SEVENTH LECTURE.

THE BEHAVIOR OF UNICELLULAR ORGANISMS.

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In recent biological writings there is manifest a growing tendency to interpret the processes taking place within the bodies of higher animals — especially the developmental processes — as a series of responses to stimuli. In the egg and the developing embryo, masses of protoplasm migrate from one position to another, cells and cell masses alter in form, changes of the most varied character are continually occurring. To explain such changes it is becoming usual to call upon chemotaxis, geotaxis, phototaxis, thigmotaxis, and other motor reactions of similar character. The prevalent ideas of these reactions, known usually under names terminating in *-taxis* or *-tropism*, have been derived to a large extent from the phenomena shown by the movements of unicellular organisms; the classic experiments of Pfeffer on the chemotaxis of bacteria and flagellates and of Strasburger on the phototaxis of swarm spores having opened a fountain from which all have felt entitled to draw. To understand the migration of a cell or mass of cells in the embryo we are referred back to experiments on unicellular organisms, wherein it is shown that the movements of the latter are controlled by chemical agents, by heat, by light, and the like. Here the vital processes are seemingly brought into the closest relation with chemical and physical ones; chemotaxis, for example, is frequently interpreted as the direct expression of chemical affinity or chemical repulsion between the substance of the protoplasmic mass and some other substance, or between two protoplasmic masses. There is thus established an immediate direct relation between the movements of organisms and movements characteristic of inorganic substances; a long step is taken toward that analysis of vital processes into simple chemical and physical ones, which is deemed by many the final goal of biological science. If these phenomena do indeed establish such a relation, they challenge the attention of every man interested in the fundamental phenomena of life; in any case, they invite complete and thorough investigation of the claims made for them. Since it is largely from the reactions of free unicellular organisms that our ideas of chemotaxis, phototaxis, and the like have been derived, it is important to study carefully the reactions of these creatures and to determine the laws which control them. We shall then be in a position to decide whether the movements of these organisms do furnish a key to the understanding of ontogenetic processes or not. It is these considerations that have impelled the investigation whose main results I shall try to present.

In studying the behavior of single-celled creatures we are forced into relation with the much debated question of the nature and importance of the activities of unicellular organisms as compared with those of higher animals and plants. Some hold that the cellular standpoint is the fruitful one for general physiology; that we must first determine the laws of action for single cells, then carry these over to the cell state, understanding the latter only as a combination of the former. Some go so far as to maintain that the reactions of unicellular organisms are of an intrinsically different character from those of higher forms, being of essentially the same nature as the reactions of inorganic bodies; this is, for example, the position of Le Dantec.[1] Others hold that the division of organisms into cells is, physiologically at least, a secondary matter; that nothing more fundamental is to be expected from the study of a unicellular organism than from that of one composed of many cells. This question can be decided, of course, only by a thorough study of both the classes of organisms thus contrasted, with a comparison of the results, to see if the study of the simpler organisms does, as a matter of fact, clear up

[1] La matière vivante, Chapters I and II.

and simplify the phenomena exhibited by the many-celled creatures. For one desirous only of getting at the real laws underlying the phenomena, the conflict on such points between high authorities[1] is very confusing, and the only recourse is to a first-hand study of the facts.

In the hope of getting light on the problems proposed and others of similar character, I shall set forth and discuss observations and experiments made upon a number of free-swimming unicellular organisms. In the investigation it was found well to begin with some single species and work out its activities, and the laws governing the same, completely enough to reveal their essential nature, then to make a comparative study of the activities of other organisms in the light of the knowledge so gained. The same method will be advantageous for the presentation of results.

I give first, therefore, some of the results of a preliminary study of the activities of *Paramecium caudatum.* This is one of the commonest of the ciliate Infusoria, living by thousands in vegetable matter decaying in water. It is a somewhat cigar-shaped creature, having a broad groove passing obliquely from one end (the anterior) to the mouth, which lies at about the middle of the length of the body. The side on which the mouth and groove lie may be called the *oral* side; the opposite one the *aboral* side. The entire surface of the animal is covered with cilia, by means of which Paramecium moves.

In beginning a study of the activities of such an organism, we are at once confronted with the question of its psychic powers. If these unicellular organisms do, as a matter of fact, possess so complicated and highly developed a psychic life as Binet, in his book on the *Psychic Life of Micro-Organisms*, has attempted to show obtains among them, then indeed there is little prospect of gaining light on simple migrations of protoplasmic masses during development, through a study of their behavior. A study of the chick or the dog would perhaps be as promising. The activities which Paramecium shows are at

[1] See, for example, Verworn, "General Physiology," and Loeb, "Einige Bemerkungen über den Begriff, die Geschichte und Literatur der allgemeinen Physiologie," *Pflüger's Archiv*, Bd. lxix, p. 249.

first view of great complexity, so that they might seem to entirely justify Binet's views as to the height and variety of the psychic powers of these organisms. These activities and their explanation have been discussed somewhat fully by the writer in a paper[1] devoted entirely to the psychological aspect of the matter, so that only so much of this aspect will be taken up at present as has a necessary relation to the questions proposed.

If we place a number of Paramecia, in the culture water in which they are found, upon a glass slide, and cover with the cover glass, we soon find that the animals, which were at first scattered uniformly, have gathered into groups in one or more parts of the preparation. Usually we find that a bit of bacterial zoöglœa forms the center of such a group; as many of the Paramecia as can do so have pressed their anterior ends against the mass, the ciliary current carrying bacteria to their mouths; others press in from behind. It is well known, of course, that Paramecia make no choice in the food which the current brings to their mouths, taking in particles of all sorts indiscriminately. The possibility may suggest itself, however, that they have gathered about these masses of zoöglœa because the latter serve them as food. The choice of food would thus occur a step sooner — the Paramecia choosing their food by gathering about it, then taking whatever comes. But if we introduce into the slide a bit of filter paper or a fine raveling of cloth, we find that the Paramecia gather about it with the same apparent avidity as about the zoöglœa, pressing the anterior end against it and remaining thus, quiet, for long periods.

This and other experiments show, therefore, that this gathering about a bit of bacterial zoöglœa or other substance is not the expression of a choice of food, but is merely a manifestation of the fact that the Paramecia react to contact with solids of a certain physical texture by suspending active locomotion and remaining against the solid. A similar reaction to solids is, of course, a very common phenomenon among organisms of different sorts; it has received the name "Thigmotaxis," or "Stereotropism."

[1] "The Psychology of a Protozoan," *Amer. Journ. of Psychology*, vol. x, No. 4, 1899.

We have in thigmotaxis one of the fundamental reactions of Paramecium, not further analyzable into simpler component reactions. As it seems to consist chiefly or entirely of a cessation of a part of the usual ciliary motion, — only the cilia in the oral groove continuing to strike strongly backward, — it may be more philosophical to consider this partly resting condition as the "normal" condition, the usual forward motion being then considered a reaction to a stimulus, due to a change or removal of the solid body against which the animal is resting, or to some other change in the environment. There seems to be no decisive reason for considering either the condition of partial rest or of the usual forward motion as more "normal" than the alternative condition; taking either as a starting point, the other may be considered a response to a stimulus.

If the Paramecia are placed upon the slide in pure water, containing no bacterial zoöglœa, or any other solid, they do not even then remain scattered uniformly throughout the preparation. On the contrary, it is usually not long before the animals are gathered into one or more close groups in some part of the slide. Paramecia are usually found in the culture jars also aggregated into groups; this, taken together with the above experimental demonstration that Paramecia, at first uniformly scattered, will soon collect into close groups without evident external cause, might be held to indicate the existence of a "social instinct" among these creatures. Another possibility suggests itself — that there may be some invisible chemical substance in the region of these groups by which all the Paramecia are attracted; so that the fact that they come near together would be a secondary result of the fact that all are attracted by the same substance.

The main results of the extended study of the conduct of the Paramecia toward chemicals, to which this possibility led, may be given in a few words. It was found that Paramecia tend to gather together and form collections in drops of weakly acid solutions, and in solutions of some salts, while they avoid alkaline solutions and solutions of the salts of the alkali metals.

Among the substances into solutions of which they gather is carbon dioxide. If a bubble of carbon dioxide is introduced into a preparation of Paramecia, they soon collect closely about it and swim in circles around it without leaving it.

It was then proved, by introducing the Paramecia into a solution of rosol, which is decolorized by carbon dioxide, that these Infusoria excrete a distinctly appreciable amount of this substance, which diffuses into the surrounding water. Whenever, therefore, a very few Paramecia get together, an active solution of carbon dioxide is soon formed, and the region becomes at once a center of attraction for the Paramecia. A most complete correspondence was demonstrated between the diffusion of the CO_2 into the water and the distribution of the Paramecia in groups, and all the phenomena exhibited by the (apparently) spontaneous collections of Paramecia could be exactly imitated by introducing CO_2 into the slide.

Thus these collections of Paramecia give no indication of "social instinct," but are merely the expression of positive chemotaxis on the part of the animals toward a certain substance. In the same way all the seemingly complex activities of these creatures may be reduced to simple factors, so that there seems no evidence to indicate the possession by them of psychic powers of anything more than the most elementary character.

We may proceed then to a closer analysis of the apparent attractions and repulsions — chemotaxis, thermotaxis, and the like; it is from a study of these that light is to be gained on the problems first proposed. We shall first consider chemotaxis.

The fact that animals and plants are attracted by certain chemical substances and repelled by others is of course well known for a large number of organisms. As to the essential nature of this phenomenon, opinions differ. As pointed out above, some hold that chemotaxis is the direct expression of chemical affinity or repulsion between the living protoplasm and the chemical. Le Dantec (*La matière vivante*, pp. 51, 52) gives geometrical figures illustrating the action between the surface of a free cell and a chemical substance diffusing in the surrounding water, demonstrating in mathematical form that as a result of this action the cell must move either toward or away from the center of diffusion of the chemical. The motion of such a protoplasmic body would be passive in the same sense as the movements of iron filings are passive when acted upon by a magnet. Delage and Herouard[1] actually state that the Flagellata have, in addition to their usual active movements, also a *passive* motion, due to the attraction of chemical substances. Perhaps the majority of biologists hold less radical views than this; yet the opinion seems widespread that in chemotaxis we are dealing with a simple primary phenomenon.

Coming now to an examination of the phenomena as exhibited by Paramecium, we will first take up positive chemotaxis, or attraction toward chemical substances. The phenomenon to be explained shows itself as follows. If into a slide of Paramecia a drop of some attractive substance (as a weak acid) is introduced, the Infusoria soon collect in the drop, forming there a dense assemblage. Now, what is the exact action of the attractive substance on the Paramecia to cause them to turn and enter the drop? Observing carefully the conduct of the animals, we find, first, that *they do not* turn toward the drop. Owing to its slow diffusion, the margin of a drop thus introduced beneath the cover glass is evident, and the Paramecia, swimming in every direction throughout the preparation, may be seen in their random course to graze almost the edge of the drop, without their motion being changed in the least; they keep on straight past the drop and swim to another part of the slide. But of course some of the Paramecia in their random swimming come directly against the edge of the drop. These do not change their motion, but keep on undisturbed across the drop. But when they come to the opposite margin, where they would if unchecked pass out again into the surrounding medium, a marked reaction is caused; the Paramecium jerks back and turns again into the drop. Such an animal then swims across the drop in the new direction till it again comes to the margin, when it reacts negatively, as before. This continues, so that the animal appears as if caught in the drop as in a trap. Other Paramecia enter the drop in the same way and are imprisoned like the first, so that in time the drop swarms with the animals. As a result of their swift, random movements when

[1] Traité de zoologie concrète, tome i, p. 305.

first brought upon the slide, almost every individual in the preparation will in a short time have come by chance against the edge of the drop, will have entered and remained, so that soon all the Paramecia in the preparation are in the drop.

Thus it appears that the animals are not attracted by the fluid in the drop; they enter it by chance, without reaction, then are repelled by the surrounding fluid. The peculiar fact that the animals, after entering the drop of the substance in question, are repelled by the surrounding fluid in which they were previously immersed will become more comprehensible after the phenomena of repulsion are considered.

Turning, then, to the matter of negative chemotaxis or repulsion, we have the following phenomenon to be explained. If into a slide of Paramecia swimming at random a drop of some repellent chemical (as NaCl) is introduced, we find that the drop remains entirely empty, not a single Paramecium entering it. Now, exactly how do the Paramecia succeed in keeping out of such a repellent solution?

Careful observation shows that when the Paramecium, swimming forward, comes in contact with the drop of repellent substance, it swims backward a short distance, then turns *toward its own aboral* side, then swims forward again. The essential point in this reaction method is, that the Paramecia always turn toward their own aboral side, without regard to the position of the stimulating drop. If a Paramecium comes obliquely in contact with the drop so as to touch it only on one side of its body, it nevertheless gives the reaction above described without modification, even though turning toward its own aboral side after backing off may carry the animal directly toward the drop, instead of away from it. In such a case the animal when it comes again in contact with the drop simply repeats the reaction. As it continually revolves on its long axis both when swimming forward and when swimming backward, the aboral side is nearly certain to lie in a new position the second time, so that the animal turns in a new direction. If this is repeated a sufficient number of times, the Paramecium is fairly certain, by the laws of chance, to get started finally in a direction which carries it away from the stimulating chemical.

It thus appears that the direction in which a Paramecium turns after stimulation by a chemical substance is not determined by the position of the stimulating agent, nor indeed by any external factor, but by an internal factor, — by structural differentiations of the animal's body. This is demonstrated in a striking manner by immersing the Paramecia directly into a chemical solution of such a nature as to act as a stimulus. The entire surface of the animal is then bathed by the chemical, so that there is nothing in the external conditions to determine in which direction the animal shall move. Nevertheless, under these circumstances, it swims backward, turns toward the aboral side, and swims forward, usually repeating the operation indefinitely. Very striking is also the experiment of causing the chemical to act first upon the posterior end of the animals. This may be done as follows: A large number of Paramecia are frequently observed with anterior ends pressed against the surface of a bit of bacterial zoöglœa (thigmotactic reaction), so that the posterior ends are all pointed in the same direction. Now, a capillary glass rod, coated with some chemical, is introduced into the water behind the Paramecia. The chemical gradually diffuses through the water, of course first reaching the posterior ends of the Paramecia. But these, when they respond, react exactly as in the other cases; they swim backward some distance and turn toward the aboral side. It often occurs that in thus swimming backward they enter the densest part of the chemical and are killed by it.

These experiments indicate that not only the direction of turning after swimming backward, but also the swimming backward itself is determined by internal factors, and is independent of the position of the source of stimulus. This conclusion seems strictly true for chemical stimuli both in Paramecium and in other Infusoria experimented with. As will be shown later, other experiments throw a light upon the cause of this uniform backward motion when stimulated by a chemical.

Summing up, then, we may say that when Paramecium is chemically stimulated it swims backward, turns toward its own aboral side, then swims forward. As a rule, the anterior end, moving forward, comes first in contact with the chemical, so that swimming backward does, as a matter of fact, usually carry the animal away from the source of diffusion of the chemical, and turning toward the aboral side before swimming forward again will, as a rule, if repeated, finally carry the animal in such a direction that it does not again come against the source of stimulus. But these are, from the physiological standpoint, matters of accident; the animal conducts itself in the same way whether the source of stimulus has this usual position at the anterior end of the animal or not. The direction of motion after a chemical stimulus, then, has no relation to the position of the chemical substance. We cannot say, therefore, that the Paramecia are *repelled* by any chemical substance — just as we were compelled to conclude that they are not directly attracted by any chemical substance.

We find, then, that the effect of chemicals on Paramecia is not to attract or repel them, but simply to cause a certain set formula of movements. Such a set formula of movements, "touched off," as it were, by stimuli of various sorts, may be called a reflex. In returning now to the question of how the apparent attraction of the Paramecia toward certain substances — that is, the fact that they collect in drops of certain substances — can be brought about through such a reflex, it is necessary to recall certain general facts in regard to the nature of reflexes. First, any change in the environment that can be perceived by the organism may "touch off" such a reflex. Second, the character of the reflex has no necessary relation to the nature of this external change, so that of a given kind of change it cannot be predicted beforehand whether it will cause the reflex or not, and changes of opposite character may produce the same reflex.

The mechanism of the gathering together of the Paramecia into a drop of some weak acid is then as follows: When the Paramecium passes from the surrounding fluid into the acid solution there is, of course, at the moment of crossing the boundary of the drop a change in its environment. Whether this change will cause the characteristic reflex or not is impossible to predict, that depending upon the internal mechanism of the organism; as a matter of fact we find that it does *not* cause the reflex. Now, after passing across the drop it comes again to the boundary where, if not stopped, it would pass out again into the surrounding fluid. At this boundary there is, of course, another change in the environment — a change in the opposite sense from that experienced in passing into the drop. Whether this second change will cause the reflex is of course likewise impossible to predict, since it depends upon the nature of the organism ; as a matter of fact we find that it *does* cause the reflex. The Paramecium is, therefore, returned into the drop and kept there in the manner already described. It seems probable that the physiological condition of the Paramecium is changed by immersion in the drop of acid, so that contact with the culture fluid now acts as a stimulus, though it before did not. It seems not impossible to conceive, however, that even without such a change in physiological condition, an environmental change from *b* to *a* might cause a reaction, when the opposite change, from *a* to *b*, would cause none. This has, as is evident from the nature of a reflex, no necessary relation to the comparative actual mechanical difficulty in passing in one direction or the other.

The one effect of a marked chemical stimulus on Paramecium is, then, to produce the characteristic reflex already described, and the apparent attraction or repulsion is determined by the fact that some chemical substances or chemical changes cause the reaction, while others do not.

Now, experimentation with stimuli other than chemical leads to the highly important observation that this same reflex is produced by stimuli of the most varied nature. Substances which seem to act upon Paramecium only through their osmotic pressure, such as solutions of sugar, cause the same reflex ; tonotaxis, then (to use the name employed by Massart), acts through the same reflex as does chemotaxis. Mechanical stimuli, produced by jarring the preparation, cause the same reflex. Heat and cold act in the same way, and the Paramecia avoid hot or cold areas and collect in regions of optimum temperature in exactly the same manner as they avoid certain chemicals and collect in others.

We are driven, therefore, to the conclusion that chemotaxis is not an activity differing in kind from the other reactions of these animals. Many sorts of changes in the environment produce a certain characteristic reflex in Paramecia, resulting in their collecting in regions of certain characters and leaving other regions vacant. Among the changes that act thus are chemical changes, and the characteristic groupings of the animals so caused are said to be due to chemotaxis; they are, however, produced in an essentially similar manner to the groupings produced by other agents. There is a unity underlying the motor activities of the Paramecia — a unity expressed in the fact that the different classes of stimuli produce identically the same reaction.

To be accurate, however, we must distinguish two less important forms of reaction to stimuli that are not manifested through the characteristic reflex above described. One is thigmotaxis; this is, however, not a motor reaction, but one characterized chiefly or entirely by a cessation of a part of the usual motion. Again, as previously set forth, it is possible to consider the partially resting condition characteristic of thigmotaxis as the primary condition; then the ordinary forward motion of the animal will be a motor reaction to a stimulus, since it is induced by a change in the environment. As will be shown, there is sufficient ground in certain other Infusoria to *compel* us to consider this forward motion as at times a reaction to stimulus; this, then, is a motor reaction which does not take place through the above-described characteristic reflex. It seems possible that the following represents the true state of the case; very weak stimuli acting on the resting individual cause the ordinary forward motion; stronger stimuli produce the above-described motor reflex.

In view of the means by which chemotaxis is brought about, it becomes more intelligible why the Infusoria may at times collect in regions of injurious substances and avoid at times areas of harmless substances. It is not a matter of attraction or repulsion at all. In the former case the injurious substance merely does not act as a stimulus to cause the motor reflex; in the second case, the chemical in question, though not injurious, does act as a stimulus. An extended investigation directed upon this point showed that the chief factor determining whether a substance does or does not cause the motor reflex of Paramecium is not the injuriousness of the substance, but is of a chemical nature.

We are now prepared to sum up the main results on Paramecium. In this animal we find that chemotaxis, thermotaxis, tonotaxis, reactions to mechanical shock, and the like, are not distinct kinds of activity; that in each case we have the same movements, merely induced by different agents. When Paramecium is effectively stimulated by any substances acting chemically or through osmosis, by heat or by cold or by mechanical shock, it responds with a reflex, which consists of the following activities: the animal swims backward, turns toward its own aboral side, then swims forward. The result of this method of reaction is that the Paramecia tend to leave the sphere of influence of agents causing this reflex, and to congregate in areas where this reaction is not caused. For chemical substances at least it is proved that the position of the stimulating agent has no influence on the direction of movement after a stimulus; the direction of movement throughout the reaction is determined by internal factors.

Is this reaction method one that is common among unicellular organisms, or is it peculiar to Paramecium? To answer this question I have studied the reactions of a considerable number of unicellular organisms belonging to the Flagellata and Ciliata. The essential point in the reaction of Paramecium, the factor that gives character to the entire response, is the circumstance that the animal after stimulation turns toward one side which is structurally defined, without regard to the nature and position of the source of stimulus. The point to which attention was primarily directed in studying the other organisms was, therefore, whether after stimulation the creature turned always toward one structurally defined side.

The organisms studied included, among the flagellates: *Chilomonas paramecium* and *Euglena viridis;* in the ciliates the following Holotricha: *Paramecium caudatum, Loxophyllum meleagris, Colpidium colpoda, Microthorax sulcatus, Dileptus anser, Loxodes rostrum*, and a species of *Prorodon;* the following Heterotricha: *Stentor polymorphus*, *Spirostomum ambiguum*, and *Bursaria truncatella*; of Hypotricha, *Oxytricha fallax* and a number of undetermined species. In several of these creatures, on account of the large size or other favorable circumstances, it was possible to use methods of investigation not available for Paramecium; in particular it was possible in a number of cases to localize very precisely the action of stimuli.

In all of the organisms named, in spite of great variations in the nature and complexity of the usual movements, the reaction method was essentially similar to that of Paramecium. In all, the direction of turning after a stimulus was toward a structurally defined side, without regard to the nature and position of the source of stimulus. With regard to the details of the reaction, as might be expected, the greatest variety exists, but the general reaction plan was the same throughout.

This method of reaction evidently has a close relation to the usual asymmetry of the cell body exhibited by these organisms. This asymmetry of the Infusoria has also a close relation to the normal method of progression through the water, as well as to the method of reaction to a stimulus. Most of these organisms, as they swim forward, also revolve on the long axis, and the resulting path is usually a spiral. The form of the body has a constant relation to the axis of the spiral, the same side being at all times directed toward this axis. The unsymmetrical structure of the body, the usual method of progression, and the method of reaction to a stimulus are thus evidently closely interrelated. In the case of a bilaterally or radially symmetrical animal one would certainly not expect that one side would be always preferred to the other in turning away from a source of stimulus, as is the case in the Infusoria.

In the case of chemical stimuli it was found for all the organisms studied that not only the turning to one side, but the swimming backward after a stimulus, was independent of the position of the source of diffusion of the chemical. The action of chemical stimuli was localized by bringing a capillary glass rod coated with some chemical compound near the anterior end, one side, or the posterior end, of the quiet organisms. In every case (except in *Euglena viridis*, which does not swim backward under any circumstances) the organisms reacted to the chemical stimulus by swimming backward, turning toward the usual structurally defined side, then swimming forward. The swimming backward, of course, sometimes carried the creature away from the densest part of the solution (when the chemical was held in front); at other times, directly toward and into the densest part (when the same chemical was held behind). In the latter case the organisms were frequently killed by swimming into the dense solution. Thus, in chemical stimuli, without exception, the direction of motion after stimulation has no relation to the localization of the stimulus.

In several of the organisms it was possible to use also very precisely localized mechanical stimuli; and the results so gained tend to modify in some particulars the general conclusions that might be drawn from a study of the action of localized chemical stimuli. Localized mechanical stimuli were produced by touching under a powerful lens any desired part of the body of the organism with a glass rod drawn to the finest hair in a flame. For Paramecium itself this method of experimentation was not satisfactory, owing to the minute size of the cell body. One point of importance was brought out in Paramecium, however. The anterior tip of the body was shown to be incomparably more sensitive than any other part. On bringing the glass hair near the anterior tip, Paramecium leaps backward almost before the hair is seen to have reached it, giving the entire typical reaction already described. Any other part of the body was so insensible that it was not possible to cause a reaction of any sort by touching it with the hair. Paramecium could be pushed about and made to alter its direction of movement mechanically, of course, but there was no active response of any sort when it was touched at any point except the anterior end.

In *Spirostomum ambiguum* essentially the same results were reached with mechanical as with chemical stimuli. If any part of the body was touched, whether anterior end, posterior end, or side, the infusorian gave the typical reaction — swimming backward, turning toward the aboral side, then swimming forward. A slightly greater percentage of cases of the typical reaction was obtained by touching the anterior end, but the difference was little; it varied in Spirostoma from different cultures.

In the other organisms on which the effects of localized mechanical stimuli were tried, particularly *Loxodes rostrum*, *Dileptus anser*, *Oxytricha fallax*, and one or two other Hypotricha, the following results were obtained: (1) The side toward which the animal turns after a stimulus is entirely independent of the side which is touched. In every case the organism turns toward one structurally defined side. If that is the side which is touched, the organism turns continually toward the source of stimulus, no matter how many times the latter is repeated; if the other side is touched, the creature of course turns away from the source of stimulus. The impression is given that it is physiologically impossible for the organism to turn otherwise than toward this one side. (2) But the forward or backward movement of the animals after a stimulus is *not* thus independent of the localization of the stimulus. If the anterior end is touched, the organism darts backward, turns toward one side, then swims forward. The posterior half of the body is very insensible, so that as a rule there is no response to a mechanical stimulus occurring here. If, however, a strong stimulus is given here, as by thrusting the tip of the rod strongly against the resting animal, the latter simply *swims forward;* if already swimming forward, it merely hastens its forward motion when thus stimulated.

Thus, in the case of mechanical stimuli in these organisms the direction of motion after a stimulus depends, *to a certain extent,* so far as backward or forward motion is concerned, upon the localization of the stimulus. This introduces a greater complexity into the psychology of these creatures than the results on Paramecium alone, or on the reactions to chemical stimuli alone would lead us to judge. The organisms do in certain respects react with reference to the localization of a stimulus affecting them. The differing results gained with chemical stimuli are probably to be interpreted, in view of the facts shown by a study of mechanical stimuli, as follows: When a chemical diffuses from a point lying behind the infusorian, it of course comes first in contact, as a very weak solution, with the posterior end of the animal. Now, as already stated, this posterior end is not at all sensitive, so that no reaction is caused. The chemical continues to diffuse until it finally reaches the very sensitive anterior end, when at once the typical reaction occurs, and the animal swims backward into the strong solution. The reaction to a chemical is perhaps then always due to stimulation at the anterior end.

Psychologically considered, we seem to have here a remarkable transitional condition toward a perception of the localization of the stimulus by the organism — a reaction with reference to the localization of the stimulus so far as motion along the axis of the body is concerned, a blind reflex, without regard to the localization of the stimulus, so far as motion to one side is concerned.

We may now summarize briefly the essential facts in regard to the reactions of the unicellular organisms studied. The reactions of these organisms may be classified into three reaction forms:

(1) One is the thigmotactic reaction. Starting with the moving infusorian, we find that it reacts to contact with solid bodies of a certain physical texture by suspending part of the usual ciliary motion, so that locomotion ceases and the organism remains pressed against the solid. Whether anything more than this cessation of part of the usual ciliary motion is concerned in the thigmotactic reaction is very difficult to say.

(2) If we start with the resting individual, the simplest reaction to a stimulus is the resumption of the usual forward motion. This is the reaction that is produced when the solid substance against which the creature is resting is removed; it is also produced in some Infusoria when the posterior part of the body is stimulated mechanically.

(3) The third, and, for our purpose, most important reaction, to which most of the so-called tactic or tropic phenomena are due, may occur in either active or resting animals. It is a reflex consisting of the following activities: the animal swims backward, turns toward one structurally defined side, then swims forward. This reaction is produced by chemical stimuli acting upon any part of the body or upon the entire body at

once, by osmotic stimuli, by heat, by cold, by mechanical shock. Its general effect is to take the organism out of the sphere of operation of the agent causing the stimulus, and to prevent it from reëntering. The fact that certain areas are left vacant is because the agencies within these areas cause this reaction; the collecting of the organisms within certain areas is due to the fact that here the reaction is not produced, while it *is* caused, by the influences active in the surrounding regions.

Thus, chemotaxis, tonotaxis, thermotaxis, and the like are unified; they are not qualitatively different activities, but are fundamentally one activity due to different causes. The tactic phenomena of unicellular organisms are brought throughout under the same point of view as the motor reflexes so well known in the physiology of higher animals.

We may now return to a brief consideration of the problems which formed the starting point of this investigation — the relation of the phenomena studied to the growth processes in the protoplasmic masses of higher organisms. Do the laws of the motor reactions of unicellular organisms, chemotaxis and the like, really give us a basis for the understanding of protoplasmic migrations and other processes in growth and differentiation?

We find that the tactic phenomena of these unicellular forms are brought about through a reflex that is in all essential points similar to the reflexes of higher animals. The nature of this reflex is closely bound up with the physiological and structural differentiations of the body of these organisms; it has a specially close relation to the asymmetry of the cell body in these Protozoa, and to the manner of the usual forward motion. These differentiations are absent in the masses of protoplasmic substance that are moved about in the processes taking place within the eggs and embryos of Metazoa. It is difficult to see how the laws controlling the movements of such substance masses can have any similarity to the laws above developed for the reflexes of free unicellular organisms. Above all, it is evident that the tactic movements of unicellular organisms are not direct expressions of simple chemical and physical laws; chemotaxis, for example, is not a direct result of chemical affinities and repulsions between the protoplasmic substance and other chemical compounds. Like all the other tactic phenomena, it is the result of a motor reflex, which may be produced by the most varied means. These tactic movements, then, do not establish an immediate relation between the movements of organisms and the movements characteristic of inorganic substances. The organism reacts as an individual, not as a substance. To my mind the facts above brought out in regard to the movements of these creatures tend, if these facts have a general validity, to deprive such movements of their supposed value for explaining or illustrating the processes of growth; in so far as the ideas of chemotaxis and the like in growth processes have been derived from the phenomena exhibited by unicellular organisms, these ideas require a revision.

Especially do the facts above brought out reveal the fallacy of the statement so often insisted upon, that the growth processes induced by chemical or physical agencies are "the same as" or "identical with" the locomotor reactions induced by the same agencies. This has been carried so far that strenuous objection has been raised even to the use of distinguishing terms for these two sets of phenomena. We are told that to distinguish as *-taxis* the motor reactions of a free organism from *-tropism* or the growth reactions of a fixed organ or organism is all wrong; the two are "identical." It is reasonably certain that the growth phenomena of plants are not brought about through a reflex that is identical with the motor reflex of Paramecium; it seems exceedingly probable that the ways by which movements are brought about as responses to stimuli in the various classes of plants and animals will present great variety. It is difficult to see what is to be gained except confusion of ideas by applying the same names to two such dissimilar activities as the motor reflex of Paramecium when stimulated by a chemical, and the bending of a plant to or from a chemical in solution.

In regard to the second question touched upon in my introduction, — the nature and importance of the activities of unicellular organisms as compared with those of many-celled creatures, and their value for explaining the phenomena shown by the higher, — the general trend of the answer is, I think, evident. I should be inclined to interpret the facts presented somewhat as follows: The claim that the motor processes of unicellular organisms form a connecting link between inorganic processes and the vital phenomena of higher creatures clearly receives no justification for the organisms studied. Every influence coming in from outside passes, as it were, through a sort of central station, where it is completely transformed to appear as a reflex action, the nature of which is conditioned by the form and structure of the organism; and the steps in the transformation are no more evident than they are in the higher forms. The reactions of these creatures are indeed simple, but not qualitatively of a different sort from those of higher organisms, so that for motor reactions of the sort studied I do not see that a knowledge of the conduct of these particular unicellular organisms really adds to our insight into the causal relations in the activities of higher animals.

On the other hand, if we dismiss any idea of getting from them knowledge of a different kind from that gained by the study of other groups, then the behavior of these Protozoa is of the greatest interest from the standpoint of comparative psychology. In these creatures we see, as nowhere else, how activities that seem so complicated and varied as to require psychological powers of a high order, are produced merely through one or two simple reflexes; it seems not impossible that the phenomena exhibited in the conduct of these organisms may in time furnish important points of support for the general theory of the origin and development of psychic powers.