American Journal of Physiology.

VOL. II.

MAY 1, 1899.

NO. IV.

STUDIES ON REACTIONS TO STIMULI IN UNICELLULAR ORGANISMS. II.— THE MECHANISM OF THE MOTOR REACTIONS OF PARAMECIUM.¹

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A^S pointed out in No. I. of these Studies,² most of the reactions of Paramecium (as well as other Protozoa) are known only in their general features. The mechanism of the reactions, — that is, the motions of the cilia by which they are brought about, has been determined for Paramecium only in Ludloff's study³ of electrotaxis and my own of thigmotaxis. It is the purpose of the present paper to supply the lack thus indicated by giving a detailed account of the mechanism of the motor reactions of Paramecium.

The far-reaching importance of an accurate knowledge of the exact mechanism of the reactions of Paramecium is apparent when we recall the sweeping conclusions that have been drawn from the results of studies on the reactions of this and other unicellular organisms. Theories of the mechanism of thermotaxis, geotaxis, and other reactions have been put forth, accompanied by deductions as to the remarkable sensitiveness of protoplasm to the various classes of reagents, and these theories have borne an important part in forming various prevalent conceptions in general physiology and in compara-

¹ SCIENTIFIC RESULTS OF A BIOLOGICAL SURVEY OF THE GREAT LAKES, directed by Jacob Reighard, under the auspices of the U. S. Fish Commission, No. 1. (Published by permission of the Hon. George M. Bowers, Commissioner of Fisheries.)

² JENNINGS, H. S.: Journal of physiology, xxi, pp. 258-322.

⁸ LUDLOFF : Archiv f. d. ges. Physiol., 1895, lix, p. 525.

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tive psychology. They depend for their validity on whether the mechanism assumed for the reactions is the correct one, and for this assumption a basis of observation has usually been lacking. As will appear, some conclusions that have been deduced with the utmost confidence lose their validity when the actual mechanism of the reactions becomes clear.

It has become the fashion to refer many processes taking place in ontogeny to chemotaxis, or other reactions to stimuli, the matter apparently being considered as therewith definitely put at rest, as if such reference permitted no further analysis. It seems often to be forgotten that movements induced by chemotaxis must be accomplished by some means, some mechanism; and upon the character of this mechanism depends largely the interpretation to be given to the process. It may aid in recalling this neglected fact to set forth the roundabout method by which certain free cells succeed in gathering about a source of attractive stimulus.

A third standpoint, from which a knowledge of the general mechanism of reactions to stimuli should be of interest, is that of comparative psychology. The stage of mental development represented by unicellular organisms has, since the work of Verworn, been studied comparatively little, at least in any thorough manner, and the disconnected phenomena observed have lent themselves to interpretation by different authors in the most varied ways. Some hold that such organisms have a complex psychology containing nearly all the elements of which the psychic life of higher animals is made up, while others maintain that the observed phenomena are explicable on the simplest grounds; that such organisms are merely automata of the most limited capabilities, and that the activities which they show require little more than the property of irritability for their explanation. It may be hoped that an exact knowledge of the mcchanism of the reactions of one of these organisms may throw further light on the question of the simplicity or complexity of the "psychic life of micro-organisms."

With these problems in mind, an examination will be made of the motor reactions of Paramecium. The organism to be studied, Paramecium caudatum,¹ is a unicellular animal belonging to the group of

¹ In the first of these Studies (*loc. cit.*) the organism used for experimentation is called Paramecium aurclia. I adopted this name because the organism has been always so called in the Jena Physiological Institute, where the work was done, and because my attention had not been called to the possibility of a mistake

ciliate infusoria, and is well known in every biological laboratory, living by thousands in vegetable matter decaying in water. It is somewhat cigar-shaped in form, having a narrow but blunt anterior

end and a broad, sharp posterior end. From the anterior end a broad depression known as the oral groove runs obliquely along one side (the oral side) to the mouth, in the middle of the body. Near the opposite side (the aboral side) are the two contractile vacuoles. The entire surface of the body is covered with cilia, by means of which the animal moves. The length of the animal is about 0.2 mm.

During its progress through the water, Paramecium comes in contact with sources of stimuli of various kinds; it strikes against mechanical obstructions, compelling it to turn aside, or it meets with various chemical substances in solution which either attract or repel it: heat, electricity, and other agents may likewise act as stimuli; to all these the animal reacts in a characteristic manner. The problem for solution is, exactly *how* is such a reaction accomplished? How does the attractive chemical compound succeed in affecting the locomotor organs of Para-



FIGURE I. Paramecium caudatum. a, anterior end; p, posterior end; ab, aboral side; o, oral side; m, mouth; g, oral groove; cv, contractile vacuoles.

mecium so that it turns toward the source of stimulus? How does the repellent compound succeed in turning the Paramecium away from the source of stimulus?

In the first of these "Studies on Reactions to Stimuli" details were given as to the general features of the phenomena shown in the reactions of Paramecium. It was there shown that Paramecia are positively chemotactic to weak solutions of substances having an acid reaction, negatively chemotactic to substances having an alkaline reaction, and to many neutral salts. I shall give here in brief only enough of the gross appearance of these reactions to make intelligible the account of the finer mechanism and the way in which this mechanism is demonstrated.

in the name. But it appears that systematists make a distinction between Paramecium aurelia, with two micro-nuclei, and caudatum, with but one. As the Paramecia which I have been studying at Hanover, N. H., have but one micro-nucleus, I must call them P. caudatum. I believe them to be identical with the organisms used at Jena, though I did not investigate the micro-nucleus there.

The method by which the reactions of Paramecium toward most stimuli is demonstrated in practice is shown in Fig. 2. Paramecia are brought upon a glass slide and covered with a long cover-glass, supported near its two ends by bits of capillary glass tubing. The



FIGURE 2. Method of testing the reactions of Paramecium.

their random swimming strike the edge of the drop, whereupon they react in a characteristic manner. If they are positively chemotactic to the substance in the drop - as they are if it is weakly acid in reaction - they soon gather in a dense swarm within the drop, as

shown in Fig. 3. If, on the other hand, they are negatively chemotactic, the drop remains entirely empty, as shown in Fig. 4. This method is of course designed especially for the demonstration of chemotaxis. Thermotaxis, or the reaction toward heat or cold, may be demonstrated in a similar manner, or better by warming or cooling one end of the slide; still better by means of the apparatus devised by Mendelssohn.1

Paramçcia swim at random throughout preparation. the Now a drop of any solution toward which the method of reaction is to be tested is introduced beneath the coverglass by means of a capillary pipette, as shown in the figure. The Paramecia in



FIGURE 3. Paramecia collected in a dense swarm in a drop of a solution to which they are positively chemotactic.

Now, how does the substance in the drop in Fig. 3 succeed in affecting the cilia in such a way as to make the Paramecia turn toward and enter the drop?

Observation of the method by which the Paramecia collect in the drop shows that the foregoing question involves an assumption which is untrue. The Paramecia in the neighborhood of the drop do not turn toward it. The animals collect in the drop in an entirely dif-

¹ MENDELSSOHN: Archiv f. d. ges. Physiol., 1805, lx, p. 1.

ferent way. Suppose the drop to have been just introduced, as in Fig. 2. A Paramecium in its random course strikes by chance against the margin. It does not react, but keeps on its way across the drop until it comes to the other side (Fig. 5). There it reacts negatively.

and turns back, swimming across the drop in another direction, till it again comes to the margin of the drop. There it again reacts negatively, and swims in a new direction, till it is turned back by the margin as before. This continues, so that the Paramecium is, as it were, imprisoned in the drop. Fig. 5 shows the course of a single Paramecium in such a drop. Other Paramecia enter the drop in the same way, purely



FIGURE 4. Negative chemotaxis toward a drop of sodic carbonate solution introduced 10 minutes before.

by chance, and remain in the same manner, until the drop swarms with Paramecia. Owing to the restless hither and thither swimming of the animals on the slide, almost every one will in a short time have come by chance against the edge of the drop, will have entered and remained. Thus in a short time we get the appearance shown in Fig. 3; almost all the Paramecia in the preparation are collected



FIGURE 5. Course of a Paramecium in a drop of attractive substance.

in the drop. We say that the Paramecia are positively chemotactive to the substance in the drop, but so far as any motor reaction is concerned, evidently a more accurate statement is that after entering the drop by chance they are negatively chemotactic to the surrounding fluid.

The same thing may be shown to be true for thermotaxis or the reaction toward heat. In place of the chemical solution, we may introduce into a slide preparation of Paramecia in cold water a

drop of water warmed to the temperature toward which the Paramecia appear to be positively thermotactic. We shall find that the Paramecia collect in the warm drop in exactly the same manner as in the case of the chemical compound just described: they enter by chance, then are negatively tactic to the surrounding cold water.

An extended examination of the reactions of Paramecium shows that this is typical for all apparently positive reactions. In and of itself, considered as a motor reaction, there is no positive taxis in Paramecium. The so-called positive taxis always acts indirectly through (apparent) negative taxis. The question of how Paramecium turns toward an attractive substance may be thrown out, with the simple statement that Paramecium does not so turn.

There remains then only the mechanism of the negative reactions to be elucidated. We may first proceed to an examination of the method by which Paramecium succeeds in keeping out of a drop of some chemical to which it is negatively chemotactic, as in Fig. 4. For this purpose a drop of $\frac{1}{5}$ per cent sodium chloride solution may be selected. To understand the negative reaction, it is necessary to recall the animal's normal method of progression through the water. The unstimulated Paramecium swims nearly straight forward, though in a slightly sinuous course, the narrower, blunter end directed forward. At the same time it revolves on its long axis. Usually, but not invariably, this revolution seems to be from left to right, but there is much variation in the direction.

Now, when a Paramecium, swimming as above described, strikes the margin of the drop of sodium chloride solution, it reverses its course, darting straight backward, — the broad, pointed (posterior) end now being in the lead. At the same time, the direction of rotation on the long axis is reversed, the Paramecium revolving (usually) from right to left. Next the animal swings on its short axis, so as to bring the longitudinal axis of the body out of the line of direction in which it was first swimming. Then the infusorian begins to swim forward again, — following a course which lies at an angle to the course it was taking when it struck the drop of sodium chloride solution. Briefly stated, the animal has adopted the very rational course of backing off, turning in a different direction, then proceeding on past the obstacle, — much as any higher animal would have done.

We may here take up two questions, upon one of which we have already a certain amount of evidence, while the second is pressed upon us by the course of events in the reaction last described. The first is, — Do different kinds of stimuli have different methods of affecting the cilia? For example, does perhaps an acid cause the cilia to strike more strongly backward, driving the animal forward; an alkali, on the contrary, cause the cilia to strike more strongly forward, driving the animal backward? In this way, at first thought, the positive chemotaxis toward acids, the negative taxis toward alkalies might be ex-

plained. The results detailed thus far have shown, however, that such a view is not tenable for an explanation of positive chemotaxis, since the latter acts only indirectly through negative chemotaxis. Nevertheless, the general question still remains, --- applicable, if not to acids and alkalies, perhaps to other chemical or physical agents. To determine the question with certainty, it will be necessary to immerse the Paramecia directly into solutions of various sorts, and observe the activities of the animals under these circumstances. At the same time evidence may perhaps be obtained on the second question referred to above, which is as follows: What causes the *turning away* of the Paramecium in the reaction toward sodium chloride, above described, after the backward course; and what determines the direction in which it turns? An obvious answer of course suggests itself, -the Paramecium turns away because it wants to get around the obstacle, and the direction in which it turns is determined by the position in which the object lies; it turns so as best to avoid the obstacle. This anthropomorphic view may perhaps be tested, and some evidence on our general question gained, by trying the effect of unlocalized stimuli, - stimuli that act upon the entire surface of the animal at once. This may of course be done by the method above mentioned, - complete immersion of the Paramecia in solutions of different kinds. There will then be no "obstacle" to get by, and, from the anthropomorphic standpoint, no excuse for turning in one direction or another.

With these considerations in mind, Paramecia are immersed directly in solutions of various sorts. This is done as follows: a solution is mixed in a watch-glass, then a quantity of water containing Paramecia is taken up with the pipette and injected energetically into the solution. They are quickly mixed thoroughly by the use of the pipette, then examined with the low power of the microscope.

The Paramecia may be first immersed in an alkaline solution, using for this purpose $\frac{1}{200}$ per cent sodium hydrate. Most of the Paramecia will be seen to swim energetically backward. This may be continued a few seconds or more, then many of the animals will be seen to turn and swim forward in a new direction. If a single specimen is watched, it may perhaps be seen to repeat the process of swimming backward, turning, and swimming forward several times; others may swim backward continuously.

Thus it appears that an alkali causes a reversal of the motion, followed by turning and swimming forward.

Let the Paramecia now be immersed in $\frac{1}{50}$ per cent acetic acid. As in the sodium hydrate, the Paramecia dart backward, only here the motion is more swift. The action of the acid seems much more energetic than that of the alkali; the Paramecia dart furiously backward for an instant, then turn quickly and rush forward for a moment, then perhaps backward again, then turn and rush forward. In a short time the backward motion has ceased; the Paramecia are all swimming forward at a furious rate, and soon they die. The difference in the action of the substances seems due to the fact that acids do not affect Paramecia at all, except when they are so strong as to be severely injurious; hence the great energy of the reaction and the quick death of the animals.

Thus acids also cause the infusoria to swim backward at first. The reaction is qualitatively the same for both acids and alkalies, only the intensity and duration of the different parts of the reaction varying.

In the same way, Paramecia may be immersed successively in a solution of some neutral salt, as $\frac{1}{5}$ per cent sodium chloride; in a solution that is effective only through its strong osmotic power, as a IO per cent solution of cane sugar; in a watch-glass of water heated to 35° C.; in a watch-glass of water at the freezing temperature. In every case the characteristic features of the reaction are the same. The Paramecia swim backward for a longer or shorter time, then turn more or less, then swim forward. This may be repeated many times. In the different solutions the different features of the reaction may be more or less pronounced, in energy and duration, but the essential nature of the reaction is the same in all.

This series of experiments gives a definite answer to the first of the two questions proposed. Evidently different stimuli do *not* have qualitatively different methods of affecting the cilia. In every case the essential features of the reaction are the same, whatever the agent causing the reaction; only the intensity of the component activities varies. Every reagent causes at first a reversal of the motion of the animal, and therefore beyond doubt a reversal of the motion of the cilia. Since the same result is obtained with stimuli of so heterogeneous and opposite a character, it follows that the determining feature in this method of reaction must be internal. The Paramecium is like a machine in which the wheels are set for a certain motion; to every application of power from whatever source it responds by this motion. It is to be noted, moreover, that while in these experiments the stimulus is continuous, the reaction is discontinuous, the motion being first backward, then sideways, then forward. The demonstration that a single stimulus does not have a single characteristic effect is therefore complete, since each stimulus causes three different motions of heterogeneous and even opposite character.

On the second question, as to what causes the turning away, and what determines the direction of turning, these experiments shed a certain amount of light, though they do not give a determinate answer. Since all these entirely unlocalized stimuli cause the turning away, it follows that the latter is not due to the localization of the stimulus: the Paramecia do not turn from nor toward the source of stimulus, — because they are completely surrounded by and immersed within it. Apparently the turning away is due, like the reversal, to an internal mechanism, not to any characteristic of the external stimulus. Neither can the *direction* in which they turn be determined by an external factor in these cases. It appears probable, therefore, that it is an internal factor that determines the direction of turning.

The next step is to try whether anything can be discerned in the structure of the Paramecium that will give a clue to the factor determining the direction of turning. The most obvious differentiations of the body of the animal are into anterior and posterior ends, and into oral and aboral sides, as shown in Fig. 1. The differentiation of the ends comes into consideration, of course, only in forward or backward motion. Has the differentiation into oral and aboral sides any relation to the turning movement? Owing to the continued rotation of the animal on its long axis, as it swims either backward or forward, it is impossible under ordinary conditions to observe whether there is any relation between this differentiation and the direction of turning. But a clue is given by the conduct of the animals when immersed in a solution of potassium iodide. This reagent has the property of almost indefinitely prolonging each of the component activities in the threefold reaction above described, and affords opportunity for a thorough analysis. When introduced directly into I per cent solution of potassium iodide the Paramecia begin, as in other reagents, to swim backward. But in potassium iodide solution this is continued six to eight minutes without change. After this they begin to turn, and this portion of the reaction is continued like the first, so that they spin around on the short axis of the body, as on a pivot, for half an hour at a time. Thus after ten minutes all the Paramecia in the watchglass will be whirling like tops. It is easy thus to have hundreds of specimens in the field at once with a low power lens, and of these many individuals will be in such a position that it is easy to determine the relation of the direction of turning to the two sides of the animal. It then appears that all are whirling toward the side that contains the contractile vacuoles, — that is, *toward the aboral side*. The direction of motion is indicated in Fig. 6. At first the Paramecia whirl as if on a pivot through the middle of the animal. Later



FIGURE 6. Direction of motion of Paramecia whirling in I per cent solution of potassium iodide.

the centre of rotation comes to lie outside the body of the animals, so that they now swim in circles. In every case the centre of the circle lies on the aboral side of the Paramecium, so that the animal is still turning toward the aboral side, though not in such short turns as at first.

Thus under the stimulus caused by potassium iodide, the direction of turning is determined by an internal factor, — the differentiation into oral and aboral sides being the deciding feature. Taking this in connection with the fact that all unlocalized stimuli cause turning, it is a natural inference that the localization of a stimulus has no effect on the direction of turning. As this seems paradoxical and improbable on general principles, however, it must be tested by observation of the reactions of Paramecium toward stimuli that are localized. Is there a difference in the reactions of the animal ac-

cording as the stimulus affects the anterior end, the oral side, the aboral side, or the posterior end? To determine the answer to this question, it is only necessary to introduce a drop of some chemical compound beneath the cover-glass of a slide preparation swarming with Paramecia, as shown in Fig. 2, and then to watch the edge of the drop with the low power of the microscope. Among the multitudes of Paramecia that strike the margin, many come against it obliquely, or touch it only on one side of the body, and their conduct is then easily observed. The reaction is the same in character as when the animal is immersed in a solution that acts as a stimulus; the Paramecium swims backward a distance, turns, and swims forward. It becomes evident at once that it *does not* turn directly away from the source of stimulus; the position of the drop seems to have little or no relation to the direction in which the Paramecium turns. Sometimes the animal

turns in such a way as to carry it away from the drop; in other cases it does not. There is no constancy in the direction of turning, and it is impossible to predict which way a Paramecium meeting the drop at a given angle will turn. In many cases the animal which at first brushed only the edge of the drop is carried, after turning, squarely against

it, as illustrated in Fig. 7, in which the numerals indicate successive positions of the animal, while the arrows show the direction of motion. In such a case the whole operation is repeated; the animal backs off, turns in a new direction, and tries again. If the obstruction is large, the Paramecium may be thus compelled to try a dozen times before getting by the obstacle; such cases are often observed.



FIGURE 7. Paramecium striking a drop on one edge (1); swimming backward (2); turning (3); and swimming forward squarely against it (4).

This description applies equally well to the case of a mechanical obstruction, and to the reactions toward a very hot or very cold solution.

The inference previously made, that the localization of the stimulus has no relation to the direction in which the Paramecium turns, is therefore confirmed. It remains now to be decided whether the factor which determines the direction of turning when the stimulus is a solution of potassium iodide is the factor in other cases also. Does Paramecium always turn toward its aboral side, whatever be the nature and position of the stimulus?

To answer this question, it is necessary to use the method of observation in gelatine, devised by Jensen. Three grams of gelatine are dissolved by heat in 100 c.c. of ordinary water, and the Paramecia are observed in the thick solution. In this gelatine solution they are able to swim only very slowly, so that all the movements can be closely studied. Any chemical can be mixed with the gelatine solution, in order to observe the effects of unlocalized stimulation, or a drop of any solution can be introduced beneath the cover-glass with the capillary pipette, for observation of the effects of localized stimuli; in fact, the Paramecia may be studied exactly as in water, the only essential difference being that they move more slowly.

The Paramecia are therefore brought into such a gelatine solution,

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and their conduct toward localized stimuli is observed. The unstimulated Paramecium swims straight forward, revolving slowly on the long axis. On coming in contact with a mechanical stimulus or a drop of some solution toward which it is negatively chemotactic, the animal swims backward very slowly, at the same time revolving slowly from right to left. Then it turns slowly, — *always toward the aboral side*. If the aboral side is above when the turning begins, the animal turns upward; if the aboral side is below, it turns downward; if to the right the animal turns to the right. This is true for a simple mechanical stimulus, for a chemical stimulus of any sort, or for a thermal stimulus; in fact, for any kind of a stimulus that can be tested in the gelatine. After some time in the gelatine solution the Paramecia are usually seen to be somewhat curved, and the curving



FIGURE 8. Paramecium curved toward the aboral side, under the influence of a powerful stimulus.

is always toward the aboral side, as in Fig. 8. A similar curving may often be observed after a strong stimulus, when the Paramecia are mounted in water. The anterior end thus curved of course acts like the rudder of a boat in turning the course of the Paramecium toward the aboral side. Never-

theless, while it aids, it is evident that this is not the only factor in the turning, since Paramecia under other conditions are seen to turn sharply, or even to revolve almost as if on a pivot, when the body is not observably curved at all.

The invariable turning toward the aboral side may, as I have since discovered, be demonstrated, without the use of gelatine, in the following way: Paramecia intermingled with masses of bacterial zoöglœa are mounted on a slide and covered with a cover-glass, which is closely pressed down, so as to leave only a narrow space between slide and cover. It will usually be found that many Paramecia are imprisoned in small crevices in the bacterial zoöglœa, so that they can swim only from one end of the crevice to the other, and at each end they must turn. The cover-glass is so close to the slide that the animals can turn only in a horizontal plane. By watching the Paramecia as they turn at the end of the crevice, it will easily be seen that they invariably turn toward the aboral side.

We find then that the question last proposed is to be answered affirmatively. Paramecium after reversing *always turns toward the aboral side*, whatever be the nature and position of the source of stimulus.

A certain feature in the normal straightforward swimming of the unstimulated Paramecium appears to be connected with this fact. As has been often noted, the course in which an individual swims is not perfectly straight, but, as seen from above, the animal seems to swerve from side to side. This swerving has been figured by Verworn¹ and others. The actual path is a narrow spiral, the animal, of course, swerving up and down as well as from side to side. Now, observation of slowly moving individuals shows that at any point in this spiral course the aboral side is on the outside of the spiral. In other words, the Paramecium as it swims continually swerves toward the aboral side. As at the same time it rotates on its long axis, the position of the aboral side continually changes, so that the resulting path is a spiral one, and the general result is the same as if the Para-

mecium had progressed in a straight line. These facts are indicated in the accompany-

path of a Parame-

cium (Fig. 9). Ap-



ing diagram of the FIGURE 9. Path of a Paramecium. The aboral side is everywhere directed toward the outside of the spiral.

parently the method of reacting to a stimulus by turning toward the aboral side is a mere accentuation of the ordinary swerving toward that side.

It will here be necessary, in order to avoid misunderstanding, to give an account of an apparent exception to the rule that the Paramecium after stimulation always turns toward the aboral side. In my previous paper on the reactions of Paramecium (loc. cit.), I gave an account of the thigmotactic reaction of Paramecium; that is, the reaction due to continued contact with a solid body. I must here supplement the account by setting forth a little more fully certain features in that reaction.

On page 303 of my previous paper is figured a Paramecium resting with its anterior end against a solid body, and exhibiting the currents caused by the cilia under these circumstances, --- that is, the currents characteristic of the thigmotactic reaction. As described in detail in the paper cited, the cilia in the oral groove at such a time beat strongly backward, driving a swift current of water toward the rear and causing a vortex to form on the oral side of the anterior half of

¹ VERWORN, M.: Psychophysiologische Protisten-Studien, 1889, p. 116.

the animal, as shown in Fig. 19 (*loc. cit.*), while the cilia on the remainder of the body are quiet, or possibly have varying motions tending to counteract the motion of translation that might be induced by the cilia in the oral groove. Meanwhile, the body of the animal remains at rest. This type of activity of the cilia is especially characteristic for resting Paramecia. But sometimes the solid body which causes the thigmotactic reaction is very small and movable, and so does not restrain in any way such motions of the animal as might naturally result from the activity of the oral cilia. In this case the Paramecium moves through the water in a peculiar way, carrying with it the small particle that has induced the thigmotactic reaction.



FIGURE 10. Motion of Paramecium in the thigmotactic reaction to a movable particle.

"The cilia beating strongly backward in the oral groove of course impel the animal forward. But as the active cilia are all on one side, there is also a tendency to move toward the opposite side. The resultant of these two motions at right angles to each other is a motion in the circumference of a circle. In fact, the animal moves forward in exactly the lines indicated by the arrows in Fig. 19, only, of course, in the opposite direction from the water currents. The ciliary motion is thus

the same whether the thigmotactic animal is at rest or in motion; in the former case the water currents move obliquely backward; in the latter case the animal moves on the same lines obliquely forward. The Paramecium is, as it were, whirled about in its own whirlpool" (loc. cit.; p. 305). An inspection of the Fig. 19 referred to in this extract shows that when the animal moves in a circle as there described, the oral side of the Paramecium must look continually toward the centre of the circle. Fig. 10 shows the successive positions of a Paramecium exhibiting the thigmotactic reaction toward such a movable particle; the arrows indicate the direction of motion of the Paramecium, while the circle indicates the path traced by the anterior end of the animal. By reference to this figure it will be noticed that under these circumstances the body moves forward tracing a curve, with the oral side always toward the inside of the curve; in other words, the animal continually turns toward the oral side. In connection with the other movements de-

scribed in these pages, it is important to recall the fact that Paramecia will be sometimes seen thus turning toward the oral side; this, however, is always in the thigmotactic reaction. It is especially frequent when Paramecia are observed undisturbed in water containing many bacteria; when the Paramecia are excited by some unusual condition this reaction is not seen. Now, it is chiefly the reaction under some exciting stimulus that forms the subject of this paper. The thigmotactic reaction is characteristic for resting individuals, and the locomotion in thigmotaxis under certain circumstances in the manner shown in Fig. 10 is an accidental matter, due to the mobility of the solid inducing the reaction. Hence, this is not properly to be accounted a motor reaction, and it is, therefore, with this brief description, left out of consideration in my discussion.

Returning, therefore, to the proper motor reactions, the final step must now be taken; the mechanism of the reactions already de-

scribed must be determined in terms of the movements of the cilia. All movements of the Paramecia result from motions of the cilia, and the mechanism of the reactions cannot be considered as analyzed into its simplest components until we know what motions of the cilia are at the basis of the general body movements. For studying the motions of the cilia two methods may be used. The first is the observation of the animals in the gelatine solution



FIGURE 11. Paramecium with cilia reversed. The large arrow in the body shows the direction of locomotion of the animal; the other arrows indicate the direction of the currents of water.

in the way already given. The thickness of the solution makes the motion of the cilia much less rapid, so that the way in which they move can be determined more or less satisfactorily. The data gained in this way may be supplemented and controlled by the second method of study. This consists in observing the Paramecia in fluid containing powdered carmine. The movements of the particles of carmine in the neighborhood of the animals show the currents caused by the cilia, and from the direction of these currents the direction of stroke of the cilia causing them may be inferred.

In the unstimulated Paramecium swimming forward the effective stroke of all the cilia is backward, urging the animal forward; the cilia as seen in gelatine give the optical effect of being directed backward, as shown in Fig. 1. On coming in contact with an effective source of stimulus, the cilia are reversed in position, now striking more strongly forward, and presenting the appearance of being directed toward the anterior end, as in Fig. 11. As a result the animal is, of course, impelled backward, or toward the broad, pointed end. It is worthy of especial notice that the cilia in the oral groove are, like all the others, now striking forward, so that a current of water passes swiftly *from* the mouth toward the anterior end, — contrary to the usual direction.

Next, after the backward swimming caused by the reversal of the ciliary motion has ceased, the animal begins to turn. At this stage



FIGURE 12. Position of the cilia as the Paramecium turns. The arrows indicate the direction of the water currents.

the cilia are found to have the following motions. The reversal of the cilia in the oral groove has ceased, and they are striking backward again, --- thus tending to drive the animal forward. The remainder of the cilia on the anterior half of the animal strike transverselv toward the oral side. This is shown in Fig. 12. This reaction was first seen clearly in Paramecia that were immersed in a $\frac{2}{5}$ per cent solution of chrome alum; it was then confirmed for other substances and for stimuli other than chemical, by the use of the gelatine solution and by observation of the currents about Paramecia in water containing powdered carmine. The arrows in Fig. 12 indicate the direction of the water currents produced by the cilia at this stage of the reaction. In the oral groove there is a strong current backward, while on the anterior half of the aboral side there is a transverse current from the aboral to the oral side. This mo-

tion of the cilia of course causes the Paramecium to turn toward the aboral side (opposite the arrows in Fig. 12), and with this observation we have determined the real mechanism of the turning.

The next step in the reaction is the cessation of the transverse stroke of the aboral cilia, so that they strike backward, as before the stimulation, driving the animal straight forward as at first.

Thus the reaction of Paramecium to any ordinary stimulus is as follows: (1) The cilia over the entire surface of the body are reversed, striking forward, thus driving the animal backward. At the same time its direction of revolution on the long axis is reversed. (2) The reversal of the cilia ceases; those in the oral groove strike

backward as at first, while those on the remainder of the anterior half of the body strike transversely, toward the oral side. This results in turning the anterior end toward the aboral side. (3) The cilia all strike backward as at first; the animal, therefore, swims straight forward again. Coincidently with (1) and (2) the body of the animal may be bent toward the aboral side, still further aiding in turning in that direction. At the end of the entire manœuvre the Paramecium is swimming forward along a course which lies at an angle to the course in which it was first swimming. The complete reaction of Paramecium to an ordinary stimulus is represented in



FIGURE 13. Complete reaction of a Paramecium. A is a source of stimulus. The numerals give the successive positions of the animal, while the arrows show the direction of motion.

Fig. 13. The rotation on the long axis could not be represented in this diagram, but all the other essential features of the reaction are shown.

This reaction is not characteristic for any particular class of stimuli, but it occurs in a more or less marked manner whenever any stimulus acts upon the animal with sufficient power to cause a motor reaction. Toward acids and alkalies, toward neutral salts and toward fluids that are active only through their high osmotic pressure; toward heat and cold and mechanical shock, the same reaction is given. Apparently a strong electric current has a related effect, since Verworn has observed that when a very strong electric current is passed through water containing Paramecia, they all swim backward, and thus collect at the anode instead of at the cathode, as is usual with a weaker current. A re-examination of the phenomena of electrotaxis in the light of the general reaction-plan described in this paper appears desirable to determine the relation of the two. Geotaxis, or the reaction of Paramecium relative to the direction of the pull of gravity, in virtue of which they usually rise to the top of a vessel of water containing them, seems more difficult to bring into relation with the general reaction above described. In view of the divergent theories of Jensen,¹ Davenport,² and others, the cause of geotaxis cannot be considered certainly known; a reinvestigation of the phenomenon in Paramecium is needed, in the light of the general method of reaction described in this paper, as well as in view of the previously unsuspected positive chemotaxis toward carbon dioxide (as described in No. I of these Studies) — a substance the distribution of which in the water profoundly influences the movements of the Paramecia. Like Miss Platt,³ I find that the Paramecia of this region do not show clear geotaxis.

Almost the only variation in this entire reaction is in the intensity of its several component activities. To a very weak stimulus, such as a mechanical obstruction in front, the Paramecium responds merely by a reversal of the cilia lasting but an instant and carrying the Paramecium backward but a fraction of its own length. The accompanying reversal of the direction of rotation on the long axis may suffice to turn the aboral side but a few degrees from its original position. The reversal is followed by a momentary transverse stroke of the aboral cilia, turning the Paramecium through but a small angle toward the aboral side. It then swims forward as before. The whole operation has caused a hardly perceptible stoppage in the course of the Paramecium. On the other hand, coming in contact with some strong chemical, such as a drop of $\frac{1}{100}$ per cent sulphuric acid, induces an intense and long sustained reaction. The Paramecium darts swiftly backward many times its own length, revolving rapidly on its long axis from right to left. Finally, the transverse stroke of the aboral cilia intervenes, in an equally powerful manner, and the animal turns sharply. It may thus turn completely around; or in some cases it may whirl more than 180°, so that the immediately following forward course takes it back again into the drop of acid. Certain chemicals exaggerate all the activities composing the reaction to a remarkable degree. Thus in $\frac{3}{4}$ per cent potassium iodide, as already described, the reversal of the cilia lasts six to eight minutes, the Paramecia all this time swimming swiftly backward; then the transverse

- ¹ JENSEN, P.: Archiv f. d. ges. Physiol., 1893, lili, p. 428.
- ² DAVENPORT, C. B.: Experimental morphology, Part 1.
- ⁸ PLATT, JULIA B.: American naturalist, 1899, xxxiii, p. 31.

stroke of the aboral cilia lasts perhaps half an hour, the animal all this time whirling toward the aboral side. In such cases the reaction loses all semblance of an attempt to escape or pass by an obstruction. In other chemicals each component part of the reaction is little exaggerated, but the entire operation is repeated many times, alternations of swimming backward, turning, and swimming forward again continuing for fifteen minutes or more. Different chemicals have a most varied effect on the reaction as a whole, though in every case the effect may be expressed as a modification of the intensity or duration of one or more of the component activities.

The absolute direction in which the Paramecium turns after its backward course is evidently determined by the position of the aboral side when the cilia on that side begin to strike transversely. The position of the aboral side at that time is a matter of chance; the animal revolves continually on its long axis, so that the position of the aboral side is continually changing, and the actual direction in which the Paramecium turns depends upon where the aboral side happens to lie when the reaction reaches the stage in which the aboral cilia begin to strike transversely. Of course this may carry the animal directly into the source of stimulus again; such cases are often observed, as has already been described and illustrated in Fig. 7. In many cases the Paramecium repeats the reaction several or many times before it succeeds in getting by the obstacle. The whole proceeding is an apotheosis of chance. If the source of stimulus is small, the process of drawing back and turning in any chance direction is likely to avoid it. Or, if it is not avoided the first time, the continual revolution on the long axis is likely to bring the aboral side into a new position next time, so that the Paramecium turns in a new direction. If this is continued long enough, a small obstruction is certain, by the laws of chance, to be evaded and passed after a sufficient number of trials. If, on the other hand, the source of stimulus is large; if, for example, the space containing the Paramecium is bounded along one whole side by a solution toward which the Paramecium is negatively chemotactic, then the reaction is repeated until by the laws of chance the course of the Paramecium is so directed as to lie in that part of the space which does not contain the repellent solution. In the case of a solution toward which the Paramecium is strongly negatively chemotactic, chance may be aided by the fact that the intensity of the stimulus usually causes an intense reaction, so that the Paramecia swim a considerable distance

backward (which in itself, of course, increases the chance of avoiding an obstacle after turning), and also turn strongly, - perhaps nearly 180°, so that the remainder of the path lies in quite a new direction. It seems probable that for most circumstances in the normal daily life of a Paramecium, this rough hit-or-miss method of reaction is quite sufficient to keep the animal out of danger and to enable it to avoid obstacles. But the utility of the reaction is left to chance, and so circumstances may arise in which the chances are against the Paramecium. Thus in the presence of a drop of some strong chemical, such as $\frac{1}{100}$ per cent sulphuric acid or cupric chloride, it will readily be seen that the chances of escape are limited. The animal responds to the first stimulus by a violent reversal of the cilia, carrying it some distance backward. If now the direction in which the transverse stroke of the aboral cilia carries it after this backward course is by chance such as to take the animal away from the drop, well and good; if, on the other hand, the Paramecium is carried a second time against the drop, it is likely to succumb at once to its poisonous effects. Observation shows that when a drop of such a substance is introduced into a preparation of Paramecia on the slide, it soon becomes surrounded by a zone of the dead infusoria. The same is true of a drop of a dense solution of cane sugar, which is injurious from its osmotic pressure. The Paramecia react when they enter such a dense solution, but the reaction is not precise enough to take them out of the destructive area before they are killed.¹

The uselessness of the reaction seems especially striking when the Paramecia are completely immersed in a solution that acts as a stimulus. Under these circumstances, when there is no obstacle to be avoided and the stimulus is not localized at all, the Paramecia respond with exactly the same reaction. Paramecia do not modify their conduct to suit the needs of the case, but give the same reaction under all circumstances. The reaction is exactly such a one as might be maintained by natural selection, acting under an environment that makes no severe demands. Since the Paramecium usually swims forward, a majority of the stimuli that affect it at all will affect the anterior end. The whole reaction to *any* stimulus is, therefore, based upon this position of the source of stimulus, without regard to the conditions in a given particular case. For stimuli acting upon the side of the body, the reaction is, therefore, a very imperfect one, the

¹ There is great variation in the repellent power of different chemical compounds. This subject will be treated by the author in a separate paper.

comparative rarity of such stimuli having led to no development of a special mechanism to suit that case. A reaction such as would permit a direct turning away from a stimulus acting upon any side of the animal would evidently involve a much more complicated mechanism, and imply a higher condition psychologically than this simple one-reaction plan. But even this serves, if repeated a sufficient number of times, for avoiding sources of stimuli acting upon the sides of the animal, and under some conditions the result is produced in a fairly direct manner. In certain cases, when the stimulus causing the reaction is very weak, and the Paramecium comes against the source of stimulus very obliquely, so as to touch it only on one side, there appears to be an almost direct turning away, toward the side opposite the stimulus. This is to be observed particularly in the

collections of Paramecia in a region containing carbon dioxide excreted by themselves. A long narrow area may thus be formed beneath the cover-glass (as shown in Fig. 14), in which the Paramecia swim back and forth; to the water outside this area they are weakly negatively chemotactic, so that when they swim against the boundaries of the area, the above-described reaction takes place, in a not very pronounced manner. A

single Paramecium swimming lengthwise of this area may strike against its lateral boundaries with one side or the other, when it will frequently (not always) be seen to apparently sheer directly off, away from the boundary, and keep on its course undisturbed. Careful observation shows that such cases are to be placed in two categories. (I) When the Paramecium comes against the boundary, the aboral side by chance already lies toward the interior of the area, so that all that is necessary is for the Paramecium to react in the usual manner, in order to leave the boundary. (2) The more interesting case is where the Paramecium comes against the boundary with the aboral side not toward the interior of the area. In this case it will be seen to hesitate an appreciable interval before turning away from the boundary. During this moment of hesitation it starts to turn toward the aboral side, which is thereby pushed further into the outer fluid, toward which the animal is negative. This induces a faint reversal of the cilia (in agreement with the general



FIGURE 14. Group of Paramecia in a region containing carbon dioxide excreted by themselves.

plan of reaction above described), so that the animal does not progress further in that direction, and may be seen to move backward a barely perceptible distance. It then tries the turning again. On account of the continual rotation on the long axis, the aboral side will now be in a new position; the animal will, therefore, turn in a new direction, and may swim victoriously into the area; if not, a new trial is made during another instant of seeming hesitation. The delay cannot be longer than it requires for the Paramecium to rotate half a turn on its long axis. The animal makes the appearance of feeling about with its anterior end, to discover the proper course to pursue; it is really trying all the time to turn toward the aboral side, but cannot go forward until this carries it into a medium that does not cause a reversal of the cilia. The direction in which the animal shall go is not selected by the Paramecium itself, but is *automatically* selected through the fact that this direction does not cause a reversal of the cilia.

This more direct method is, however, only possible in cases where the negative stimulus is very weak, so as to cause only a very faint reversal of the cilia. With a stronger stimulus the animal shoots back as much as half its length, or more, so that it is now separated from the source of stimulus by a perceptible interval (as in Fig. 13); it is, therefore, free to turn in any direction. Hence, it as frequently turns at first *toward* the source of stimulus as in any other direction. Moreover, even with the weakest stimulus, not all individuals turn in the more direct way just described; many individuals in such an area as shown in Fig. 14 react essentially as shown in Fig. 13. The latter figure shows the *typical* reaction, of which the method just described is a less usual special case.

For the case of complete immersion in a solution that acts as a stimulus, the reaction seems under experimental conditions to be ludicrously imperfect and useless. Under the normal conditions, however, it perhaps serves the Paramecium very well even for this case. Suppose that the Paramecium in its headlong course finds that it has entered completely a circumscribed region of solution having injurious properties. Evidently, to immediately reverse the cilia and swim a long distance straight backward is as likely to rescue the Paramecium from its perilous position as anything it could do, and if this straight course backward does not bring it at once out of the injurious solution, it is perhaps likewise sound practice to change the direction of motion. As under other circumstances, the reaction depends upon chance for success, but the chances are fairly favorable. It is interesting to see how so simple and invariable a method of reacting can meet so well the demands made upon it.

Finally, for the very rare case of stimuli acting upon the posterior end, no provision whatever seems made. It is only when swimming backward in response to a stimulus from in front that a stimulus is likely to act upon the posterior end, — and this is apparently so rare that it can safely be neglected. In cases where animals swimming backward come in contact with something that would act as a stimulus if it affected another part of the body, the cilia continue to strike forward. The normal reaction would be of course to reverse the stroke of the cilia, making them strike forward; as, however, they are already striking forward, there is now no change. Thus Paramecia swimming backward may often be seen to press the posterior end against a mechanical obstruction met in the backward course, and remain there, the forward stroke of the cilia driving them continually against it. Or in the case of chemical stimuli, Paramecia swimming backward often cross the boundary between two substances, when this boundary seems an insuperable obstruction to individuals swimming forward. This is particularly striking when a drop of weak acid is introduced into a slide of Paramecia. As detailed in my previous paper (loc. cit. p. 269, Figs. 7 and 8), the Paramecia gather in a ring about such a drop, and are then negatively chemotactic to the inner, more strongly acid part of the drop, and also to the outer fluid. Therefore, they swim about in a ring of some width, surrounding the drop of acid; if they strike against either the inner or the outer boundary of this ring, the cilia are reversed, so that the animals return into the ring. But if a Paramecium on striking the drop of acid at the inner boundary of the ring reverses its cilia strongly and swims backward, it may, if it reaches the outer boundary while swimming backward, cross this boundary without the slightest hesitation, and swim away into the surrounding water, though if it had come against the outer boundary while swimming forward, it would have been at once forced back into the ring by the reversal of its cilia. In cases, however, where a Paramecium swimming backward comes in contact with a source of very strong stimulus, the next step in the reaction is induced, — the Paramecium begins whirling on its short axis, - a proceeding which serves a purpose as little as would the continued swimming backward.

The collection of Paramecia in the region of a given attractive

stimulus, as in positive chemotaxis or positive thermotaxis, evidently depends equally upon chance. Nothing acts as a direct attraction to Paramecia. Their habit of swimming continually through the water is what must be relied upon to bring them into the sphere of activity of any agency. In this seemingly random swimming they are frequently met by influences which cause in a slight degree the reaction I have described, as is shown by the frequent slight jerks backward, followed by a slight turn in a new direction. In this way the Paramecium follows the line of least resistance, as it were, and finally may come into the region of a chemical toward which it is positively chemotactic, or into a region of optimum temperature. If now it proceeds on its course across the optimum territory, on coming to the farther boundary it passes into a region of such a nature as



FIGURE 15. Thermotaxis of Paramecium. The right end from a to c rests upon a water bath heated to 40° C.; the opposite end, from f to d, rests upon ice.

induces the negative reaction; the animal turns away and after some repetitions is directed back into the optimum region. The actual process by which this takes place in the case of ther-

motaxis may be detailed, since my account differs so completely in principle from that of Mendelssohn,¹ who first gave a careful description of thermotaxis, — and since this process affords a very striking example of what might be called the automatic selection of movements.

Four strips of capillary glass tubing, enclosing a rectangular space, are fixed on a slide by means of Canada balsam (Fig. 15); the enclosure is then filled with water containing Paramecia, and covered with a long cover-glass. The Paramecia are scattered uniformly throughout the enclosure, swimming in all directions (the two ends being at first not empty, as they appear in the figure). Now one end of the slide for about a fourth of its length (from a to c) is allowed to rest on a water bath heated to about 40° C., while the other end, from f to d, rests on a piece of ice. Soon it will be noticed that the Paramecia at the heated end, between b and c, are in violent mo-

¹ MENDELSSOHN, M.: Archiv f. d. ges. Physiol., 1895, lx, p. 1.

tion. They swim rapidly, some forward, some backward, now and again turning quickly and shooting in a new direction. No particular direction is preferred; the animals simply swim swiftly in any chance direction. Now those which by chance cross the line at c-c, coming into a region of low temperature to the left of c, cease their violent movements, while those which have started in a different direction keep up their headlong course until they also cross the line c-c, which they must inevitably do, purely by the laws of chance, if they continue to be active. Thus in time all the Paramecia which were in the heated region at the right of c will have crossed the line c-c, leaving the heated space empty. Meanwhile, it is not filled again, because any Paramecia to the left of c that may swim toward the heated end, react by reversal of the cilia and turning, when they come to the line c-c separating the hot from the cooler region. Thus the Paramecia have entirely vacated the region to the right of *c*, simply by keeping up their undirected movements, until by chance a practicable one carries them across the line. At a certain time after the beginning of the reaction a stream of Paramecia will be seen crossing the line c-c from right to left, since any other movement in this region causes a reversal of the cilia and turning.

At the other end, in the region resting on the ice, the cold does not act like the heat in greatly heightening the activities of the animais: it does, however, stop the thigmotactic reaction, so that all the Paramecia are set in motion, though perhaps very slowly. (If the cold is allowed to act suddenly and strongly, the Paramecia are simply benumbed, and remain where they are.) Some of the Paramecia thus swim by chance across the line d-d; the reaction is not, however, so quick and sharp as in the case of too high a temperature, and a number of stragglers will remain benumbed in the cold region. But those which are to the right of d, whether originally so, or after having crossed the line d-d from the cold region, do not cross this line again, since when they come to the line the cold causes a reversal of the cilia and a turning away. The cold region, therefore, gradually becomes emptied of Paramecia, like the hot space at the opposite end of the slide. The Paramecia in the middle region of the slide may now swim undisturbed anywhere between c and d, but as soon as they attempt to swim across the line c-c or d-d, the reaction sets in, and they are turned back. After a time, therefore, practically all the Paramecia are gathered in the optimum region between d and c, while the ends of the enclosure are empty. The

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result is not due to direct swimming toward the optimum temperature, nor a direct swimming away from the hot or cold region, but by a sort of "automatic selection" of movements. The Paramecia in the two ends keep swimming hither and thither, until a chance movement in the right direction carries them into the optimum zone. Motion takes place in any direction till one is automatically selected by the fact that it brings the Paramecium into new conditions. The analogy of this to the natural selection of structures is obvious.

Mendelssohn, who described the phenomena of thermotaxis in Paramecium without a knowledge of the finer mechanism of the reaction, assumed that the Paramecia turned and swam *directly* toward the optimum region from either end. In a Paramecium approaching a source of heat, the anterior end would thus be slightly warmer than the posterior end. Mendelssohn assumed that the directive control exercised by temperature must be due to this slight difference in temperature between the anterior and posterior ends of the same He found that in a trough 10 cm. long, a difference of animal. three degrees Celsius between the two ends of the trough was sufficient to cause the Paramecia to collect in the warmer end. The average length of a Paramecium being about 0.2 to 0.25 mm., it was easy to calculate that there was a difference in temperature of about 0.01° C. between the two ends of a Paramecium swimming lengthwise in the trough. It was, therefore, concluded that the Paramecia were sensitive to a difference in temperature of 0.01° C. But, as shown above, the method of reaction is much coarser than that assumed by Mendelssohn; the animal swims from one side of the optimum region to the other, not reacting at all until it comes to a region decidedly hotter or colder. The sensitiveness to temperature differences may, therefore, be much less than that given by Mendelssohn. In a trough with the optimum temperature at one end and changing gradually to the other, the only difference that one can be certain of their appreciating is that between the positive and negative limits of their excursions. If a single Paramecium swims back and forth over a stretch of 5 mm. lying between the cooler and warmer regions of the trough, then it must be concluded that it is sensitive to the difference in temperature between points 5 mm. apart; sensitiveness to any less difference is not proved. Similar considerations apply to other sources of stimuli, since the mechanism of reaction is the same for all classes of stimuli. It is evident that the sensitiveness of Paramecium to different agents may have been greatly overestimated.

Moreover, similar deductions as to the sensitiveness of other organisms must be considered insecure until the exact mechanism of their reactions has been determined.

While the general reaction I have described is evidently from certain standpoints an extremely simple one, yet it bears strongly marked the distinctive features of reactions to stimuli as we know them in the higher organisms, - namely, the lack of any direct and apparent relation between the effect and the cause. In studying the activities of inorganic matter, it is possible to establish relationships of cause and effect -- often through a somewhat extended chain from the first cause to the final effect — that may be clearly perceived as causal relations, --- so that the effect could be predicted from a knowledge of the first cause and the attendant conditions. On the other hand, in dealing with the activities of living bodies, we are confronted with phenomena in which the steps connecting cause and effect cannot be traced; such phenomena are called reactions to stimuli. Evidently, one of the chief objects in the investigation of the activities of living bodies must be the attempt to resolve reactions to stimuli into the chain of causes of which we must believe them to be composed, so that a series of steps can be traced, each satisfactory from a causal standpoint, from the original cause to the final effect. Can we hope by a study of the simplest unicellular organisms to approach such a resolution of life activities into connected chains of cause and effect? As a hypothetical example of such a resolution may be cited Verworn's theory of the chemotactic movements of Amœba toward oxygen; if this theory is true, the relations of cause and effect are clearly traced from the original cause to the final effect. In the case of the comparatively complicated organism Paramecium, it was perhaps scarcely to be expected that any clear evidence of the actual causal relation between stimulus and reaction should be made apparent, and as a matter of fact, we find, from a causal standpoint, an absolute gulf between them. It is not even possible to trace such general relations between the contractility of the cilia and the nature and position of the sources of stimuli as have been assumed by various authors; Jensen,¹ for example, assumes that a stimulus acting upon one side of the Paramecium causes the cilia of that side to beat more strongly, thus turning the animal away from the source of stimulus; some such relation might perhaps have been reasonably anticipated. But we find that the most varied and

1 JENSEN, P.: Archiv f. d. ges. Physiol., 1893, liii, p. 471.

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even opposite stimuli produce the same reaction, and that stimuli at one end, at the side, or acting over the entire surface of the animal at once, produce the same result. The reaction appears to be purely arbitrary, without any relation to the nature of the cause. It evidently depends upon the internal mechanism of the body of Paramecium, and this mechanism is so complicated that we are quite unable to trace the steps which lead from cause to effect.

For all practical purposes, therefore, the reactions of Paramecia present phenomena not a whit simpler for a causal understanding than the activities of a highly developed Metazoan. The mechanism of the unicellular organism, lacking as it does a complex nervous system, may, as a matter of fact, be simpler than that of a Metazoan, but in both cases the mechanism is of sufficient complication to interpose for our understanding an absolute break between stimulus and reaction; hence the study of the Protozoan gives no deeper insight into the essential nature of such reactions than does the study of a Metazoan. Whether the reactions of such a comparatively undifferentiated lump of protoplasm as Amœba will really prove of any more value for such an insight remains to be seen; certainly Amœba is deserving of a thorough experimental study from this standpoint.

Thus the principal intrinsic interest of this investigation lies not so much in the fact that the organism studied is a mass of protoplasm constituting but a single cell, as in the fact that it represents a very low place in the psychological scale. From the psychological standpoint, the reactions of Paramecium are extraordinarily simple. We have in this animal perhaps as near an approach to the theoretical reaction postulated by Spencer and Bain for a primitive organism, --namely, random movements in response to any stimulus, - as is likely to be found in any living organism. The motions are strictly random, so far as the position of the source of stimulus is concerned; the animal always swimming, after stimulation, in the direction of one of its own ends (the posterior) and turning toward one of its own sides (the aboral), without regard to the relation of these directions to the source of stimulus. And by the repetition of the reaction the direction of movement is frequently changed, - always without relation to the localization of the stimulus. It appears not to have been foreseen, theoretically, that such random movements would of themselves if continued carry the animal out of the sphere of influence of the agent causing them and keep it from re-entering. To accomplish this result, it is only necessary that the direction of motion should be changed at the moment when the stimulus begins to act, and at intervals so long as its action continues.

It is evident from this method of reaction that Paramecia are neither directly attracted nor directly repelled by any agencies. It is often assumed that it is a universal property of living organisms to react in two opposite ways toward stimulations, — to be attracted by some and repelled by others. In view of the reactions of Paramecium this assumption must fall to the ground, as certainly not universal, and possibly not nearly so general as has been supposed. The mechanism of the reactions of most simple organisms remains yet to be ascertained.

In regard to the position in the psychological scale to be assigned to Paramecium, the following may be said. The organism responds to any stimulus by a definite, well-characterized reaction. The same may be said of the isolated muscle of a frog. The intensity of the reaction varies with the nature and intensity of the stimulus: this also is true for the muscle. Under certain influences the Paramecium remains quiet; likewise the muscle. The directive relations of the motions performed are determined both in the Paramecium and in the muscle by the structure of the organism, not by the localization of the stimulus. There seems, then, no necessity for assuming anything more in order to explain the reactions of Paramecium than to explain the reactions of the muscle. We require, therefore, little or nothing more than irritability, or the power of responding to a stimulus by a definite movement, to account for the activities of Parame-Since the direction of motion of the Paramecium has no cium. relation to the position of the source of stimulus, there is no need to suppose that the animal has anything related to a knowledge of this position. Moreover, it exercises no choice, --- the direction of motion being always the same with reference to the parts of the animal. Ι do not see that we are compelled to assume consciousness or intelligence in any form to explain the movements of this creature.

SUMMARY.

I. Paramecium has a single motor reaction, by which it responds to all classes of stimuli. This reaction consists of the following activities. (I) The direction of the stroke of the cilia is reversed, over the entire surface of the animal, so that they strike forward, driving the animal backward. (2) The reversal ceases; the cilia in the oral

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groove strike backward, as at first, while the aboral cilia of the anterior half of the body strike *transversely toward the oral side*. This *results in turning the animal toward the aboral side*. The anterior end may, if the stimulus is strong, be curved toward the aboral side, thus aiding in turning toward that side. (3) The cilia all strike backward as at first, driving the animal forward again. At the end of the reaction the Paramecium is swimming forward on a path which lies at an angle to the path on which it was moving at first.

2. The intensity and duration of the different parts of this reaction vary with the nature and intensity of the stimulus.

3. Paramecia do not turn directly toward a beneficial source of stimulus, nor directly away from an injurious source of stimulus, but the reaction is always as stated under I. That is, localized stimuli, acting on one side or one end of the animal, have the same effect as stimuli acting upon the entire surface of the body at once. The direction in which the Paramecium turns after a stimulus is determined by internal factors, and is expressible in terms of the animal's structure; it has no relation to the position of the source of stimulus. The *absolute* direction in which the animal turns is a matter of chance; if it does not carry the animal away from the obstruction the first time, the entire reaction is repeated till it does.

4. *Positive* and *negative taxis*, as applied to Paramecia, are merely convenient terms for expressing the fact that the animals form collections in the regions of certain influences and do not form such collections in others; the terms do not express motor reactions. Paramecia are not directly attracted or repelled by any agencies or conditions. The collections formed in the regions of certain agencies are due to the fact that these agencies cause *no motor reaction*.

5. Different classes of chemical or physical stimuli do not have qualitatively different methods of affecting the stroke of the cilia.

6. In view of the mechanism of the reactions, the sensibility of Paramecium to different agents has probably been much overestimated, since it is not the differential effect on the anterior and posterior ends of the animal that induces the reaction.

7. In the reactions of Paramecium the steps between cause and effect cannot be traced, opposite causes producing the same effect, and the same cause if continued producing opposite effects. The nature of the reaction is conditioned by the internal mechanism of the animal's body.

8. The reactions of Paramecium indicate that the organism stands at the very bottom of the psychological scale. Simple irritability, or the property of responding to a stimulus by a fixed set of movements, seems sufficient to account for its activities.

The results presented in the foregoing paper were obtained in connection with an extended study of the chemotaxis of Paramecium, carried out in the Laboratory of the United States Fish Commission for the Biological Survey of the Great Lakes during the summer of 1898, and continued at Dartmouth College during the following autumn. It is a pleasure to acknowledge here my indebtedness to Prof. J. E. Reighard, the Director of the Survey, and to the officials of the United States Fish Commission for assistance and courtesy in every way in carrying on this investigation, as well as for permission to publish the present paper.

Dartmouth College, Hanover, N. H., Jan. 17, 1899.