it is the plus change—the change from less resistance to greater resistance—that causes the reaction, the animal will become oriented with anterior end downward. To both cases we could apply the detailed analysis given in the account of the reactions to water currents, above.

Thus as to the nature of the effective stimulus in gravitation, our analysis leads to results agreeing with the conclusions of DAVENPORT (1897). This author holds that the reaction to gravity is due to the fact that the organism "experiences greater resistance (friction + weight) in going upward even to the slightest extent than in going downward (friction – weight)" (*l. c.*, p. 122). What I have set forth above is the way in which this difference in resistance acts in orienting the organism.

The stimulus induced by the variations in the resistance due to gravity is of course a very light one, and observation shows that it is easily modified or masked by other stimuli. Chemical, mechanical and electrical stimuli overcome the reaction to gravity, hence the necessity of having the Paramecia in nearly pure water and in a clean tube if the reactions to gravity are to be seen clearly. If these conditions are not fulfilled, the Paramecia may collect in any part of the tube, through reactions to chemical stimuli, and to contact with solids. It may perhaps be said in general that the reaction to gravity shows itself only when the animal is not subjected to other effective stimuli.

JENSEN (*l. c.*) showed that when placed on the centrifuge Paramecium reacts with regard to the direction of the centrifugal force in the same way as to gı ıvity. The animals orient themselves and swim in the direction opposite to that in which the centrifugal force tends to carry them. In these experiments the conditions are of course present for the same sort of reactions that we find under the action of water currents and of gravity. In one phase of the spiral course the movement of the unoriented animal is assisted by the centrifugal force, in another resisted; the changes thus produced lead to reaction and orientation in the way already described.

Summary.—The reactions to water currents ("rheotaxis"), to gravity ("geotaxis") and to centrifugal force are in Paramecium essentially the same, and due to similar conditions; they may be summed up as follows: The unoriented individual is subjected, owing to its spiral course, to repeated changes of pressure and of the resistance to its movements; in one phase of the spiral the motion is assisted, in another resisted. These changes induce the usual reaction; through the consequent increased swerving toward the aboral side, with the revolution on the long axis, the animal occupies successively many different positions, till one is found in which these changes no longer occur, when there is no further cause for reaction. Such a position, in which the relation of the movement to the resistance remains constant, is found only in orientation with the axis of the spiral path coincident with the direction of the force in question. Under the action of the three agents named, as a rule it is the minus change that induces reaction; hence the animal directs itself against the operation of the forces at work.

B. Behavior during Conjugation.

The behavior during conjugation is not brought about through the avoiding reaction, yet the conditions determining it seem of the same character as those determing behavior produced through the reaction named, so that it should be considered in relation with the latter. It is not my purpose to give here a full account of the behavior during conjugation, but merely to point out the part played in this behavior by the usual "action system" of Paramecium, above set forth.

Paramecia during a period of conjugation are perhaps in a "physiological state" differing from the usual state, so that they react differently from usual, uniting in pairs. Yet it is remarkable how much of their behavior at such times is due to precisely the same features that are always present, taken in connection with a physical modification of the body substance. I have not thus far been able to observe at such times any method of reaction differing from the usual ones. The factors bringing together two individuals seem to be chiefly the following.

1. At these periods of conjugation the oral surface of Paramecium is adhesive, through some physical modification of the protoplasm. As a result of this modification other Paramecia coming in contact with the oral surface become attached. The position of the two Paramecia is of no consequence, nor the way in which the contact is brought about, provided only that one animal comes in contact with some part of the oral surface of another. As a result of this fact, the individuals in a crowded culture become stuck together in all sorts of bizarre ways, and evidently without any previous definite reaction on the part of the individuals concerned. Two specimens will be seen feeding on the bacterial zoogloea and moving in opposite directions over its surface; one crosses by chance the path of the other,

and in passing its posterior end drags across the oral surface of the latter. Thereupon they stick together, and a struggle ensues, each individual trying to pursue its forward course and not succeeding, till one finally drags the other one backward (Fig. 13, at the upper left hand corner). The second speci-

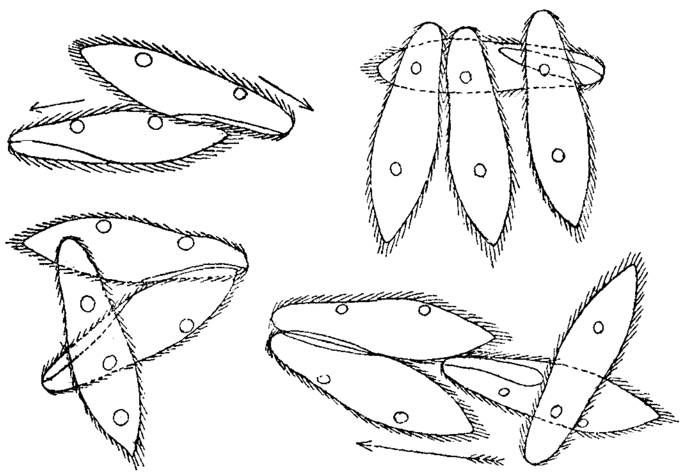


Fig. 13. Irregular adhesion of individuals, observed in cultures of Paramecia in which conjugation was taking place. These groups move about irregularly, remaining attached, in spite of the struggles of the individuals.

men may be dragged about through the water or over obstacles of all sorts, till finally the adhesion gives way and they separate. Specimens thus become adherent in every possible way, provided merely that some part of the oral surface of one of the individuals enters into the adhesion. Many such cases are clearly not early stages of any ordered conjugation, and they often separate after one individual has been dragged about for some time much against his struggles.

Again, often more than two individuals thus adhere; groups of three, four or five are seen, adhering in all sorts of irregular ways, and apparently struggling to free themselves. A number of such cases of irregular adhesion are shown in Fig. 13, from a culture in which conjugation was taking place freely. It is evident that such groups as are shown in this figure cannot be interpreted as due to any will or desire of the animals, and this becomes still more evident when one observes the accidental manner in which they are formed, the way in which the individuals are dragged about against their efforts, and their struggles to free themselves—at times resulting successfully. I have even seen moribund individuals, and individuals undergoing fission thus attached irregularly to the oral surface of other specimens.

2. A second important factor in bringing about conjugation is found in the usual ciliary movements of the animals and in the currents produced by these movements. As we have seen in the foregoing pages, there is a strong current passing backward along the oral side of Paramecium, so that there is a tendency for all sorts of objects suspended in the water to be carried to the oral groove. This tendency is of course operative on other Paramecia in the neighborhood as well as upon lifeless objects. In the case of two Paramecia close together this tendency is of course reciprocal; each tends to draw the other to its own oral groove. Thus if two Paramecia are swimming along close together, there is a strong tendency, through their usual movements, for them to come together with oral surfaces in contact. Under ordinary conditions this is often seen, but does not lead to conjugation, because the oral surfaces are not adhesive. But when the oral surfaces are adhesive, as we know them to be at periods of conjugation, then the animals stick together. The remainder of the process falls outside the field of "behavior." The relations just pointed out show why in a conjugating culture so many more individuals are found in contact by their oral surfaces than in the irregular ways shown in Fig. 13; the irregular adhesions occur only through unusual accidents.

Thus when the oral surfaces of Paramecia become adhesive, the usual movements lead to attachment by these surfaces, such as we find in conjugation. All the phenomena seem to be intelligible on the basis of these factors alone, though it may be possible that there are certain modifications of the usual behavior in periods of conjugation.

C. Responses to Stimuli not brought about through the "Avoiding Reaction."

The behavior which we have thus far considered is brought about chiefly through the avoiding reaction; the general method is that of "trial and error." Though the most important features of the behavior of Paramecium are produced in this way, there are certain other reactions in which the method of "trial and error" does not play the chief, or at least the only part; in these the relation of the direction of movement to the source of stimulus is, in certain features at least, more direct. These reactions we shall take up next, though only with the reaction to the electric current shall we deal here in detail. A list of these reactions was given on page 450. Local contraction of the body as a response to stimulation has been dealt with sufficiently above (page 457), and in the paper of STATKEWITSCH (1903). MASSART (1901) gives a thorough study of the discharge of trichocysts as a response to various stimuli, while STATKEWITSCH (1903) gives details as to the production of this reaction by induction shocks. The reaction to contact by coming to rest has been described in detail in a previous paper by the present author (JENNINGS, 1897), and in a more recent paper by PÜTTER (1900). These matters, then, we need not consider further here.

1. Forward Movement as a Response to Stimulation.

In a previous paper (JENNINGS, 1900) I showed that many Infusoria respond to a stimulus which affects only some other part of the body than the anterior end, by moving forward. I did not succeed in showing this for Paramecium, owing to difficulties of technique in working with so small an animal. In the meantime ROESLE (1902) has observed that when a specimen is stimulated at about the middle of the body by collision with another specimen, it responds by moving forward. I have recently been able to confirm this result experimentally. A small glass rod may be drawn out so fine that the tip is hardly visible under a magnification such that the differentiations in the body of Paramecium are conspicuous and cilia are plainly seen. With the tip of such a rod it is possible to stimulate Paramecium locally, without jarring the animal as a whole. It is then found that a mechanical stimulus back of about the anterior one-third causes a movement forward. It is notable that at the anterior end the lightest touch produces a strong avoiding reaction, whereas an equally light stimulus elsewhere produces no reaction whatever. I was not able to confirm with the rod ROESLE'S view that the region about the mouth is especially sensitive, but this seems highly probable on general principles, as well as in view of ROESLE'S results; the technical difficulties of reaching precisely the region about the mouth with the rod are very considerable.

A very powerful stimulus even on the posterior part of the body induces the avoiding reaction. But this may be due to the mechanical transmission of the shock to the anterior end.

Apparently a very light, unlocalized stimulus likewise produces forward swimming, as I noted in a previous paper (1899, *a*, p. 104). This is true of a slight jarring of the vessel containing resting individuals. ROESLE (1902) states that an induction shock sometimes has the same effect, though as STATKEWITSCH (1903) shows, this stimulus usually produces the avoiding reaction.

2. Reaction to Electricity.

Part Played by the Action System.—The reaction to the electric current presents certain features not found in the reactions to other stimuli. According to the account of this reaction in the foundational paper of LUDLOFF (1895), the cilia on the cathode half of the body of Paramecium strike forward, those on the anode half backward. The inevitable result is that any specimen not in line with the current will be turned directly around, until the anterior end is toward the cathode. The reaction seems, according to this account, to be much simpler and more schematic in character than the reactions to other stimuli, the characteristic "action system" seeming to play no differential part. But the recent papers of PEARL (1900), PÜTTER (1900) and WALLENGREN (1902, 1903) show that the reaction to the electric current is in many ciliates more complex and less schematic than had been supposed. As first brought out in the paper of PEARL (1900), there seems to be an attempt by the animal to react in the same way to the electric current as to other stimuli (PEARL'S "reflex factor"), but this is modified or masked by certain effects peculiar to the current (PEARL'S "forced movements"). Cilia of different parts of the body under the influence of the current thus differ in their method of action and force of stroke. WALLENGREN (*l. c.*) shows that whether anodic, kathodic or transverse electrotaxis is produced depends upon the peculiar action of the cilia of certain regions of the body. Thus the "action system" of the organisms does play a part in determining the reaction to the electric current, though not so exclusive a part as in the reactions to the stimuli met under natural conditions of life. The corresponding relations have never been brought out for Paramecium;[1] this I shall try to do in the following.

PEARL (1900) confirmed LUDLOFF'S schematic account of Paramecium, though at the same time he showed, as noted above, that in certain other ciliates the "action system" (his "reflex factor") does play an important part in determining the reaction to the electric current. Though the results of LUDLOFF and PEARL on Paramecium are correct so far as they go, they are incomplete. The "action system" does in reality play a much larger part in determining the reactions to the electric current than would appear from the accounts of the two authors named. This is most clearly seen in the fact that when the anterior end is directed toward the anode at the moment the current is made (Fig. 14, *b*) the animal always reaches the position of orientation with the anterior end to the cathode by turning toward the aboral side, as in the reactions to other stimuli. Under these conditions the cilia of both the oral and aboral sides beat backward in the anterior half of the body (Fig. 14, *b*); since the cilia of the oral groove are more powerful than the opposing

[1] It is somewhat peculiar that these relations are not dealt with in the recent extensive and valuable paper of STATKEWITSCH (1903, *a*).

aboral ones, they turn the organism toward the aboral side. But this is aided by the fact that the cilia of the aboral side of the anterior half of the body strike obliquely toward the oral side. So far then as the anterior half of the body is concerned, this reaction is the same as that produced by other stimuli. In the posterior half, directed toward the cathode, another factor plays a part, to be taken up later; but this has under the present conditions no effect on the reaction.

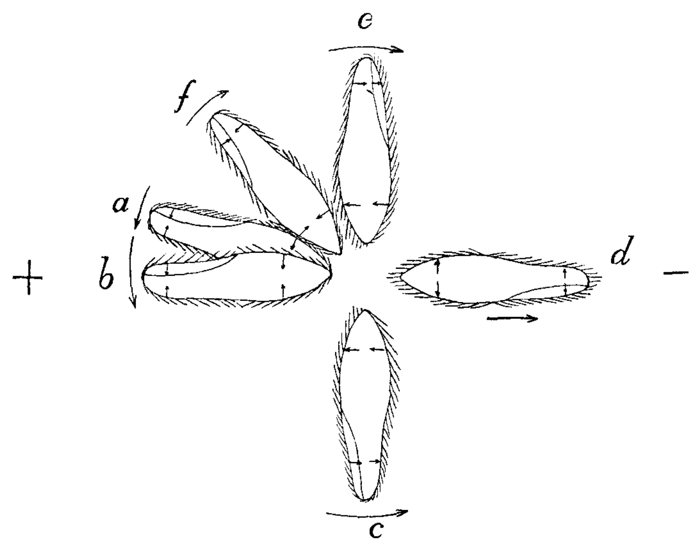


Fig. 14. Diagram representing the action of the cilia and the direction of turning in Paramecia occupying different positions with relation to the electric current. The small arrows within the outlines of the body represent the direction in which the cilia of the different regions tend to turn the animal; the larger external arrows represent the actual direction of turning. In all positions from *a* to *d* the turning is toward the aboral side; at *e* it is toward the oral side.

Even when the animal lies in a very slightly oblique position, so that orientation would be reached somewhat more quickly by turning toward the oral side (Fig. 14, *a*), the turning is still toward the aboral side, the strong oral cilia striking backward and driving the animal toward the aboral side. Further, when the animal is transverse to the current and the aboral side is toward the cathode (Fig. 14, *c*), the turning is of course toward the aboral side, as inspection of the figure shows it must be. Indeed, in any position from *a* through *b* and *c* to *d*, Fig. 14, the animal attains orientation by turning toward the aboral side, as in reactions to other stimuli. These results follow even when the movements of the cilia are precisely those described as typical by LUDLOFF, the greater effectivess of the oral cilia determining the direction of turning.

On the other hand if the animal is transverse to the current with the oral side toward the cathode (Fig. 14, *e*), it turns directly toward the *oral* side, until the position of orientation is reached. In this turning toward the oral side the electrotactic reaction differs from the motor reactions to other stimuli, the factor peculiar to the action of the electric current playing here the essential part. In the typical case where the cilia act as described by LUDLOFF, all the cilia tend to produce the turning toward the oral side, as Fig. 14, *e*, shows.

Between the position shown in Fig. 14, *e*, in which the animal turns toward the oral side, and that in Fig. 14, *a*, in which it turns toward the aboral side, there is of course an intermediate position in which the tendencies to turn in the opposite directions are in equilibrium. In such cases the animal retains its position until the normal revolution on the long axis has occurred, bringing the body into the position shown in Fig. 14, *f*, with aboral side to the cathode. The animal then of course turns at once toward the aboral side, into the position of orientation. A similar method of reaction in certain positions has been described by PEARL (1900, p. 101, "type III") for Colpidium, and by WALLENGREN (1902, p. 365) for Opalina. The tendency to turn in two opposite directions at once, as it were, so that the animal no longer reacts in a co-ordinated way, is very characteristic for the reaction to the electric current, distinguishing this reaction from all others.

Altogether, in nearly three-fourths of all possible positions the animal attains orientation by turning toward the aboral side; that is, the "action system" of Paramecium—PEARL'S "reflex factor"—determines to this extent the reactions to electricity, as it does still more completely the reactions to other stimuli. In practical experimentation with free swimming Paramecia the turning toward the aboral side plays even a larger part than is indicated in the discussion just given. Thus, if the current is frequently reversed, the Paramecia practically always become re-oriented by turning toward the aboral side, since after the reversal the anterior end is directed to the anode as in Fig. 14, *b*; in this position, as we have seen, the turning is always toward the aboral side. It is only by taking special pains to close the current when the animal is in such a position as is shown in Fig. 14, *e* that it can be caused to turn toward the oral side. The result is then due to an effect peculiar to the current, which will be taken up later.

The "action system" in Paramecium further plays a part in the reactions to electricity in the fact that the response on breaking the circuit, and the response to a single induction shock, take the character of the typical "avoiding reaction." This response at the breaking of the circuit is described by PEARL (1900, p. 113); the response to induction shocks by STATKEWITSCH (1903, p. 48).

Again, the "action system" of Paramecium plays a part in the fact that the path followed during the reaction to the constant current is a spiral of the usual sort, the animal revolving to the left and swerving toward the aboral side. Thus there is during the reaction to the current an obliqueness in the stroke of the cilia similar to that found under usual conditions. Certain variations in the spiral path under the action of the electric current will be taken up later.

Peculiarity of Reaction to the Electric Current.—On the other hand, it is clear that a factor exists in the reaction to the electric current which is not found, so far as known, in the reactions to other stimuli—a factor not supplied in the "action system" as observed in the movements under the natural conditions of existence. This is the factor shown in the turning toward the oral side under certain conditions; the factor that causes the animal to try at times to turn in two opposite directions at once—PEARL'S "forced movement factor." What is its nature?

The characteristic phenomenon of the reaction to the electric current is the contrasted action of the cilia in the cathode and anode regions of the body (Fig. 14), as described by LUDLOFF (1895). But it is to be observed that the action of the cilia in the anode region is identical with that which occurs under the influence of any other stimulus. The work of ROESLE (1902) and STATKEWITSCH (1903) shows that under induction shocks the stimulation is primarily at the anode, and that the effect of this stimulation is similar to that of stimulation by other means; the cilia are reversed for a short time, so that the animal swims backward; then it starts forward in a new direction (STATKEWITSCH, 1903). Under the constant current, after the circuit has been closed and the conditions have become constant, the anode cilia are directed backward, as under usual conditions, so that so far as they are concerned the animal swims forward in the normal way. It is then in the continued reversal of the cathode cilia that the peculiar action of the current manifests itself; these cilia oppose the normally acting anode cilia, giving rise to the conflict in direction of turning and of progression that is so striking a factor in the reactions to electricity. LUDLOFF's account of this peculiar action of the cathode cilia is excellent, but certain points brought out by LUDLOFF are not included in the schema usually copied from his work, and this has given rise to certain misconceptions. This has been shown in the recent valuable paper of STATKEWITSCH (1903 *a*). My own results confirm those of STATKEWITSCH on this point; since they were obtained quite independently of the work of STATKEWITSCH,[1] and by a different method of experimentation, I will set them forth. The essential point is that the reversal of the cilia in the cathode region of the body does not typically include just half the body, as is usually set forth. On the contrary, it begins in a weak current with a very slight effect limited to the point of the cathode end of the body, and as the current becomes stronger it spreads gradually backward, until it finally includes almost the entire body. STATKEWITSCH

[1] My experimental work was completely finished and the first draft of this paper written when STATKEWITSCH's paper appeared.

(1903 *a*, p. 92) determined this by direct observation of the cilia on animals in viscous media of various sorts, inventing a number of new media for this purpose. My own results were obtained by observation of the currents produced by the cilia. These observations were made by the use of India ink in the water containing the animals, as set forth above (p. 442); they add certain features to the results set forth by STATKEWITSCH.

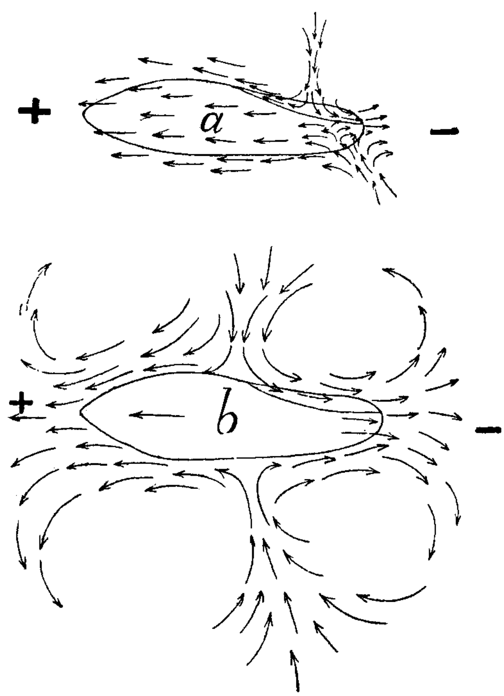


Fig. 15. Currents of water produced by the action of the cilia in the reaction of Paramecium to the electric current. *a*, electric current weak, water currents reversed only at the anterior tip—most markedly in the oral groove; *b*, electric current strong. The arrows show the direction of the water currents.

With a weak electric current the ciliary currents, after orientation is reached, are everywhere backward. At the very anterior tip (directed to the cathode) the currents are perhaps a little less strongly backward than when the animal is not subjected to electricity. This agrees with the results of LUDLOFF and of STATKEWITSCH (1903 *a*), who found that in a weak current only the cilia at the cathode tip are reversed (Fig. 16, *1*). An additional feature to be observed from the movements of the ciliary currents, is that in the oral groove the cathode effect is more marked than elsewhere, and shows itself by repeated reversals of the ciliary current in the anterior part of this region, lasting but an instant.

With a stronger current the effective stroke of a part of the cilia of the anterior region of the body is reversed, so as to be forward. At first this includes only a small part of the anterior region of the body, and this result is reached first in the oral groove, where a water current passes continually forward even when the electric current is so weak that over the remainder of the anterior part of the body the water currents are still backward or at rest (Fig. 15, *a*). As the electric current is made stronger, the currents pass forward over the entire anterior half of the body. This is the stage usually considered typical, though as STATKEWITSCH (1903 *a*, p. 93) points out, it is only one point in a series of continuous

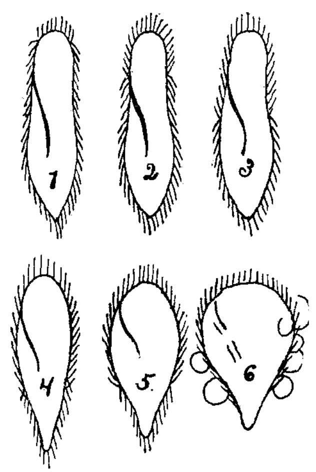


Fig. 16. Different stages of the reaction of the cilia to the electric current, after STATKEWITSCH (1903 *a*). The cathode is conceived to be above, the anode below. In a weak current, only a few cilia at the tip of the cathode end are reversed (1). As the current becomes stronger (2, 3, 4, 5, 6) more and more of the cilia are reversed, until in the strongest currents practically all of the cilia strike forward.

changes. At this stage there is still an alternation at intervals in the direction of the effective beat of the cilia of the anterior half of the body, giving the movement a jerky character. As the electric current is made stronger the forward water currents on the anterior half of the body become constant and more powerful; the currents on posterior and anterior halves separate at about the middle of the body, and water is drawn from all sides to supply them, making the animal the center of a sort of cyclonic disturbance in the water (Fig. 15, *b*), which gives a most extraordinary appearance. At this stage the forward movement of the animal is much retarded, owing to the strong backward stroke of the cilia on the anterior half of the body.

With a still stronger electric current the forward ciliary currents in the anterior (cathodic) region of the body become still more powerful and extensive, seeming to begin even behind the middle, though the precise boundaries of the two sets of currents are very difficult to determine by this method of observation. There comes a period when the effect of the two sets of currents are equal, and the animal neither advances nor retreats, but retains its position, revolving rapidly on the long axis. It is clear that the forward stroke of the anterior cilia just balances the backward stoke of the posterior cilia. Often the two sets of cilia alternate in obtaining the upper hand; the animal is driven backward a distance, then forward again. If the electric current is made still more powerful, the forward currents in front become still stronger and more extensive; they gain the upper hand permanently, and the animals are driven backward toward the anode.

For stronger electric currents it is not possible to determine by observation of the ciliary currents the distribution of forward and backward striking cilia. But this has been determined from direct observation by STATKEWITSCH (1903, *a*); his results are shown in Fig. 16. The reversal of the cilia, beginning with a weak electric current at the cathodic tip, extends backward as the current becomes stronger till it finally includes practically the entire body surface.

In view of these results, the known facts as to the reaction to the electric current may be formulated at follows. First, the current stimulates in the same manner as any other stimulus; this stimulation has origin at the anode. Second, the results of this stimulation are interfered with or overcome by an effect peculiar to the electric current, and having origin at the cathode. This peculiar effect is shown in a progressive reversal of the cilia, beginning with a weak current at the cathode tip, and gradually extending toward the anode end, until with a strong current it affects almost or quite the entire body. Without this second factor, the reaction to the electric current would apparently take place in the same way as the reaction to gravity or to currents of water. The first factor mentioned corresponds to PEARL'S "reflex factor," the second to his "forced movement factor."

Thus in the reaction to the electric current the point especially demanding explanation is the cathodic reversal of the cilia; it is this which distinguishes this reaction from all others. As STATKEWITSCH (1903, *a*, p. 79) has emphasized, "the reaction of the cilia is the first and fundamental phenomenon of galvanotropism." Any theory of the reaction to the electric current is of value just in so far as it promises to aid us in understanding the peculiar action of the current on the cilia. Theories which attempt to account for electrotaxis on certain general considerations, without taking into account the effect on the cilia, are at the present time anachronisms; they close their eyes to the real problem that needs solution.

As to the fundamental nature of the change in the protoplasm that induces the cathodic reversal of the cilia, which forms the distinctive feature of the reaction to the electric current, the conclusions drawn from the thorough and extensive work of STATKEWITSCH (1903, *a*) are most worthy of consideration. For details reference must be made to the original work of STATKEWITSCH;[1] we may say here that the author comes to the conclusion, after extensive experimentation as to the chemical and physical effects of the electric current on the organisms, that the current disturbs the usual equilibrium of the processes of metabolism in such a way as to produce a change in the normal backward stroke of the cilia, in the manner described above (*l. c.*, p. 158)—this change beginning at the cathode end, and progressing, as the current is made stronger, over the entire body.

[1] A German translation of parts of STATKEWITSCH'S Russian text is to appear, I understand, in VERWORN'S *Zeitschrift für Allgemeine Physiologie*.

Cause of Backward Swimming in Strong Currents.—The observations described above on the direction of the effective beat of the cilia as the current becomes stronger throw light on the disputed question as to the cause of the swimming backward toward the anode in a strong current. LUDLOFF (1895) explained this backward movement as due to the fact that in a strong current the effectiveness of the reversed stroke of the anterior (cathodic) cilia becomes increased, till it overcomes the forward effect of the posterior cilia. According to LUDLOFF'S view, then, the animal swims actively backward in a strong current, just as it swims actively forward in a weak current. On the other hand PEARL (1900, p. 123) holds that in a strong current the animals are borne passively backward to the anode by the cataphoric effect of the current—the electrical convection—while their active movements tend to carry them to the cathode. In other words, he holds that in a strong current the electrical convection becomes more effective than the stroke of the cilia, thus carrying the animal backward. DALE (1901, p. 354) holds the same view. WALLENGREN (1902) adopts this explanation, for Opalina, without expressing an opinion in regard to Paramecium. Which of the two explanations is correct?

As the account given on preceding pages (pp. 490 492) shows, the observations on the direction of the effective beat the cilia are throughout in accordance with the explanation given by LUDLOFF, and no other factor is required to account for the phenomena which actually occur. When the animal is swimming backward to the anode the effective beat of a large portion of the cilia is demonstrably forward, producing currents equal or superior to those due to the backward stroke of the other cilia. This forward stroke of the anterior cilia must inevitably tend strongly to drive the animal backward, so that at the best only a very small part in the phenomena could possibly be attributed to the electrical convection. The direct impression from observations is that the result is fully accounted for without bringing the electrical convection into the matter at all.

The further question arises as to whether the electrical convection is competent to produce the effect ascribed to it on the view of PEARL and DALE With the strength of current used, is the electrical convection sufficiently powerful to carry the bodies of Paramecia, considered merely as pieces of material of a certain size and weight, toward the anode at the rate at which the Paramecia move backward? Observation shows that even smaller, non-living particles are not carried toward either pole at any such rate. Further, Paramecia that have been killed in ether, chloroform, chloretone or formalin are not moved to either electrode by the electrical convection. BIRUKOFF (1899), who maintains the efficacy of electrical convection, endeavors to explain the fact last cited as follows. The dead Paramecia do not remain suspended, but sink to the bottom, and it is a necessary condition for the effective operation of electrical convection that the solid particles in question should remain in suspension.

Obviously then in order to test this matter we must arrange experiments in such a way that the dead Paramecia shall remain for some considerable time suspended. This is easily done by placing them in a vertical tube, or by placing the slide bearing the Paramecia in a vertical position. The electrodes are then introduced at the upper and lower ends of the tube or preparation. The Paramecia sink slowly through the water, and thus remain a long time suspended, not being in contact with any solid objects till they reach the bottom.

With living specimens under these conditions the reactions are identical with those in horizontal preparations. If a weak current is used, the Paramecia hasten to the cathode, both when this is at the upper, and when it is at the lower end of the tube. If a stronger current is used, and the upper end of the preparation is made the anode, the infusoria swim backward against the pull of the gravity to the anode, at the upper end. With lifeless Paramecia on the other hand no such effects are produced. The dead animals simply sink steadily, whatever the strength of the current, in spite of electrical convection toward cathode or anode.

Thus whatever it is that causes the Paramecia to move backward to the anode in a strong current is competent to lift the animals against the force of gravity. The electrical convection is not competent to produce this result. It is therefore evident that the electrical convection is not the essential agent in producing the movement of Paramecium backward to the anode. The observations previously detailed show clearly what *is* the agent producing this result.

BIRUKOFF (1899) held even that the usual movement to the cathode was produced by the cataphoric effect, or electrical convection. This had of course been disproved long before the paper of BIRUKOFF was written As an additional disproof, we may note that the experiments just described show that the electrical convection is not competent to produce the effect observed in the movement to either cathode or anode. It is to the movements *of the cilia* brought about by the electric current that we must turn for the real factors producing the movements to cathode or anode.

Relations between Contact Reaction and Reaction to Electric Current.—In a previous paper (1897) I described what I called an interference between the contact reaction ("thigmotaxis") and the reaction to the electric current, and in a later paper PÜTTER (1900) considerably extended our knowledge of the phenomena in question. The interference described consisted, so far as Paramecium is concerned, essentially in the fact that specimens showing the contact reaction respond less readily to the electric current than do free specimens, and the response, when it occurs, is intermittent. For Stylonychia PÜTTER held that a further effect was evident, in the fact that thigmotactic specimens take up a transverse position with respect to the electric current, while the free specimens swim directly to the cathode.

I wish to bring out here certain further points in regard to the interference between the contact reaction and the reaction to the electric current. These are the following:

1. In my previous paper I described this interference only for the case of Paramecia in contact with a mass of detritus. But the Paramecium need not be in contact with such a mass in

order to show the interference described. It occurs also when the animals are in contact with a clean glass surface, or the surface film of water. This is particularly evident when the Paramecia are subjected to a moderately strong current on the slide in a thin layer of water, without a cover. They swim as usual toward the cathode. But when a specimen in its spiral course comes against the glass slide or the surface film, it at once stops. It may stop only an instant, or it may remain at rest for some time, or it may show certain peculiar movements, to be described later.

2. The effect of thigmotaxis appears not merely in a decrease in sensitiveness to to the current, but in a change in the method of reaction to the current. PUTTER (1900) showed that in various Hypotricha individuals in contact with a surface take, in the current, a nearly transverse position with the left side (bearing the peristome) to the cathode, while free swimming individuals become oriented with anterior end to the cathode. Similar relations are to be observed in Paramecium, though less frequently than in the Hypotricha, because Paramecium is less often in contact with the surface. But when a large number of individuals are subjected to the current in a thin layer of water (with or without a cover glass), the phenomena are evident. The free specimens swim as usual, with anterior ends to the cathode. Those that come in contact with the surface film or the glass, stop, as described above. If they do not quickly resume the forward course, they soon take up a position nearly transverse to the current, with the oral side or peristome directed toward the cathode (Fig. 17). In this position they may either remain quiet, or may move forward transversely (or obliquely) to the current, keeping in contact with the surface. The effective beat of the cilia, as determined by the movements

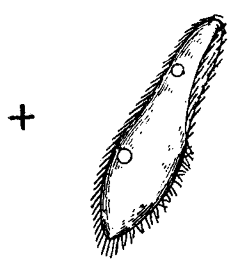


Fig. 17. Transverse or oblique orientation of Paramecium to the electric current when in contact with a surface.

of the particles of India ink, is now everywhere backward, save in the oral groove, where it is usually forward, though at intervals it here passes backward for a moment.

If while in this position the direction of the current is reversed, so that the oral surface is toward the anode, the oral cilia strike strongly backward. This has one of two effects. Sometimes it causes the animal to be detached from the surface; in this case it turns toward the aboral side until the anterior end is directed to the cathode, then it swims forward in that direction, like other free swimming specimens. Or the animal may still remain in contact with the surface; in this case it turns toward the aboral side, until the peristome or oral surface is again directed toward the cathode. Then it remains quiet, or resumes its forward movement transverse to the current. In cultures where the specimens are much inclined to be thigmotactic, one often observes in this way marked transverse electrotaxis in a large number of individuals; by repeatedly reversing the current they can be driven from one side of the preparation to the other and back again, always transversely or obliquely to the current.

ROESLE (1902) observed that Paramecium reacts much more readily to induction shocks when the peristome is directed toward the anode than in other positions. ROESLE interprets this as showing that the peristome is more sensitive than other parts of the body surface. While this conclusion is *a priori* very probable, I am not sure that the facts cited really demonstrate it. When the constant current is made, the animal lying against a surface with peristome to the cathode, there is a reaction, which is, however, ineffective in causing a movement of the animal's body. The reaction consists in a weak reversal of stroke of the oral cilia, as is shown by the forward movement of the particles of India ink in the oral groove. This forward stroke of the oral cilia has very little locomotor effect, and does not overcome the attachment of the animal to the surface; it could not be observed without the presence of the particles of India ink. It is possible that this reaction occurs also with induction shocks, and escaped observation, owing to the fact that ROESLE used no method of rendering the currents visible. When the circuit is closed with the peristome to the anode, on the other hand, the oral cilia strike strongly backward, and this has a powerful locomotor effect, driving the animal forward, or, if the current continues, turning it toward the aboral side. ROESLE'S observations are then fully explicable on the basis of the known action of the current on the cilia, as described first by LUDLOFF, together with the stronger locomotor effect of the oral cilia when striking backward, a difference that is evident in many ways. I must then agree with the conclusion of STATKEWITSCH (1903), reached on other grounds, that the results of ROESLE do not demonstrate the greater sensitiveness of the peristome.

Thus we find under certain circumstances a "transverse electrotaxis" of Paramecium under the action of the constant current, as in many other infusoria. This transverse orientation is of course of an entirely different character from that obtained by STATKEWITSCH (1903 *a*, pp. 24-32), with rapidly alternating currents.

3. In a strong electric current the contact reaction causes not merely a stoppage of the forward course, but actual swimming backward. If the Paramecia are in a thin layer of water, through which a rather strong current is passed, all the specimens that are not in contact with upper and lower surfaces swim forward, in the somewhat cramped manner, as if against resistance, that is characteristic of the swimming in a strong current. But when a specimen comes in contact with the glass surface below or the surface film above, it begins to swim backward. This may last for but an instant, while the accidental contact continues, or if the animal remains in contact the backward swimming continues a long time. If a very thin layer of water is used, so that the Paramecia can hardly avoid coming in contact with a surface, most of them swim backward, though as soon as a specimen becomes free from the surface, it darts forward. With a slightly thicker layer of water, often about half the individuals are free and swim forward, while the other half are in contact and swim backward. The same individual

may alternate frequently in the direction of swimming, according as it comes in contact with the surface, or becomes free from it. To obtain these results in a sharply defined way, it is necessary to vary the strength of current until exactly the proper intensity is found.

The cause of this peculiar effect of contact seems to be as follows PUTTER (1900) has shown that one effect of the contact reaction is to cause the cilia of the region posterior to the place of contact to cease effective action. In the strong current the cilia of the anterior half of the body tend to drive the animal backward, while the posterior cilia force it forward; the latter are a little the more effective, so that the animal on the whole moves forward. In the spiral course the body, swerving toward the aboral side, comes in contact with the surface at about its middle. Thereupon, in accordance with the observation of PÜTTER, above mentioned, the cilia behind this spot, driving the animal forward, cease to beat, while the cilia in front of this spot, driving it backward, continue their action. Hence the anterior cilia now gain the upper hand, forcing the animal backward.

In his recent valuable papers (1903, pp. 46-47; 1903 *a*, pp. 46-56), STATKEWITSCH maintains that there is no real interference between the contact reaction and the reaction to the electric current, but that the animal in contact with a solid is reached only by a weaker current than the free swimming individuals, hence it reacts less markedly. Animals showing the contact reaction are usually in contact with a heap of detritus; STATKEWITSCH holds that the electric current divides, a portion of greater intensity passing through the water, a weaker portion through the heap of detritus and the Paramecium.

This simple physical theory would of course be very satisfactory if it explained the observed facts, but this it does not do. It is based on the assumptions (1) that the so-called interference is shown only when the animal is in contact with a heap of detritus; (2) that the interference appears only as a weakening of the reaction, not as a change in its character. Both of these assumptions, as I have shown above, are incorrect. As to the first one, the Paramecia, as we have seen, show the interference described even when the animal is in contact only with a clean glass surface, or with the surface film of the water. It is evident that this cannot be explained as due to the dividing of the current and the passage of a weaker portion through the object with which the animal is in contact. STATKEWITSCH's observations on this phenomen (1903 *a*, pp. 45-52) were made only on individuals in contact with a bit of detritus, and he assumes that this is a necessary condition for the production of the supposed interference.

As the second assumption mentioned, I have shown above that the contact reaction produces not a mere weakening of the effect of the electric current, but actual changes of a most decided character in the way the reaction occurs. Paramecia in contact with a glass surface or the surface film take up a transverse position, or move backward, in the same current which produces forward movement in free swimming specimens. These effects cannot possibly be explained as due to the dividing of the current into weaker and stronger portions, as supposed by STATKEWITSCH.

PÜTTER (1900) had already set forth that in Stylonychia the contact reaction has the effect of producing a transverse orientation in the electric current. STATKEWITSCH, however, tries to show that this transverse orientation is merely the effect of a weak current. But when one examines attentively his evidence for this (1903 *a*, pp. 43-44) it seems apparent that all the specimens which showed transverse orientation were in contact with a surface, and he does not mention the existence of transverse orientation in free swimming specimens. Thus his results are equally well explained on PÜTTER's view that the transverse orientation is due to the contact reaction. In Paramecium STATKEWITSCH expressly states repeatedly (for example, 1903 *a*, p. 57) that the effect of the weak current is to cause movement toward the cathode, and he never in his extensive and thorough study of the reaction of Paramecium to electricity observed transverse orientation to the constant current. The transverse orientation of Paramecia that are in contact, described above, cannot then be accounted for as due to the weakening of the current affecting them. This is true *a fortori* of the swimming backward of individuals that come in contact with a surface, for such swimming backward occurs under other conditions only in *stronger*, not in weaker, currents. There is no escape from the conclusion that the contact reaction interferes with and modifies in a striking manner the reaction to the electric current.

STATKEWITSCH'S view that the supposed interference between the effects of the two stimuli is to be explained in the simple physical way he sets forth seems based largely on an *a priori* conviction that the electric current *must* always produce the same reaction when it acts upon the same organism with the same strength (see for example STATKEWITSCH, 1903, p. 46). This conviction appears in a most curious way in his attempts to demonstrate the correctness of his view. In his earlier paper (1903, p. 47) he promises to demonstate in his final paper that the supposed interference does not exist, but is to be explained by the division of the current, in the way above set forth. In the final paper this promised demonstration takes the following form: "For demonstration of this condition it is not necessary to search out any methods of registration; for this purpose the very objects on which we are experimenting can serve most excellently; a more sensitive galvanometer than Paramecium, indeed, one need not demand. Its reactions to the current present unchanging, definite phenomena, taking place in accordance with law, dependent on the strength of the acting current. The orientation with relation to the cathode, the increase in the rapidity of progression up to a definite limit, the changes in the form of the body—all these appear at a definite intensity of the current, which demonstrates in an immediate way that through the bit of detritus and the protist attached to it passes a current of less intensity than in the neighboring fluid, where the reactions of the infusoria are more pronounced" (1903 *a*, p. 55, translation). Now, the question at issue was whether the electric current of a given strength does as a matter of fact always produce the same reaction on the same organism, as STATKEWITSCH holds, or whether on the contrary the contact reaction may interfere with it, as set forth by PÜTTER and myself. In attempting to demonstrate the former alternative in the manner given above, I submit that STATKEWITSCH merely assumes its truth, and uses this assumption for disproving the second alternative—after which disproof the first alternative of course emerges triumphant. We have here a clear case of reasoning in a circle.

The general fact that the reaction to a certain defined stimulus may be modified by the reaction of the organism to other stimuli, present or past, is perfectly well established for the behavior of lower organisms. In a recent paper (1904, *a*) I have developed this point in detail, and have adduced many examples from the reactions of the Ciliata. The contact reaction is especially effective in modifying the reactions to other stimuli. This appears in the reactions to many agents besides electricity. PÜTTER (1900) has shown that the contact reaction interferes largely with the reaction to heat, a result which I have confirmed, especially for Stentor. I have often observed that the contact reaction inhibits to a large degree the reaction to mechanical shock. Paramecia and other infusoria when free swimming react strongly to a light touch with a glass point at the anterior end, giving the "avoiding reaction" in a pronounced form. But when thigmotactic they often do not respond at all to such a touch. Again, attached specimens of Stentor cærulus do not react to light in any way, while unattached individuals react decidedly (JENNINGS, 1904). STATKEWITSCH surely cannot expect us to take seriously in opposition to such well defined facts his objection that the concept of the contact reaction is indefinite, and that we cannot *measure* its effect (1903 *a*, p. 56). The effect of the contact reaction on the cilia has been described in a perfectly definite way by PÜTTER (1900) and by myself (1897), and we certainly cannot be asked to shut our eyes to the existence of such striking phenomena because no one has devised means of measuring them.

Irregularities in the Reaction to the Electric Current.—There are certain irregularities in the reaction to the electric current that deserve mention. First, one often observes that while most of the specimens in a preparation are reacting precisely and strongly, a few specimens do not react at all, swimming about at random. Second, one at times observes single specimens that swim toward the anode, while all the others go toward the cathode. This is most likely to be observed after the current has been reversed several times, though it is sometimes seen at the beginning of the experiment. After repeated reversal of the current, one sometimes makes the following observation. A specimen is oriented and swimming toward the cathode; on reversal of the current it retains its orientation and continues to swim forward—now of course toward the anode. A third very peculiar irregularity that is less unusual than the others is the following. In a ratner strong current the animals are swimming slowly and in a rather cramped way toward the cathode. Now the current is reversed, whereupon, without turning around, they swim rapidly *backward* to the cathode. By repeatedly reversing the current, the animals may sometimes be caused to alternate several times, first swimming forward, then backward, retaining throughout the same position. But usually after swimming backward a short time toward the cathode, the animal turns around and swims to the cathode in the usual way. All these irregularities are so comparatively unusual that I have not been able to determine precisely the nature of the ciliary movements.

Reaction of Paramecia to Electricity when in Solutions of Chemicals.—GREELEY (1903) has recently raised anew the question as to the significance of certain peculiarities of the reaction to the electric current when the animals are in solutions of certain chemicals. He points out that in acid solutions Paramecia move to the anode, whereas, under usual conditions, where the solution is alkaline or neutral, they move to the cathode. This he attempts to bring into relation with the observations of LILLIE (1903), who shows that cell constituents containing much nucleic acid migrate to the anode as an effect of electrical convection, and that the tendency to migrate to the anode decreases with the decrease in acidity. In this way we seem to be on the road to a direct physical explanation of electrotaxis. In criticism of the views of GREELEY, so far as hitherto brought out, the following must be said:

1. All thorough work thus far shows that the essential point in the reaction to the electric current is the method in which the current affects the cilia. No attempt has been made to show how the known effects on the cilia could be produced through the factors emphasized by GREELEY, and it would undoubtedly be difficult or impossible to bring the two into relation.

2. The movement toward the anode is not limited to acid solutions, but is known to take place in a still more striking way in various salt solutions, especially in a solution of sodium chloride. I have observed it even in a solution of sodium bicarbonate, having of course an alkaline reaction.

3. The movement to the anode in such solutions is backward. It has been so described by LOEB and BUDGETT (1897, p. 532), by PÜTTER (1900, p. 297), and so far as I am aware, by every one who has described it carefully, and I can myself confirm this fact. The organisms thus become oriented in the same manner, with anterior end to the cathode, as under usual conditions. Further, these same solutions produce backward swimming even without the use of the electric current. We have then all the existing features of the reaction fully accounted for without taking into consideration the factor considered essential by GREELEY. The electric current taken by itself accounts for the orientation in the usual way; the chemical stimulation taken by itself accounts for the swimming backward; the combination of the two accounts for the swimming backward to the anode.

4. The swimming to the anode continues only as long as the chemical stimulation exists. As soon as the organism has had time to become acclimatized to the chemical, *it swims as usual to the cathode.* This has been shown by PÜTTER (1900), and by STATKEWITSCH (1903 *a*), and I can confirm it. Often it is but a few moments that the swimming backward to the anode continues.

In view of all these facts, it cannot be held on the evidence thus far brought forth, that the phenomena observed in acid solutions, as described by GREELEY (1903), have any special significance for the theory of electrotaxis, such as that author assumes. The known facts point to the following general statement of the phenomena. Immersion in chemicals, of various characters, causes the organism to swim backward. If at this time the Paramecia are subjected to the electric current, they continue to swim backward, and, becoming oriented, therefore pass to the anode. This movement to the anode ceases as soon as the stimulating action of the chemical ceases.

In order to make out a case for the theory advanced by GREELEY, it will be necessary to show clearly that this general statement is incorrect.[1]

IV. PRESENT POSITION OF INVESTIGATION OF THE BEHAVIOR OF PARAMECIUM.

I believe it may be said that we are now able to make a general, qualitative survey of the chief facts and factors in the behavior of this representative of the unicellular animals. There are doubtless still some dark points; the reaction to the electric current, for example, is still hard to place in the general scheme of behavior, though recent researches have gone far toward clearing up this matter. But it is true that we know, in a general way, most of the chief methods of action of this animal, and the way in which these are affected by the chief classes of external conditions. There still remains the investigation of the intimate physiological processes underlying the gross features of the reactions, and especially the quantitative study of the phenomena which the qualitative examination has brought out. Our present knowledge, then, amounts to a preliminary survey, showing us in the gross the phenomena which require investigation in detail. Attempted quantitative study of phenomena of which the qualitative, purely descriptive, features

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[1] Since the above was written, GREELEY'S final paper has appeared (*Biol. Bull.*, Vol. 7, pp. 3–32). It raises many interesting questions, which I hope to touch upan later. (Note added during correction of proof.)

are uncertain, is likely to be misleading and worthless; this has been too often illustrated in the investigations on the reactions of unicellular animals. We cannot measure things till we at least know what we are measuring; if we attempt it our results have only the appearance of accuracy, and are likely to fall to the ground as soon as the qualitative nature of the phenomena is worked out and found to be different from what we had assumed. It is for this reason that the present writer has limited himself thus far almost entirely to qualitative work. Now that the qualitative survey has been made, I believe that if its results are held clearly in mind, quantitative work can be done with some hope of understanding the significance of the data which our measurements bring out. But in view of the pecu liar and complicated action system of Paramecium, quantitative results will always have to be interpreted with the greatest care, and it must be realized that that method of investigation which examines only the beginning and end of an experiment, without troubling itself as to what the organism does in the meantime, is likely to be most misleading. Further, in view of the peculiar character of the action system of Paramecium, and the large part it plays in determining the behavior under stimulation, the utmost caution is necessary in transferring the conclusions obtained with this animal to other organisms having a different action system.

The work on which the present paper is based was done at the Naples Zoological Station while the author was a Research Assistant of the Carnegie Institution of Washington. It is a pleasure to acknowledge my indebtedness to the Carnegie Institution for making the work possible, and for permission to publish the present paper.

Pozzuoli, Italy. April 26, 1904.

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