STUDIES ON REACTIONS TO STIMULI IN UNICELLULAR ORGANISMS. IX. — ON THE BEHAVIOR OF FIXED INFUSORIA (STENTOR AND VORTICELLA), WITH SPECIAL REFERENCE TO THE MODIFIABILITY OF PROTOZOAN REACTIONS.[1]

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THE only infusorian whose behavior is at present known with any degree of fulness is Paramecium. This animal is a type of the free-swimming infusoria; while Paramecium does at times come to rest, as a rule it is found in rapid movement, — especially when under experimental conditions.

The behavior of an animal which is fixed in a definite position will necessarily be of a different character from that shown by such an organism as Paramecium. Stentor and Vorticella furnish examples of such animals, and, as will appear, their behavior differs much from that of Paramecium, — showing indeed a much higher development.

As compared with an organism continually in motion, a fixed animal offers many advantages for the experimental study of behavior, for one may keep the same individual continuously under observation, or return to it at longer or shorter intervals. It is thus possible to observe changes in behavior, and to determine whether the reaction to a given stimulus is modified by previous subjection to the same or different stimuli.

The present paper is based upon a study of the behavior of the following organisms: Stentor rœselii Ehr., Stentor cæruleus Ehr., several species of Vorticella, Epistylis flavicans, var. procumbens, and Carchesium polypinum Lin. Stentor is much more favorable for such work than any of the Vorticellidæ, and Stentor rœselii is in many respects the most favorable as well as the most interesting of the organisms studied. I shall therefore make an account of the behavior of this animal the basis of the paper, comparing the others with it.

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[1] Contributions from the Zoölogical Laboratory of the University of Michigan, No. 57.

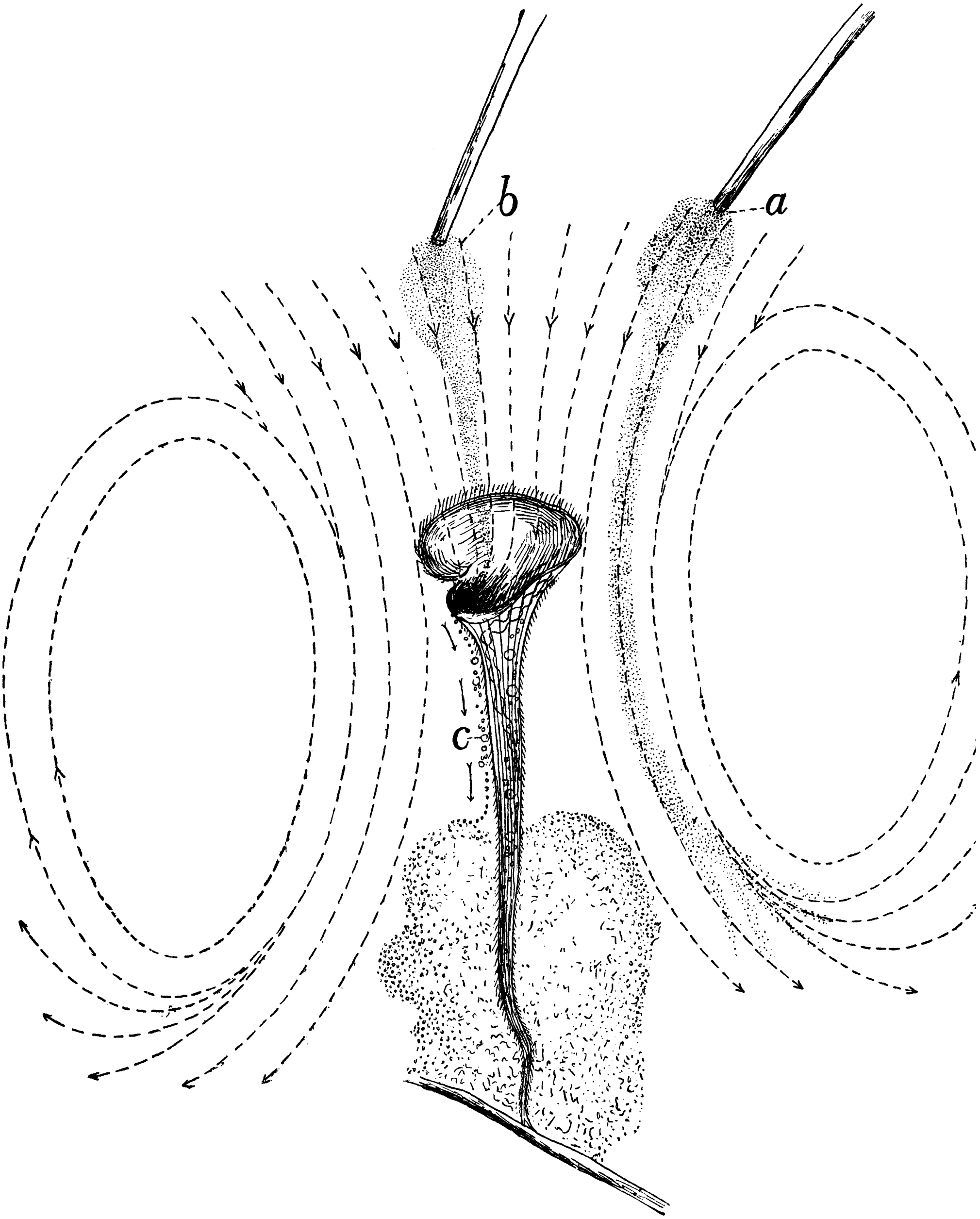

FIGURE 1. — Stentor rœselii, showing the currents caused by the cilia. At *a* a chemical is introduced a little to one side of the disc, showing that it does not reach the animal. At *b* a chemical is introduced above the disc; it is carried directly to the mouth. At *c* particles are seen passing along the ventral surface of the body to the edge of the tube.

A. THE BEHAVIOR OF STENTOR RŒSELII EHR.

For understanding the behavior of an organism when subjected to stimuli, it is necessary to have well in mind the structure of the animal and its normal movements when unstimulated, — a consideration too often neglected in work on behavior.

Stentor rœselii Ehr. (Fig. 1) is a colorless or whitish animal consisting, when fully extended, of a slender, tapering, stalk-like body, bearing at its larger end a broadly expanded disc. The surface of the body is covered with longitudinal rows of fine cilia, and bears also a considerable number of fine long setæ, which disappear at times, and are said to be retractile and extensile. The disc is surrounded by a circlet of large compound cilia or membranellæ. These make a spiral turn, passing on the left side into the large buccal pouch, which leads to the mouth. The mouth thus lies nearly in the middle of what may be called the oral surface; this surface is considered ventral in determining right and left. The disc is covered with rows of fine cilia which are nearly parallel with the circle of membranellæ. The smaller end of the tapering body is known as the foot; here the internal protoplasm is exposed, sending out fine pseudopodia, by which the animal attaches itself to objects (Fig. 2).

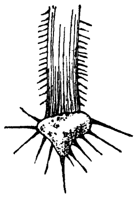

FIG. 2. — Foot of Stentor rœselii, after Johnson ('93), showing the pseudopodia.

The body contains, next to the surface, many fine contractile fibrillæ, the myonemes, through the action of which the animal may contract into a short oblong or conical form (Fig. 3).

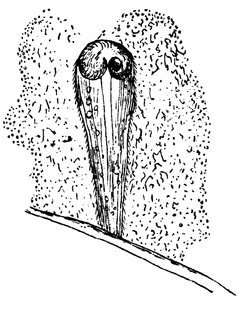

FIG. 3. — Stentor rœselii, contracted into its tube.

Stentor rœselii is usually attached to a water plant or a bit of débris by the foot, and the lower half of the body is surrounded by the so-called tube. This is a very irregular sheath, formed of flocculent material of all sorts, partly held together by a secretion from the Stentor. It is frequently nearly transparent, so as to be almost invisible. The manner in which the tube is formed will be described later.

Movements of cilia in the unstimulated animal.[1] — The membranellæ and cilia of the oral disc are in continual motion in the extended animal; the nature of this motion is best seen by adding something to the water to make the currents induced by the cilia visible. When finely ground sepia or carmine is added to the water, the currents caused by the cilia are seen to be as follows: The mouth of the animal forms the bottom of a vortex, towards which the water above the disc descends from all sides (Fig. 1). Only the particles in the water near the axis of the vortex really strike the disc, — those a little to one side shoot by the edges without touching. These latter curve outward again after reaching a point below the disc, and thus a whirlpool is produced, — some of the particles returning upward so as to reach again the downward current at a point some distance from the Stentor. But most of the particles which thus miss the edge pass downward and out of the sphere influenced by the Stentor.

Particles which reach the disc pass to the left, toward the buccal pouch, showing that the beat of the membranellæ has a component which drives to the left as well as downward, — the real movement of the current being thus a left spiral. The particles thus reaching the buccal pouch are whirled about within it a few times, then they may take one of two courses. They either pass down into the mouth at the bottom of the pouch and thus into the internal protoplasm, or they are whirled out over the edge of the pouch, in the mid-ventral notch. In the latter case they usually pass backward toward the foot of the animal, along the mid-ventral line, as shown at *c* in Fig 1. Apparently the body cilia in this region keep up a backward current. The particles reach the edge of the tube, where they may cling, thus aiding to build up the tube.

In determining whether certain given particles shall pass into the protoplasm or out over the edge of the disc, there seems to be no indication of sorting by the cilia and of choice, — though this would not be at all surprising in view of what we know of choice in Amœba, and of corresponding phenomena in inorganic fluids (see Rhumbler, 1898, or the brief resumé in Jennings, 1902). But in Stentor, as long as the disc remains extended, whenever particles of any sort are allowed to reach the disc in large numbers, some are taken into

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[1] It is doubtless to be held that the animal is never really unstimulated; the use of this term signifies merely that no special stimulus is acting on the animal, beyond what is supplied by the usual conditions of existence.

the protoplasm, while others pass over the edge and away, without regard to the nature of the particles (provided they are not too large; see p. 30). This is true, for example, of sepia, carmine grains, unicellular algæ and débris of all sorts. When large numbers of minute unicellular algæ pass into the buccal pouch, apparently the proportion taken into the protoplasm is the same as in the case of sepia or other non-nutritious particles. It seems evident that whether a given particle shall or shall not be taken into the internal protoplasm depends upon the mechanical conditions governing the spiral currents in the pouch. Many of the particles in the current never reach the minute mouth at all, and these are whirled over the edge in continuation of their spiral course; those which are so situated in the vortex as to be carried directly to the mouth are taken in. Of course Stentor does exercise a sort of choice (as will appear below), by changing its position, reversing the ciliary current, or contracting when injurious substances are present in the water, but there is no indication of a sorting and selection of particles brought into the pouch by the usual currents.

When stimulated, Stentor rœselii may contract into its tube (Fig. 3). Such contractions do not as a rule take place except in response to well marked stimuli. This was the rule throughout my observations, extending over many days. Undisturbed individuals observed without interruption for an hour or more did not contract at all during that time. In this respect Stentor differs from Vorticella, which contracts at short intervals, even when the conditions are apparently quite uniform (see Hodge and Aikins, 1895).

Reactions to stimuli. I. Mechanical stimuli. — We will first consider what Stentor does when touched or struck by small objects, — its reactions to simple mechanical stimuli. Such stimuli are often received in the normal life of Stentor, and there is a surprisingly full and complicated set of reactions to them, as compared with the simple reactions of Parmecium.

We will suppose that small solid bodies are brought with the water currents to the disc. This may be controlled experimentally by drawing a glass tube to a long, excessively fine capillary point, filling the tube with water containing finely ground sepia, and bring the point near the Stentor. What the animal does depends upon a number of different conditions.

Normal movements continued. — At first the normal currents are not changed; the particles pass into the pouch, and some are taken into the internal protoplasm, while others pass out over the edge of the pouch at the mid-ventral notch, as described above. If the particles are minute, do not cling together into large masses, are not excessive in number, nor mingled with any stimulating chemical, the currents continue this normal course indefinitely.

Bending toward the source of stimulus. — If a small object merely touches gently one edge of the disc, the Stentor may bend over toward the object (Fig. 4). This reaction may be seen when a small organism comes against the disc of Stentor, then attempts to swim away. The Stentor bends in that direction, so as to keep in contact with the object as long as possible. In the culture dishes containing Stentors there were many free heads of Epistylis, and these frequently swam thus against the Stentors, giving rise to the above described reaction. The Epistylis heads were not held at all, but were merely followed as far as possible by bending.

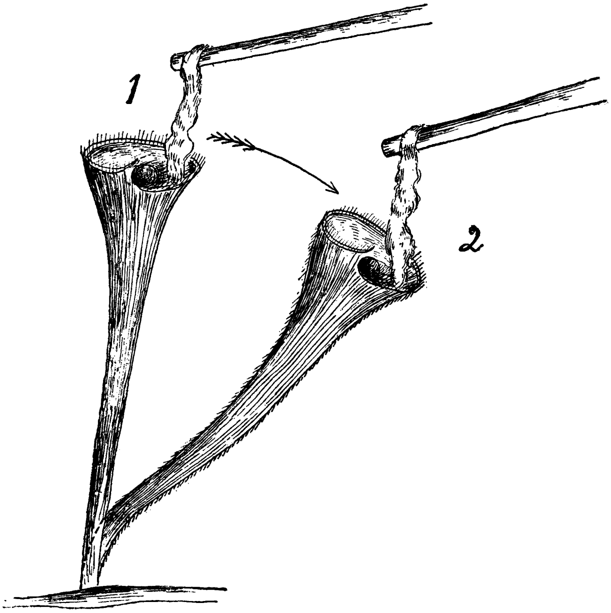

FIGURE 4. — Stentor rœselii bending in the direction of a slight mechanical stimulus. At 1 a bit of débris is allowed to touch the edge of the disc, and is then pulled to the right. The Stentor follows it, bending into the position shown at 2.

This reaction may be produced experimentally by tickling the edge of the disc with the tip of a minute glass rod drawn out to the finest possible hair.[1] The Stentor bends over toward the side touched, and if the rod is moved very gently to one side, follows it.

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[1] These and similar manipulations were carried out under the Braus-Drüner binocular microscope, the use of which renders very simple many experiments and observations which would otherwise be difficult.

If the rod trembles a little too much, the Stentor will contract suddenly, as described below. The most satisfactory way of producing the reaction is to get a bit of soft flocculent débris from the bottom of the dish to cling to the rod. This débris may then be allowed to come against the disc, and is then gently pulled to one side. The Stentor follows it, often bending far over. This experiment is represented in Fig. 4. The animal may thus bend in any direction, — to the right, to the left, or toward the oral or aboral side.

Bending away. — If the stimulus is a little stronger, as one produced by a large hard object, or by the objects becoming too numerous, as when a dense cloud of sepia reaches the disc, or when the objects are accompanied by a weak chemical stimulus, as is the case with carmine grains, then another reaction is produced. The animal bends away from its present position. This is thus to a certain degree the opposite of the reaction last described, but is not so precisely localized a reaction as the former one. In this reaction the organism shows the influence of its spiral, unsymmetrical structure, in that, as in the case of Paramecium, it always turns toward a structurally defined side. The reaction in Stentor is as follows: the animal twists on its long axis one or two turns, then bends over toward the aboral side. It thus bends into a new position, but it does not always bend *away* from the source of stimulus; in some cases this reaction carries the animal toward the source. In the latter case the reaction is repeated.

In most cases where the source of stimulus is not large, this reaction succeeds in removing the Stentor from its action. Thus, if a capillary tube containing sepia is held close to the disc, when the animal bends over toward the aboral side the particles of sepia no longer reach the disc, and the animal is relieved from the stimulus (Fig. 5). Much experimentation shows that this simple reaction is more effective in getting rid of stimuli of all sorts than might be anticipated. If the first reaction is not successful in accomplishing this end, it is repeated.

Reversal of the ciliary current. — If the turning toward one side does not relieve the animal (or in some cases before this is tried), so that the particles continue to come in a dense cloud, the ciliary current is suddenly stopped and apparently reversed for an instant. The particles in the pouch or against the disc are thus thrown off. The reversal lasts but an instant, then the current is continued. If the particles still continue to come, the reversal is repeated two or three times in rapid succession. If this fails to relieve the animal of the stimulus, the next reaction (contraction) usually supervenes.

Sometimes this reversal of the current takes place before the turning away described above, and it may be followed by that reaction. But usually the turning away occurs first.

The reversal is produced under various circumstances. It occurs when a very large number of particles reach the disc at once, so that there is a tendency to clog the pouch, or when a large hard object, such as one of the loricate Ciliata, gets into the pouch. I have seen Coleps gotten rid of in this way. It occurs also when some chemical, as a weak salt solution, is mingled with the particles, or when the chemical alone reaches the disc (see the reactions to chemical stimuli, below).

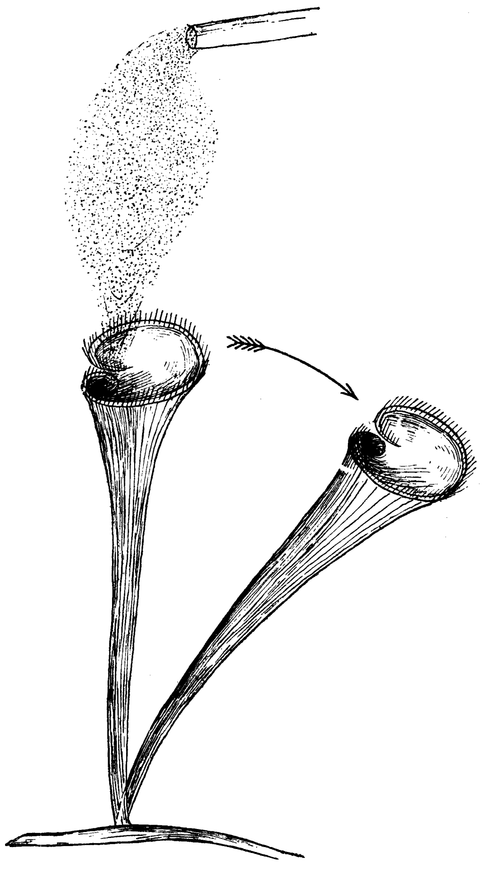

FIGURE 5. — Stentor rœselii bending away when a quantity of sepia or of some chemical reaches the disc. The animal bends toward the aboral side.

Contraction. — If the animal does not succeed in getting rid of the stimulus in either of the ways above described, or if the stimulus is a very powerful one to begin with, the Stentor suddenly contracts. The body becomes short and club-shaped or oblong, and the Stentor disappears within its tube (Fig. 3). Here it usually remains twenty to thirty seconds, then rather slowly extends, so that from the moment of contraction to the moment of complete extension an interval of 40 to 50 seconds has usually elapsed.

When, in extending, the body of the Stentor has become about half or two-thirds its original length, the ciliary disc begins to unfold and the cilia to act, causing the current to reach the disc as before. If with the current the stimulus again acts upon the animal (as when the sepia or the chemical is kept near), immediate recontraction follows.

This may be repeated many times. To certain sorts of stimuli, as will be seen later, Stentor may get accustomed, so as to unfold and behave in the usual manner while the stimulus continues undiminished. We will consider for the present the case where the continuance of the stimulus involves continued repetition of the reaction. This case is realized when a dense cloud of carmine grains is kept where it will strike the Stentor as soon as it expands, or when various chemicals are kept in this position. In such a case the contractions are repeated, as above described, usually for a period of ten to fifteen minutes. Often the animal, after a number of contractions, remains within its tube a longer time than at first. But more often there is little change in the time of contraction until toward the end of the period of ten or fifteen minutes. If the stimulus continues, the next phase of the reaction now sets in, described in the following.

Abandonment of the tube. — After the stimulus has been thus repeated at every unfolding of the Stentor for ten to fifteen minutes, the animal contracts violently several times, without intervening full extension. The short clavate body merely lengthens a little, then contracts suddenly and powerfully into a still shorter mass. This is repeated until the attachment of the foot of the Stentor at the bottom of the tube is broken, and the animal is free. It now leaves the tube and swims away. The animal may swim forward out of the anterior opening of the tube, but if this takes it into the sphere of operation of the stimulus, as will very often be the case, it may force its way backward through the substance of the tube, and thus gain the outside, swimming backward. It then swims away, to form a new tube elsewhere.

Behavior while free. — While thus swimming through the water, after leaving its tube, Stentor takes on the characteristic behavior of the free-swimming infusoria, such as Paramecium. In the open water stimuli are almost lacking for the guidance of the animal, hence its behavior is, paradoxical as this may seem, much less free and varied than is that of the fixed infusorian, or the infusorian creeping on the bottom; it becomes quite stereotyped. The writer has previously given (Jennings, 1899*b*) an account of the main features in the behavior of Stentor polymorphus when swimming in the open water. The behavior of Stentor rœselii is essentially similar in character. It rotates to the left on its long axis as it swims, and at the same time it swerves toward one side, — apparently toward the right aboral side. Its path thus becomes a spiral, like that of Paramecium (for the significance of this spiral swimming, see Jennings, 1901). When the Stentor in its course comes into the region of a stimulating chemical or other stimulating agent, the animal swims backward a little, turns toward the right aboral side, and swims forward again. In all these respects its behavior is essentially like that of Paramecium, as described in the second of these studies (Jennings, 1899*a*), so that it will not be described in detail here. At first after leaving the tube the Stentor is strongly contracted, of a very short oblong or club-shaped form. Usually as it swims it gradually extends a little, taking a long conical form, but remaining much shorter than the fixed specimen. The animal thus swims rapidly for some time about the vessel in which it is confined. It may be observed that the Stentor as it swims secretes over the posterior half of its body a transparent mucus or sticky substance of some sort, since carmine grains or other small particles in the water often cling to the posterior half of the body, or are trailed along some distance behind it, — the mucus evidently pulling out to form threads.

On coming against the surface film or the smooth surface of the glass, the Stentor behaves in a peculiar way. The (only partly unfolded) disc is applied to the surface, and the animal creeps or spins rapidly over the surface, often revolving to the left; sometimes not revolving, and always progressing in the direction of the right aboral side or angle of the disc.

On coming in contact with a bit of plant tissue or débris (consisting in the cases observed largely of worm-castings), the Stentor usually creeps rapidly over the débris, keeping the ventral surface against it. It thus follows all the irregularities of the surface, as rapidly and neatly as this would be done by one of the Hypotricha. This may continue for some time, the animal seeming to explore the object thoroughly; then it may leave the débris and swim about freely again for a period. At times the Stentor becomes attached to a piece of débris by the secreted mucus. This is drawn out to form a thread, often several times the length of the Stentor; by means of this thread the Stentor remains suspended in the water, as it were, whirling about on its long axis. It may thus remain partially attached for some time; then the thread is broken by a sharp contraction of the body, and the animal swims away.

Formation of a new tube, and attachment of the foot. — Finally (in three cases that were timed, after fifteen to twenty minutes) the Stentor forms a new tube and attaches itself. This is done as follows. The animal, coming to a small heap of débris, creeps over it with ventral surface against it, as above described, exploring it thoroughly. It becomes evident that mucus is being secreted over the surface of the posterior half of the body, since particles of débris stick to the body, or are trailed behind it. Finally, in a certain region, often between two masses of débris, the animal begins to move backward and forward, through a distance of only about three fourths of its own length (when contracted). This is kept up for about two minutes, and results in the formation of a short mucus sheath, from the secretion on the outer surface of the Stentor. This process is illustrated in Fig. 6. Now the foot is pressed against the débris at the posterior end of the sheath, where it adheres, — doubtless by the extrusion of pseudopodia, as illustrated in Fig. 2. Now the Stentor extends its body to the full length, — and we find it in the usual attached condition, with the lower half of the body surrounded by a transparent tube of mucus.

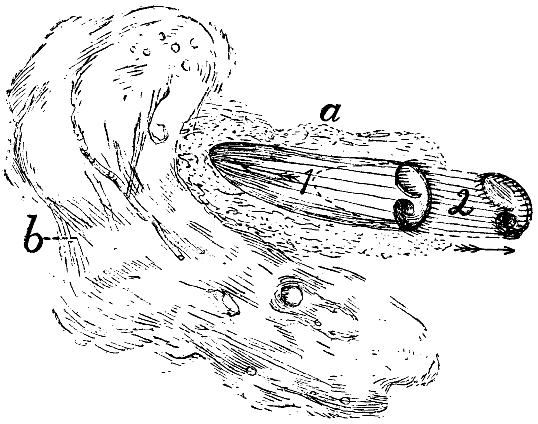

FIGURE 6. — Illustrating the movement of Stentor in forming a new tube. The animal oscillates between the positions 1 and 2, giving off mucus, which forms the tube. *a*, mucus forming the tube; *b*, débris.

The above account is drawn from observation of the process of settling down and forming a tube in several specimens, and seems to be typical. In one case observed, however, the animal attached itself to the smooth surface of the glass, and this time the process differed. After wandering about for some time, as described above, the specimen applied its disc to the bottom of the vessel, and revolved for some time on its long axis. Then it ceased revolving, and slowly bent its body till the foot reached the bottom, — the body becoming nearly straight again and tangential to the surface, before this was accomplished (Fig. 7). The foot attached itself to the bottom, then the disc was lifted up, and the body took a position perpendicular to the surface. The animal was now attached in the usual way, though the beginning of the tube had not been made. The tube in such a case is formed later, automatically, as it were, by the secretion of mucus on the surface of the body. This becomes compacted and confined to the posterior half of the body by the contractions of the Stentor in responding to stimuli.

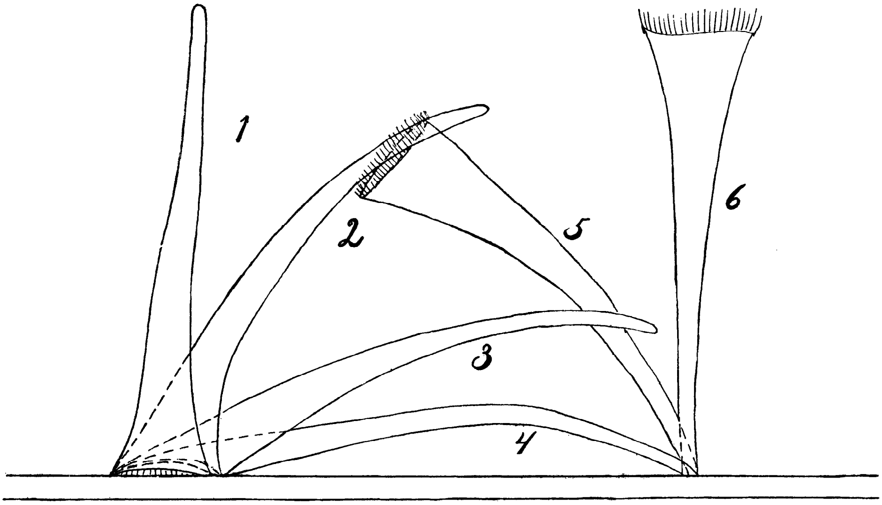

FIGURE 7. — Illustrating the manner in which Stentor rœselii attaches itself to a smooth surface. The figures 1–6 represent the successive positions occupied by the Stentor.

Usually, however, the tube is formed before the attachment of the foot, in the manner first described.

Having thus described the typical series of reactions when Stentor rœselii is subjected to mechanical stimuli, or to a combination of mechanical and chemical stimuli, we may return and consider the effect of some other stimuli, as well as a number of matters of a different character.

II. Chemical stimuli. — Results essentially the same as those above described are obtained in stimulating Stentor rœselii by means of chemicals. But there are certain points which are of much importance for understanding the method by which such organisms react to chemicals; these will be brought out here.

When a chemical of sufficient strength to act as a stimulus, yet not strong enough to be destructive, is allowed to reach the disc of an attached Stentor, the same series of reactions is given as has been described above, — changing position, reversal of ciliary current, contraction, and final abandonment of the tube. These results were obtained with a weak solution of methyline blue; with the red filtrate from carmine in water, with $\frac{m}{100}$ NaCl, with $\frac{m}{100}$ HCl, and with $\frac{m}{10}$ cane-sugar. In the latter case the effect was evidently due to the osmotic action of the sugar, as will be shown later. Other chemicals were not tried.

After it was found that Stentor would bend directly toward the source of a weak mechanical stimulus, as described above, it was thought possible that an opportunity might be here presented for demonstration of positive or negative chemotropism, — a bending to or from the source of diffusion of a chemical. In other infusoria the writer has been unable to observe a direct turning toward or away from the source of diffusion of any chemical, so that this seemed an opportunity not to be missed. The experiments in this direction developed certain facts which are of much significance for understanding the reactions not only of Stentor, but of other ciliates and flagellates, to chemicals.

The attempt was made to localize very accurately the action of the stimulus, by the use of fine capillary tubes, bringing the chemical near to one side of the body, — so that it might affect one side alone. The Stentor might then be expected to bend toward or away from the side affected. This involves no difficulty in manipulation, but an insuperable difficulty is at once met in the course of the currents produced by the cilia of Stentor. Chemicals placed at one side do not reach the animal at all, as will be seen by an inspection of the course of the currents in Fig. 1. The chemical at *a* is carried past the animal without touching it. This is rendered evident when some colored chemical, such as a solution of methyline blue, is used. If the point of the tube is moved farther toward the front of the Stentor, the solution is involved in the central vortex and is carried directly to the buccal pouch and the mouth (as at *b*, Fig. 1).

Thus unilateral stimulation with a dissolved chemical, elsewhere than at the mouth, is practically impossible. This is true also when the chemical in solution is advancing with a broad, plane front, as illustrated in Fig. 8. In such a case the solution does not reach the Stentor uniformly distributed, as determined solely by the movements of the ions. On the contrary, as soon as the advancing solution has arrived within a certain distance of the animal, a small cone of the substance is drawn out by the vortex, directly toward the disc of the animal. The point of this cone reaches the buccal pouch and mouth of the Stentor, long before the rest of the chemical has affected the animal. This is very clearly seen when colored chemicals are used.

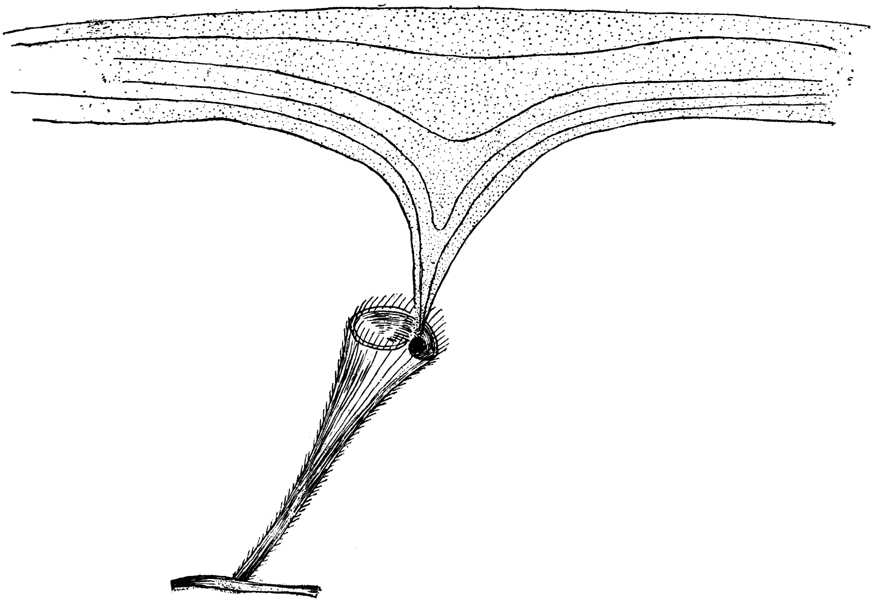

FIGURE 8. — Illustrating the way in which an advancing chemical is drawn out in the alimentary vortex, so as to reach the mouth and disc of Stentor without affecting the remainder of the body.

The result is that the animal always receives its stimulus from a chemical at a certain definite spot, — the mouth or buccal pouch, — while the rest of the chemical remains some distance away. It is obviously impossible for the animal to orient itself in accordance with the natural lines of direction of the diffusing ions. If the organism turns away from the side affected by the chemical, it will of course turn toward the aboral side, — that opposite the mouth, without regard to the original direction of the source of diffusion of the chemical, — and this is exactly what the animal does.

Parallel conditions exist in the other infusoria. In Paramecium, for example, a strong current, corresponding to that which reaches the buccal pouch in Stentor, passes along the oral groove to the mouth, the current over the rest of the body being slight in comparison. When a colored solution is used, and a nearly or quite quiet Paramecium is found, it may be observed that an advancing chemical behaves in much the same way as in Stentor. A cone of the solution is drawn out opposite the anterior end of the Paramecium, and passes down the oral groove to the mouth (Fig. 9). The Paramecium receives its stimulus from the chemical, therefore, on the oral side, —and responds, like Stentor, by turning toward the aboral side, — usually after swimming backward some distance.

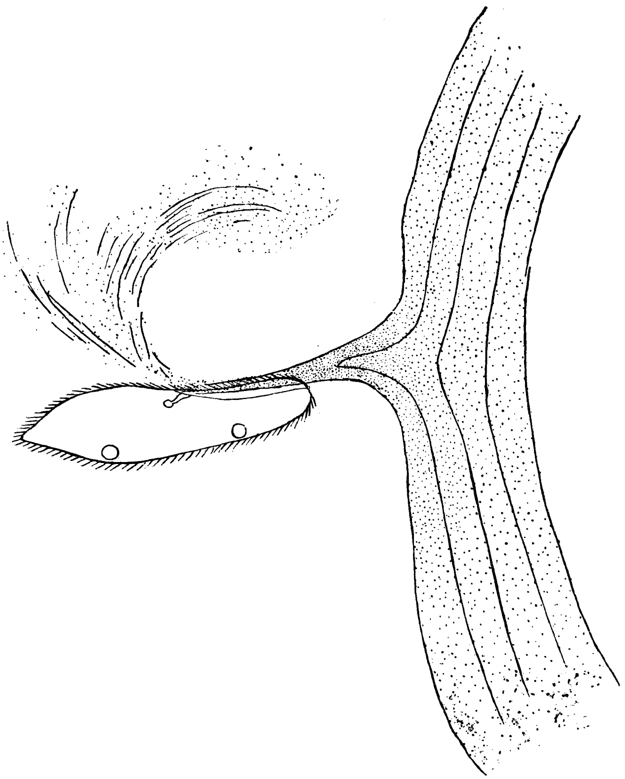

FIGURE 9. — Paramecium, showing how an advancing chemical is drawn out by the alimentary vortex, so as to reach the oral side without affecting the rest of the body.

These examples show that we are not justified in expecting the ciliate infusoria in which similar conditions occur to orient themselves to the lines of direction of diffusing ions, as presupposed by some current theories of the reactions of organisms to chemicals. The organisms are active, and determine for themselves where the stimulus shall first affect them. It is not at all surprising, therefore, that they have not been found thus to orient themselves.

In the Flagellata, owing to the minute size of the body, it is impracticable to determine by experiment whether the conditions for stimulation are or are not the same as those just described for ciliates. But in view of what is known of the movements of the flagella in these organisms, with resultant formation of a vortex having its apex at the mouth,[1] together with the known asymmetry of most flagellates, it can hardly be doubted that the conditions are practically identical with those found in the ciliates. In this group, then, as in the Ciliata, we should not expect to find the organisms orienting themselves to the lines of diffusing ions; they do not permit the ions to follow alone the laws of diffusion, but actively intervene to determine the distribution of the substance in solution. These facts certainly deserve consideration in all work on the reactions of Ciliata and Flagellata to chemicals.

Similar considerations apply to the reactions to other stimuli, in so far as the distribution of the agents concerned depends upon currents in the water. This would be the case, for example, with the reactions to heat and cold, in so far as the stimulation is due to differences in the temperature of the water in different regions. Figures 8 and 9 would serve equally well for the conditions when we have an advancing region of water which is warmer or colder than that about the infusorian. The warmer (or colder) water would be drawn out into a cone and then into a stream, which would affect only the oral side of the animal. It is therefore not surprising that we do not find a direct orientation produced by heat and cold in these animals, the so-called thermotaxis being brought about through the mediation of the " motor reaction " (backing and turning toward the aboral side; see Jennings, 1899*a*, page 334).

To radiant heat, to light, and to the electric current, these considerations, of course, do not apply, as the distribution of the stimulating agent in these cases is not affected by currents in the water.

The fact that Stentor and Paramecium (as well, of course, as many other infusoria) are first stimulated by a chemical on the oral side, and that they respond by turning toward the opposite (aboral) side, seems to indicate that the reaction of these organisms is, primitively

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[1] See DELAGE et HEROUARD, 1896, pages 306–312, for a full account of the movements of the flagella and the formation of the alimentary vortex.

at least, truly a localized one. The reason why in reacting they always turn toward the same side would be merely because they are always stimulated on the same side (the opposite one). If this is true, we should expect them, if the stimulus were in some way made to affect the other (aboral) side, to turn toward the oral side, contrary to their usual habit. This may have been the original condition of affairs, and possibly infusoria may exist in which it is realized even at the present time. But that it is not true for most of the infusoria is shown by the reactions to localized mechanical stimuli, as described in the fifth of those studies (Jennings, 1900). It there appears that when ciliates are stimulated on the (unaccustomed) aboral or right side, they respond by turning toward that side, — exactly as when they are stimulated on the opposite side. The unilateral method of reaction has become strongly stamped upon the organisms, being indicated in the unsymmetrial form.

III. Osmotic stimuli. — As in the case of Paramecium, sugar seems not to affect Stentor through its chemical qualities, but only through its osmotic action, so that opportunity is given for determining the nature of the reaction to changes in the osmotic pressure of the surrounding medium. $\frac{m}{30}$ cane-sugar (about 1 per cent) caused no reaction whatever, though electrolytes of the same osmotic pressure caused a marked reaction, — showing the effect to be due to the chemical qualities, in the latter case. When Stentor was flooded with $\frac{m}{10}$ cane-sugar, there was no reaction for seven or eight minutes. By this time the plasmolyzing effect of the solution was very evident; the animals had shrunk considerably. Now there was a sudden strong contraction, the animal remaining contracted several minutes. It then let go its hold and abandoned its tube, forcing its way backward out of the latter.

Even with $\frac{m}{1}$ sugar (about 34 per cent) the response was not immediate. The animal conducted itself normally for about twenty seconds after it was flooded with the solution. By this time shrinkage due to plasmolysis is very evident to the eye; the animal contracts and finally leaves the tube.

B. OTHER FIXED INFUSORIA.

In giving an account of the behavior of some other fixed infusoria, I shall confine myself largely to a comparison with Stentor rœselii, bringing out the resemblances and differences, and entering into details only in case of important differences or additional features.

STENTOR CÆRULEUS EHR.

Stentor cærulus differs from S. rœselii in form and in its blue color, and it is usually larger, at least in this region. It does not inhabit a tube, and though frequently attached, it is much more inclined to a free life than is S. rœselii, so that it is often found swimming freely in large numbers.

In an attached Stentor cæruleus the ciliary currents are essentially like those of S. rœselii, and parallel statements may be made for both species as to the ingestion of food particles.

Stentor cæruleus is much more sensitive than S. rœselii; otherwise its reactions to mechanical and chemical stimuli are of the same general character, though with several important points of difference.

Stentor cæruleus does not usually bend over toward a solid object touching one side of the disc, as does S. rœselii. A large number of experiments on this point gave uniformly negative results.

When the particles of solid substance which are brought against the disc by the water currents are too large, too numerous, or mingled with some chemical, the animal responds, as does S. rœselii, by twisting somewhat on its long axis, then bending toward the right aboral side into a new position; by reversing the ciliary current for an instant, and repeating this; by contracting the body; and finally by breaking from the point of attachment and swimming away through the water. In these reactions there is little that is essentially different from the corresponding reactions of S. rœselii. A favorite method of changing the position when stimulated is shown in Fig. 10. The specimen backs strongly until the stalk is doubled near the foot. The animal then straightens the body into the position

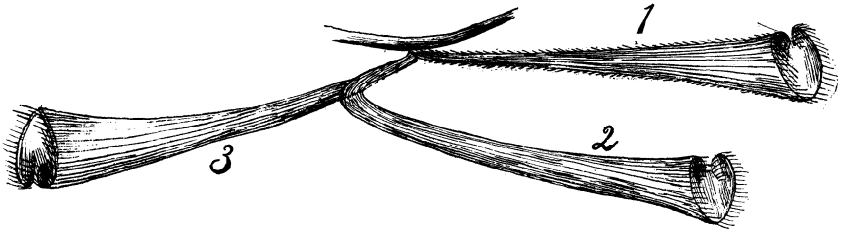

FIGURE 10 — Method by which Stentor cæruleus often changes position when stimulated. The animal occupies first the position 1, then pushes backward into the position 2, with stalk bent, then straightens into position 3.

indicated by the part next to the foot, — thus at an angle of 180° with its previous one.

Stentor cæruleus has recourse to the last step in the series of reactions, — the abandonment of its place of attachment, — much more readily than does S. rœselii. In the latter species I was unable to force the animal to leave its place by mechanical shocks alone. Specimens were stimulated by striking the disc with a glass rod, sometimes for an hour continuously, yet the animals did not leave their place. Stentor cæruleus, on the other hand, will sometimes break its attachment the first time it is struck with the rod. There is much variation among different specimens on this point; usually it requires many such strokes to produce the result, and all the other reactions in the series are tried first.

After leaving the place of attachment, Stentor cæruleus swims through the water in a rather wide spiral, revolving to the left. The body is usually somewhat curved toward the oral side, and apparently as a consequence of this, the animal swerves continually toward the oral side. The tendency to deviation thus caused is corrected by the revolution on the long axis. When the free-swimming Stentor receives a mechanical or chemical stimulus, it swims backward a little, then turns toward the right aboral side. The behavior of the free-swimming Stentor is thus essentially similar to that of Paramecium.

As the Stentor swims about well extended, frequently protoplasmic projections may be seen extending from the tip of the foot. These are viscid, so that bits of débris stick to them and are dragged about; sometimes other infusoria, such as Paramecium, coming in contact with the foot, are thus dragged along. I have seen two Stentors become attached to each other through the accidental coming together of the two posterior tips. If a small glass rod is placed against the tip of the foot, the Stentor may frequently be dragged backward by it, owing to adhesion.

Often Stentor drags its foot over the bottom or over pieces of plant material. Sometimes it stops in such a position, and in a few seconds the foot is securely fast and the animal is anchored anew.

Stentor cæruleus, unlike S. rœselii, reacts to light. The reactions of this and some other ciliates to light will be treated in a separate paper.

VORTICELLA.

Owing to its minute size, Vorticella is much less favorable for a study of behavior than is Stentor. I was especially desirous of investigating it however in connection with certain statements made in a very interesting paper by Hodge and Aikins (1895). These authors investigated chiefly the question of the rhythmical character of the activities of Vorticella. They kept a single Vorticella under observation without a moment's intermission for a period of twenty-one hours, besides intermittent study for a number of days. The observations showed "that a Vorticella works continuously and shows in its life no period of inactivity or rest, corresponding to periods of rest in higher animals. In other words, a Vorticella never sleeps." During five days the cilia were in continuous motion, and food was continuously taken.

Incidentally, Hodge and Aikins made a number of observations on other points. One of these was in regard to the modifiability of reactions in Vorticella. An attempt was made to feed the individual under observation upon yeast plants, by introducing some of a pure culture of these organisms into the preparation. "This attempt resulted in an interesting demonstration of the educability of Vorticellæ. At first they took this, to them, newly discovered food with great avidity, filling their bodies to distention with food vacuoles of the yeast. In a very few minutes, however, the entire meal was ejected with volcanic energy. Not a single torula was allowed to remain in the body, and for several hours at least — how long the memory lasted was not determined — the individual could not be induced to repeat the experiment."

It is much to be regretted that further details are not given in regard to this interesting experiment. We are not told whether the Vorticella continued its normal behavior and took in other food during the time in which it refused the yeast. It might be that the animal was merely injured by the food, and took nothing more into its body until it had recovered. We are not informed in what way Vorticella refused later to take the yeast, — whether by contracting, by reversing the ciliary current and turning the yeast out of the pouch, or in some other way. Yet upon these points depends largely the interpretation that shall be given to the observation.

I have endeavored, and as I judge with some success, to reproduce the essential features of this experiment. I have not succeeded with the yeast, for the Vorticellæ at once contracted, in my experiments, when the yeast culture was introduced. But a similar result may be obtained in a very simple way. In the case of the yeast culture we have a fluid containing various chemicals in solution, and holding in suspension many small bodies. These conditions may be imitated by grinding up ordinary carmine in water. A little of the carmine goes into solution, as may be shown by filtering the water, which will be found to have become red. This red solution was found to act as a slight chemical stimulus, on both Vorticella and Stentor.

When some of this carmine and water is added to the water about the Vorticella, the course of events is about as follows. For a short time — ten to fifteen seconds, or sometimes more — the current caused by the cilia is kept up in the usual manner, and many of the carmine grains are taken into the internal protoplasm, forming red food vacuoles. Then there is a sudden contraction of the stalk, the ciliary disc closing at the same time. This is repeated several times, the ciliary disc however remaining closed while the stalk partly extends and recontracts. Then usually the Vorticella extends in a new direction. If the carmine continues to be present, the contractions are repeated for ten or fifteen minutes or more. Then the stalk may remain extended, but the ciliary disc remains closed, so that no more carmine is ingested. This condition lasts as long as the carmine is present in large quantities.

Thus in this case, as in that described by Hodge and Aikins, Vorticella at first ingests a certain substance which it later refuses. This is also true of Stentor, as will be seen by consulting the account above given of the behavior of Stentor when much carmine is added to the water containing it. In no case was Vorticella observed to throw out the granules which it had already ingested, as described by Hodge and Aikins, but this is perhaps an unessential difference, as of course this has nothing to do with the "educability" of the animal.

In this experiment, I am convinced that the refusal of the Vorticella to continue to take the substance is due to a too great stimulation, either in the quantity of material, or, more probably, in the strength of the chemical action of the substance, rather than to any precise choice in the kind of substance ingested. There is evidence for this in the following fact. If the quantity of carmine in the water is greatly decreased, so that only scattered grains are left, the

Vorticella or Stentor no longer reacts to these, and they are ingested, gradually forming red vacuoles in the endosarc. Whether this would have been true in the experiment of Hodge and Aikins the data they have given do not enable us to judge.

In regard to a point closely connected with the above, the attitude of Hodge and Aikins must, I think, be considered uncritical. This relates to the sorting of food by the cilia. Among the "psycho-reflexes" of Vorticella, Hodge and Aikins include "3. Sorting of particles by the sensory cilia; the driving of food toward the mouth, and the driving away of waste particles." Further "When a particle is touched by the cilia an act of choice is apparent, and in accordance with this choice the particle is carried toward the mouth or whirled away." "Particles scarcely visible under the microscope are sorted with the greatest apparent precision." "A prime condition of the creature's life must be ability to distinguish food from that which is not food."

Beyond these general statements quoted no details are given. The authors report no critical observations or experiments as to what substances are ingested, what rejected in this sorting process. It is well known that investigators that have made such experiments have concluded that no such sorting takes place. Thus Verworn (1889, page 150) found that Vorticella ingests carmine grains, indigo, and chalk crystals, and I have myself observed the same facts. These are substances which cannot serve as food, so that Hodge and Aikins are certainly mistaken in their belief that "a prime condition of the creature's life must be the ability to distinguish food from that which is not food." Such organisms as Vorticella and Paramecium grow and multiply in situations such that the substance brought to the mouth by the currents consists largely of food, without any sorting; when this condition disappears, the organisms quickly die. The ingestion at the same time of some substances which do not serve as food is not particularly injurious to the organism, as these are simply passed out of the body with the waste matter at the time of defecation.

The impression that a sorting and selection takes place among the particles brought to the mouth probably arose from the following observations. Vorticella, as well as Stentor, brings to the buccal pouch in its alimentary vortex many more particles than are taken into the body. When the water contains many particles a continuous stream of these may be seen passing out of the buccal pouch. From this it is most natural to conclude that the material has been sorted, the valuable particles ingested, and the particles which are not nutritious turned away. But experiment does not support this conclusion. Thus, when all of the particles are of the same sort, either nutritious or not, part are taken into the interior, while a large portion are turned away. This is true on the one hand of grains of sepia, which are quite insoluble and non-nutritious; it is true, on the other hand, also, when many nutritious unicellular algæ are brought to the mouth. In the latter case, as in the former, many more of the particles are turned away than are taken in. The explanation of these facts is evident when one considers the mechanism of the alimentary vortex, as has already been pointed out by Verworn (1889). A large, strong current of water is carried toward the disc of the Vorticella. Inevitably, much of the water misses the disc completely, and the food particles which it contains never touch the animal. Another portion of the water strikes the disc, but not all of this can enter the relatively small buccal pouch, so that many of the food particles which strike the disc are whirled away again into the water. In the same way a rapid whirlpool is formed in the buccal pouch, but only a small part of the water in this can reach the relatively minute mouth, and it is only from this small part that the food can be taken. Thus there is a continual stream of particles passing out of the pouch, that have never come in contact with the mouth.

These mechanical considerations explain also the following noticeable fact. When the water contains but few particles, whether nutritious or not, only a few are ingested, while a large proportion of them are whirled out of the pouch and away. When the number of particles in the water is great a large number are ingested in a short time, without regard to whether they are or are not useful as food. The number of particles ingested depends primarily upon the number which reach the mouth opening, and this is only a small proportion of those involved in the general ciliary vortex.

This question of the sorting power of the cilia is, I take it, merely one of fact, and not one involving any important principle. What we know of choice in the Rhizopoda, and the parallel phenomena in inorganic fluids, to which reference has already been made, shows that there would be nothing new in principle if the cilia of Vorticella exercised choice in the same way. But the facts seem to indicate that they do not. Choice in these animals seems to be shown only in such phenomena as the reversal of the ciliary motion, bending over into a new position, and contraction, — these being, of course, different methods, somewhat crude perhaps, of rejecting certain things, and thus of exercising choice.

C. Becoming Accustomed to Stimuli.

Are the reactions of such organisms invariable, or does the reaction to a given stimulus depend on previous subjection to the same or different stimuli? The problem of the modifiability of the reactions of these lowest organisms is one of great interest, but one on which there exists but little precise experimental data. Scattered allusions to changeability in the reactions of the lower organisms are to be found in the literature, especially with relation to what might be called acclimatization to stimuli. Massart (1901, page 8) states that it is often to be observed that organisms which have reacted several times in succession, at short intervals, to a given stimulus, lose, little by little, the power of responding to this stimulus, but that this is doubtless to be attributed to fatigue. Loeb (1900, page 228) has discussed such a case in the reactions of worms to a shadow, as described by Nagel, and has attributed the lack of reaction when the stimulus is repeated to "a simple after effect of the stimulus, a case that we often meet with in the physiology of both animals and plants." Davenport (1897, page 108) gives an example drawn from the behavior of one of the organisms at present under consideration. "When an organism has been stimulated by contact for some time, it at last becomes changed, so that it no longer responds as it did at first. Thus, Dr. W. E. Castle informs me that he has seen a colony of Stentors, in an aquarium, being constantly struck by Tubifex waving back and forth, yet the Stentors did not contract as they usually do when struck."

Such contractions in the fixed infusoria furnish a most favorable opportunity for an investigation of this matter, and I therefore undertook to obtain some precise experimental data upon the subject. Experiments were made upon Stentor rœselii, S. cæruleus, Vorticella, Epistylis, and Carchesium.

First, the conditions described in the observation by Castle, above cited, were imitated, by striking the extended infusorian with a fine glass rod or hair, under the Braus-Drüner stereoscopic binocular. The chief difficulty in these experiments is to make the successive strokes approximately equal in force. This can be done but very imperfectly; nevertheless the results are clear.

The first stroke, whether light or heavy, given to an individual that has been undisturbed for an hour or more, almost invariably results in causing a quick contraction. This is true for all the organisms worked with. The animals remain contracted a minute or less, then slowly extend. At the instant when extension was complete, another stroke was given. This, and several successive strokes usually caused the same reaction as the first one. After ten or a dozen reactions, however, the organisms usually did not contract as soon as touched; the stroke had to be repeated one or more times before reaction was caused. A typical series for Stentor cæruleus is given in the following. The figures represent the number of strokes in each case before contraction took place, — a contraction occurring thus at each dash:

1—1—1—1—1—1—1—2—2—1—2—1—2—4—1—1—1—1—1—2—6—10—1—2—9—13—3—14—7—3—2—3—3—9—18— (at this point the Stentor pulled its foot loose and abandoned its place).

As is evident from the above, there is much irregularity in the number of strokes required to cause contraction. This is due, partly at least, to the practical impossibility of giving successive strokes of equal force. But the Stentor responded at first to the lightest possible touches, while later it required a considerable number of smart strokes to cause contraction.

Sometimes there is a ready response only to the first touch, as in the following series (Stentor cæruleus):

1—22—25— (breaks away).

1—1—40— (breaks away).

In these cases the organism does not remain entirely oblivious to the blows, but after it has ceased to react by contracting it continually changes its position, by twisting, then turning toward the aboral side, as if trying to escape from the blows. The final reaction, in Stentor cæruleus, is to break away from its attachment and swim away.

In Stentor rœselii, Vorticella, Epistylis, and Carchesium, similar results were obtained, save that these organisms never broke away from the attachment as a result of such mechanical stimuli. A typical series for an individual of Epistylis flavicans, var. procumbens, was as follows:

1—1—1—1—1—1—1—2—33—25—7—13—36—20—14—13—13—33—9—30—3—31—226.

In another series the results were as follows:

1—22—10—3—3—1—1—22—59—125— (continuous blows for 1 min.) — ($\frac{3}{4}$ min.) — ($1\frac{1}{2}$ min.) — ($4\frac{1}{2}$ min.).

Some series show greater irregularity than the above. As in the case of Stentor, during the latter part of the experiment the Epistylis continually changed its position, as if trying to escape from the blows.

A typical series for Stentor rœselii, obtained in this case by jarring with the rod the leaf to which the Stentor was attached, is as follows:

1—1—1—1—1—1—1—1—1—1—1—1—3—1—5—1—1—3—1—3—3—48—40 —2—250—36—36—154.

The results for Vorticella are similar. In a typical case the animal contracted after each of the first nine strokes. Then the contractions became less sudden; two or more strokes were required to produce them. After about twenty contractions the Vorticellæ could be tapped almost indefinitely without causing further contraction.

Carchesium polypinum is a tree-like colony composed of many Vorticella-like individuals, attached to the branches of a common stalk. The stalk muscles of the individuals are not continuous throughout the colony, so that it is possible, though not usual, for each individual to contract separately.

Carchesium shows very markedly the acclimatization to a stimulus. Observing first the reactions of a single individual that is repeatedly stimulated, it is found that its stalk contracts strongly at every stroke. But after about five minutes there is a marked change in the readiness to respond. Several strokes are required to cause contraction. Still later the stalk ceases to contract when the individual is struck, though for a time the peristome is folded inward and the ciliary motion ceases after every stroke, without contraction of the stalk. When thus continuously stimulated, usually the stalk contracts at intervals of two or three minutes, — though the strokes come as often as one per second.

The effect of the stimulation of a single individual on the colony as a whole is interesting If a single individual in an otherwise undisturbed colony is struck with the glass rod, usually the entire colony contracts at once, forming an almost solid ball. Apparently the sharp contraction of a single individual, by jarring the colony, acts as a stimulus to cause the contraction of all the other individuals. If the stimulus is repeated (on the same individual) as soon as the colony has become extended, usually only about half of the colony contracts. The third time only the large branch reacts to which the individual stimulated belongs. After this the number of neighboring individuals contracting when the single individual reacts is variable, ranging usually from half a dozen to thirty or forty. When the condition is reached where the individual, continually stimulated, reacts but once in two or three minutes, nearly the entire colony contracts with it.

What is the explanation of this failure to react to a stimulus to which the organism at first reacts readily? Three possibilities present themselves. (1) The lack of reaction might be due to fatigue of the contracting apparatus (corresponding to muscular fatigue in the higher animals). (2) It might be due to fatigue of the sensory function, so that the organism no longer perceives the stimulus (corresponding to fatigue of the sense organs in higher animals). (3) It is possible that the phenomenon cannot be explained as fatigue, so that all we can do is to formulate the facts, calling it an "after-effect," or other name which carries no implication as to its nature. We should perhaps have parallel phenomena for this also in the case of a higher organism, which reacts to a sudden, unexpected shock, but does not react a second time, though the stimulus is repeated, and is perceived by the organism.

Some farther data needed for forming an opinion as to which of these possibilities represents the truth may be obtained by varying the experiments. Striking the animal with the glass hair is a rather brutal method of experimentation; reactions may be produced with much slighter stimuli, and the results are much clearer.

For this purpose weak currents of water may be employed. This was done as follows: A tube 28 cm. long and of 5 mm. bore was drawn to a very fine capillary point and then filled with water. When the capillary end is below, there is of course a slight current of water from the tip, due to the pressure of the water in the tube above. Now the tip was brought close to an individual of Epistylis, so that the current flowed against the latter. At once the animal contracts. If the current is continued the Epistylis soon unfolds, and continues open and active in spite of the current. If now the tube is removed, so that the current no longer acts, then in a few seconds is restored, the animal does not react. Moving the tip of the tube over to a fresh specimen, this reacts at once. Moving it back to the first specimen, this does not contract. With a large colony of Epistylis, it was possible thus to test many specimens;

invariably the animal reacted to the stimulus of the current the first time, but later did not. In a very few cases a certain individual would react also to the second or third or even fourth stimulus, but soon ceased, and in a large majority of cases the animals reacted only the first time.

In Stentor rœselii the same results were obtained. The animals invariably reacted to the first stimulus of the current, but none of the numerous individuals studied reacted to a repetition. Stentor cæruleus behaves in a similar manner. In this species the individuals often respond only once by contraction, even to the stimulus of a stroke with the glass rod; after the first contraction they react only by bending over into a new position.

A large colony of Carchesium polypinum was situated just beneath the surface of the water. Touching the surface film with a needle, the colony at once contracted strongly. It was allowed to expand, and the surface film touched as before. There was no contraction. Repeated touching of the film caused no reaction, except the first time. Jarring the branch to which a colony was attached gave rise to a parallel series of phenomena.

From these results it is clear that the lack of reaction cannot be due to fatigue of the contractile elements. It is possible, as I have demonstrated by experiment, to keep Stentor continuously contracting for an hour at a time. Yet the animal responds only once to a weak stimulus; it cannot be supposed to have been so fatigued by this single contraction that it cannot contract farther.

It seems evident also that the failure to react after the first time cannot be due to fatigue of the sensory or perceptive power. It can hardly be supposed that a single stimulus would result in such fatigue that further stimuli are no longer perceived. Moreover this supposition is directly negatived by the fact that in many cases there is other proof that the organism does continue to perceive the stimulus. Thus, with Stentor cæruleus, as described above, at the first stimulus by tapping with the glass rod the animal contracts suddenly and strongly. After this it no longer contracts, but the fact that it perceives the stimulus is shown by its bending far over first in one direction, then in another, as the stimuli are continued, as if trying to avoid the blows. The impression made on the observer is very much as if the organism were at first trying to escape a danger, and later merely trying to avoid an annoyance. Similar phenomena may be observed with Epistylis and Vorticella.

Thus the third alternative seems the only conclusion to which we can reasonably come, in view of the facts. The organism becomes changed after stimulation, in such a way that it no longer reacts to a stimulus to which it at first reacted. There is a difference in the physiological condition of the organism before and after the stimulus. One can hardly avoid comparing these phenomena with the fact that in a higher organism a sudden unexpected touch or other stimulus will cause a reaction or "jump," when the same stimulus, not unexpected, causes no reaction whatever. It seems not improbable that the phenomena are similar in fundamental character in the two cases.

This resemblance is increased by certain further considerations. It is only when the stimuli are non-injurious that the unicellular organism ceases to respond upon repetition of the stimulus. If the stimulus is very powerful or injurious, the reaction is continued indefinitely. I attempted to accustom Stentor to the stimulus from a very minute quantity of $\frac{m}{150}$ NaCl, brought close to it with a minute capillary tube. Though the stimulus was repeated at very short intervals for an hour steadily, the Stentor reacted in every case; there was no indication of becoming accustomed to the stimulus.

The changes to be observed in the character of the reactions to a given stimulus when repeated show the same relation to the nature of the stimulus. As described in the first part of this paper, when the stimulus continues, and is powerful so that the reactions also continue, the reaction does not remain the same, but there is a series of different reactions. This series is a progression from less effective to more effective reactions, culminating in the animal's abandoning its place. On the other hand, as we have seen above, the reaction is sometimes changed also in the case of a weak stimulus, as when Stentor is tapped with the glass rod. But in this case the progression is in the opposite direction, — from a strong, effective reaction (contraction) to a weak one (bending over to one side.) The course of the reaction series, whether from less intense to more intense, or vice versa, depends upon the nature of the effect of the stimulus on the organism.

D. ANALYSIS OF THE OBSERVATIONS, WITH DISCUSSION OF THEIR BEARINGS ON CERTAIN GENERAL PROBLEMS.

The examination of the behavior of Stentor shows a striking contrast with the known behavior of Paramecium, in the much greater complexity and adaptability of the former. In Paramecium the behavior seems made up of a few simple reflexes, with little variation or adaptability. In Stentor, on the contrary, this is far from being the case. This difference is due, I believe, to the different method of life. Paramecium is typically a free-swimming organism. As I have pointed out elsewhere,[1] in the open water there are few stimuli to guide an organism, the conditions being nearly uniform in all directions. Especially is this true in the case of an organism which, like Paramecium, is not sensitive to light. The result is the development of a few simple, almost machine-like devices for governing locomotion. Such a device is the spiral course, preventing the organism from aimless wandering in circles; such a device is the invariable turning toward a certain structually marked side when stimulated, which is so striking in Paramecium. On the other hand, an organism on the bottom is continually receiving stimuli of varied character, and it develops in consonance therewith a varied behavior. This difference between the behavior of free-swimming organisms and that of those which live on the bottom is very great, and its importance is not usually recognized. Even in the same individual the behavior becomes of a very different type on changing from one of these situations to the other. Stentor when free-swimming has the same simple behavior shown in Paramecium, while in Paramecium and other infusoria the behavior is greatly modified by contact with surfaces.[2]

Proceeding to an analysis of the behavior of Stentor, it is evident in the first place that the same external stimulus is not always answered by the same reaction, but that the reaction given depends largely on the history of the individual (and thus upon its present physiological condition). Thus we find the following to be true: —

1. After reacting to a given stimulus one or more times, if the stimulus is not a harmful one, the organism may cease to react, though the stimulus is repeated without change.

2. After reacting to a given stimulus the first time by a very pronounced reaction (contraction), the organism may later react, if the stimulus turns out to be a non-injurious one, by a very slight reaction, as by bending over to one side.

3. In the case of a stimulus which must in the long run be classed

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[1] See JENNINGS, 1901.

[2] On some of the modifications in the behavior of organisms when in contact with surfaces, see especially PÜTTER, 1900, and JENNINGS, 1897, pages 305–312. There is opportunity for further investigation in this matter.

as harmful, as when a dense cloud of carmine is added to the water, a series of reactions is to be observed, becoming of more and more pronounced character, until by one of them the organism rids itself of the stimulus. The course of events in such a case is usually as follows: —

a. No reaction at first; the organism continues its normal activities for a short time.

b. Then a slight reaction by turning into a new position, a seeming attempt to keep up the normal activities and yet get rid of the stimulus.

c. If this is unsuccessful, we have next a slight interruption of the normal activities, in a momentary reversal of the ciliary current, — tending to get rid of the stimulus.

d. If the stimulus still persists, the animal breaks off its normal activity completely, by contracting strongly, — devoting itself entirely, as it were, to getting rid of the stimulus, — though retaining the possibility of resuming its normal activity in the same place at any moment.

This reaction is repeated many times, the organism extending and immediately re-contracting as soon as the stimulus is perceived. In this case it is interesting to note that the organism now responds at once to a stimulus (by contracting) to which it at first did not respond, or to which it responded only by a reaction of different, less decided character. In paragraph 1 above we have the opposite case, where the organism ceases to respond to a stimulus to which it at first did respond.

e. Finally, if all these reactions remain ineffective in getting rid of the stimulus, the animal not only gives up completely its usual activities, but puts in operation another set, having a much more radical effect in separating the animal from the stimulating agent. It abandons its tube, swims away, and forms another one in a situation where the stimulus does not act upon it.

It is to be noted that this series of reactions is not of such a character that each step necessarily produces the next one; on the contrary, the bringing into operation of any step depends upon the ineffectiveness of the preceding ones in getting rid of the stimulus. The series may cease at any point, as soon as the stimulus disappears.

Further, the succeeding reactions are not mere accentuations of the preceding ones, but differ completely in character from them, being based upon different methods of getting rid of the stimulus.

Throughout the whole of the series of reactions the stimulating agent remains without change. The differences in reaction are due then to changes in the organism, — to such changes as in a higher organism might be called changes in the "state of mind." Here we may perhaps call them changes in the " state of protoplasm," though without implying that the two expressions are fundamentally different in signification.

It is clear that it is impossible to bring such behavior under the rubric "tropisms" or "taxis," or to present it as purely reflex in character; we must at the very least take into consideration physiological states of the protoplasm, as well as reflex factors. To gain a really satisfactory insight into the behavior, it is necessary to go farther than this, and to take into consideration the ends to be attained by the different reactions and changes in reaction, — though whether this necessity has its foundation only in the human way of looking at things, or is really inherent in the behavior of Stentor, is a question on which there may be difference of opinion. In any case it will be well to analyze the behavior a little farther from this point of view. So far as outward appearances go, Stentor seems to react, like a higher organism, not merely to a stimulus now present, but to what is to come, — to the results of the action, as well as to the present conditions. The changes in the reactions, as the stimulus continues, seem to be directed toward the end of getting rid of the stimulus, — a different method being tried when one method fails. In the method of formation of a new tube, the same apparent reference to an end to be attained is forced upon the attention; there is no visible stimulus for the backward and forward movement of the Stentor, which results in the formation of a new tube; no reason that can be seen for this movement, except that it does form a tube.

We have thus in this unicellular organism the outward signs of action directed toward the accomplishment of certain ends, and thus, in so far, of intelligent action. There are, of course, a number of different ways of interpreting such phenomena. To say that the reaction is really directed toward the accomplishment of an end, is to say that the animal reacts, not merely to a present external stimulus, but also to a non-present result of its reaction. This is only possible if the organism has already, at some previous time, experienced this result, so that the latter has left a trace; has modified the organism, — changed its physiological condition. The organism when stimulated reacts in accordance with, or in consequence of, this modification, as well as in response to the external stimulus; the result is action directed toward an end.

Thus in action directed toward the accomplishment of an end there is an element in the organism, — a "trace" or "modification," corresponding to the result to be attained, and due to previous experience of this result. But a different view is often taken of action which appears outwardly to be directed toward the accomplishment of a certain result. In many such cases it is maintained that the organism really has no trace or modification corresponding to the result attained. In the case of Stentor, it would be held that the organism has become a sort of mechanism which gives a definite series of responses, when energy of such and such a character acts upon it under such and such conditions, for such and such a period of time. The result follows just as a precipitate is produced in a chemical reaction. The difficult problem according to this view is how reactions happen to be produced that are adapted to the accomplishment of certain ends. This is explained (usually) by natural selection.

In many of the instincts of higher organisms, such a view as that last set forth seems forced upon us by the fact that the organism has had no opportunity to get impressed upon it any trace or modification corresponding to the result to be produced. The animal responds before it has ever experienced the result. Cases of this sort will occur to every one.

In Stentor, however, this difficulty perhaps hardly exists, since it is not possible to separate sharply the given Stentor from its ancestors that may have experienced the results of any given reaction. Since each Stentor arises by simple division of a previous Stentor, there is here no special difficulty in the inheritance of acquired characters. If a given Stentor has become modified by certain experiences, there is no evident reason why the two Stentors derived from it by division should not retain this modification. Hence we have no absolute ground for maintaining on this basis that in Stentor the apparent reaction with reference to the result to be attained is not really a reaction with such reference. In other respects, we seem to have the same problem in attempting to explain the behavior of Stentor that we have in the instincts of higher animals.

It may not be out of place, finally, to indicate the bearing of the behavior of Stentor on the problem of consciousness in the lower organisms, a matter which has been much discussed of late. I do not see that there can be any objective criterion of consciousness, hence this question in strictness does not fall within the field of an investigation directed to the end of determining what observation and experiment can tell us of the behavior of an organism. But it may be of interest to point out the relation of the phenomena described to certain questions that have been raised. In former papers (Jennings, 1899*a*, page 339; 1899*b*, page 13), I expressed the opinion that in Paramecium the behavior was comparable to that of an isolated muscle, and that " we are not compelled to assume consciousness or intelligence in any form to explain its activities." This statement is, of course, well within the facts, as far as objective investigation can give them to us, yet it is perhaps of little significance, since it could probably be made for any organism, outside of the self. The behavior of Paramecium is of a character to emphasize strongly the possible machine-like character of the activities of the lower organisms. In Stentor we have a very different case, showing that the behavior of Paramecium cannot be considered a type for that of all infusoria. Paramecium has become adapted in its behavior to a very simple set of conditions, and its behavior is of corresponding simplicity. In the behavior of Stentor, we find all the outward indications of action directed toward the accomplishment of certain ends. We have then the same ground for attributing consciousness to Stentor as to higher animals which show behavior of a similar character, — no more, no less.

In a recent paper Minot (1902) has expressed the opinion that " the function of consciousness is to dislocate in time the reactions from the sensations," — to inhibit the direct reactions at certain times; to cause reactions at certain times to stimuli that have occurred previously. " This disarrangement . . . seems to me the most fundamental and essential characteristic of consciousness that we know, — " " — and so far as we know, it belongs exclusively to consciousness."

Judged by this criterion (substituting "stimulus" for "sensation" as used by Minot) we should clearly have to attribute consciousness to Stentor. As shown above, this organism at certain times inhibits the reactions to stimuli, to which at other times it reacts strongly. Moreover, the nature of its reactions to a given stimulus depends upon stimuli previously received, and this I think is all we can mean when we say that an animal reacts at a certain time to a stimulus previously received. I confess that Dr. Minot's criterion seems to me by no means an absolute one; and that unconscious mechanisms could be constructed, and indeed do exist, in which there is a dislocation in time between the action of an outer agent upon the machine and the reaction of the machine, similar to that which we find in organisms. It is nevertheless interesting to find the behavior of a unicellular organism falling within the category that would be considered conscious by Minot.

If we consider now the criterion held by Loeb and Bethe, — that consciousness depends upon associative memory, upon the power of learning, — it is perhaps not so easy to decide where Stentor stands. The changes in reaction when the stimulus is long continued; first no reaction, then bending into new position, then reversal of the ciliary motion, then contraction many times repeated, and final leaving of the tube, could perhaps be considered cumulative effects of the stimulus, and hence as not giving evidence of associative memory. But this of course leaves quite out of consideration the fact these different reactions are all adapted, by different methods, to getting rid of the stimulus, and it is exactly this adaptation to an end that furnishes the real problem. How does the organism happen to give these particular reactions, thus adapted to the accomplishment of an end? If it gives these particular reactions as a result of experience, it has learned, hence, on the hypothesis we are considering, it has consciousness. If it has not learned to give these purposive reactions, the only alternative hypothesis as to how this has come about is, so far as I am aware, through the action of natural selection upon chance movements.

All together, it must be clearly recognized, I think, that objective study can give us nothing final on the problem of whether consciousness does or does not exist in the lower organisms. We can have indeed no absolute proof of the existence of consciousness outside of ourselves. Whether one holds that Stentor and Paramecium have or have not consciousness will depend chiefly upon his general system of philosophy, which is of course not mainly determined by observation and experiment.

E. SUMMARY.

The foregoing paper comprises a study of the behavior of Stentor rœselii, Stentor cæruleus, and Vorticella.

Taking Stentor rœselii as the type, the following are the most important points brought out:

I. In the unstimulated Stentor the ciliary motion causes a vortex whirling to the left and descending to a point on the left oral side. Only a small part of the water or suspended material in the vortex reaches the mouth. The unstimulated Stentor does not contract.

II. Under the influence of slight mechanical stimuli, as when carmine grains or other small objects are carried to the disc by the vortex, the behavior is as follows: —

A. For a time the normal behavior may be continued, some of the particles being ingested.

B. In some cases the Stentor may bend toward an object touching one side of the disc (" positive thigmotaxis ").

C. With repeated weak stimuli, the Stentor may react the first time by contraction; then cease to react farther, though the stimulus is continued. Or the animal may react the first time by contraction; later by merely turning to one side, as described in paragraph 1, below.

D. When the objects striking the Stentor are very numerous or large or are combined with a chemical stimulus, or are otherwise unfavorable, there is a series of reactions, as follows: —

1. The Stentor first bends into a new position, by twisting on the long axis, then bending toward its aboral side. It may thus rid itself of the stimulus; if not, this reaction is usually repeated a number of times.

2. If the reaction described above does not rid the animal of the stimulus, it next reverses the ciliary current for an instant. This reaction may be repeated a number of times.

3. If the stimulus still continues, the animal next contracts into its tube. This reaction is repeated many times, if the stimulus continues, and usually the period during which the animal remains contracted becomes longer.

4. Finally, if the stimulus continues, the animal lets go its hold and abandons its tube. It swims away through the water, its behavior while free being similar to that of Paramecium. After a time it forms a new tube, by a peculiar process, in another place, where it is not affected by the stimulus, and remains there.

III. Under chemical stimuli (1) the reactions are essentially the same as above described for mechanical stimuli, the series 1–4 described above taking place in a similar manner. (2) The distribution of a diffusing chemical approaching the Stentor is determined by the ciliary vortex of the Stentor. The result is that the chemical arrives at the mouth and oral surface of the Stentor before it touches any other part of the body; the latter may remain for a long time quite unaffected. Hence the conditions necessary for the orientation of the body in lines of diffusing ions are not present, and such orientation cannot occur. This is true also for other ciliate infusoria; probably also for flagellates.

Similar considerations apply also to the reactions to temperature variations in the water.

IV. To osmotic stimuli Stentor responds only after plasmolysis is far advanced.

V. In Stentor cæruleus the behavior is essentially similar to that of S. rœselii, — the same series of reactions being given to continued stimuli. The following differences are to be noted: —

1. Stentor cæruleus does not bend toward a weak mechanical stimulus at one side of the disc, as does S. rœselii.

2. Stentor cæruleus has no tube and abandons its place of attachment much more readily than does S. rœselii.

VI. In general the reactions of Vorticella are similar to those of Stentor, though it was not observed to abandon its place as a response to stimuli.

VII. Stentor, Vorticella, Epistylis, and Carchesium were found to become accustomed to repeated mechanical stimuli, so that they cease to respond by contracting when the stimulus is repeated. This is not due to fatigue, since they frequently respond only to the first stimulus. It is likewise not due to lack of perception of the stimulus, since after ceasing to contract they often give other evidence that the stimulus is perceived.

VIII. On the whole the behavior of Stentor is complicated, as compared with that of Paramecium, and shows considerable power of adaptation. Whether the animal reacts to a given stimulus or not, and how it reacts, depends upon previous subjection to this stimulus, and upon the previous method of reacting to it. If a stimulus continues, the animal gives a series of reactions which are not invariable in order or length of continuance; each reaction of this series is adapted, by a different method from the others, to getting rid of the stimulus. These reactions, together with the method of forming a new tube, have the appearance of being directed toward the accomplishment of definite ends.

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