The Interpretation of the Behavior of the Lower Organisms
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Source: *Science*, New Series, Vol. 27, No. 696 (May 1, 1908), pp. 698-710
Published by: American Association for the Advancement of Science
Stable URL: https://www.jstor.org/stable/1633003
Accessed: 11-04-2020 07:10 UTC

DISCUSSION AND CORRESPONDENCE

THE INTERPRETATION OF THE BEHAVIOR OF THE LOWER ORGANISMS

IN my recent volume on the "Behavior of the Lower Organisms" are set forth certain views which have called forth discussion and criticism.[1] In response to many questions which indicate that there is a general interest in the subject, I wish here to reexamine some of the matters raised.

Objections have centered about my discussion of certain general theories of behavior, particularly of the tropism theory, and of certain applications of the theory of selection. Some of the criticisms are clearly just; others seem to me to rest upon misunderstanding, while still others show actual differences of opinion. To set in a clear light these different categories is my present wish.

The only question of importance is: How far is there a real difference of opinion, among workers familiar at first hand with the phenomena, in regard to (1) the actual, experimental facts of behavior, (2) the general and important laws or principles underlying these facts. Divergences due to different lines of interest, different fields of investigation and different understanding of terms merely obscure the essential point and need to be cleared away. To make clear the objects and meaning of different investigators sometimes reveals harmonious diversity in place of conflict; when this result is not reached, it at least shows precisely where opposition lies, and suggests experimentation that shall turn opposition into agreement.

It will greatly facilitate the attainment of these ends if I first set forth briefly certain purposes and principles that guided me in the preparation of my account.

1. My book was designed mainly as a topographic survey of the field of behavior in the lowest organisms. My primary purpose was to give the reader a clear idea of the observable facts, so that he might gain somewhat the same impression that he would from seeing the phenomena themselves. To aid in this, I characterized as typical such phenomena as were fairly representative of the behavior in general, while phenomena that were rare or unique, like the reaction to the electric current, I said were not typical and gave an inadequate idea of the nature of behavior. This, while strictly true, has led to misunderstanding; certain critics have assumed that I considered such phenomena as of no importance *from any point of view*. I believe that there is nothing in my treatment that gives ground for this assumption. Special cases of this form of criticism will come up in later paragraphs.

2. The most important characteristics of behavior have always seemed to me those shown in the biological interrelations of the physiological processes: in the relations of behavior to preserving the organism, to supplying the requirements for metabolism, and in general to keeping the other physiological processes in progress. These adaptive or regulatory characteristics of behavior furnished the problem to the solution of which attention was in my book mainly directed. Therefore I characterized as "important," "significant," and the like, mainly those features of behavior which seemed to lead toward an understanding of its regulatory character. Other investigators, not having this problem in the center of interest, have considered quite other matters as the important ones. Thus Torrey (*l. c.*) holds that we find the most important features of behavior in precisely those features that are not regulatory. Judgments of importance are of course relative; importance *for what?* is the question. I take it that the question in which Torrey is primarily interested is that regarding the nature of the immediate change which occurs in living matter when an external stimulus acts upon it.

3. We now come more directly to the content of the work. Years of investigation had convinced me that the complexity of the problems of behavior had been underestimated; that even in the lower organisms we are compelled to deal with an immense number of

[1] See especially Torrey, in SCIENCE, September 6, 1907; Loeb, *The Journal of Experimental Zoology*, Vol. 4, No. 1, 1907, and *Pflüger's Archiv*, Bd. 115, 1906, p. 580; Parker, SCIENCE, October 25, 1907.

complex and little-understood factors, rather than with a few simple ones.

In my book I therefore attempted, by citation of precise experimental data, to show the great number of factors which play a part in determining behavior; to show that changes in the internal system which makes up the organism are of equal importance for this, with changes in the external system which makes up the environment; and I set forth particularly those remarkable relations of dependence and support between the acts of behavior and the other physiological processes, that are commonly spoken of as adaptation.

4. My positive contention that behavior in the lower organisms is complex, varied and variable, so that it is not easily predictable, led me to a criticism of theories which represented such behavior as simple, uniform over wide fields, and unequivocally determined by single external factors. I found a theory of this character to be widely held; I met it in opposition at every turn as my papers began more and more to present behavior as complex; and I found this view presented regularly under the name of the "tropism theory."

This then was the reason for my attack on the tropism theory. I criticized it, not as a mere statement of one of the factors that make up the complex phenomena of behavior, but as a view of supposed extremely wide applicability, which maintained the simplicity and uniformity of the behavior of the lower organisms. I tried to show that there was no single schema into which most of the behavior of the lower organisms could be forced. How far it was just to identify the view criticized with the tropism theory we shall inquire in a moment; here it is most important, if we wish to get a clear understanding of the grounds of apparent conflict, to grasp the fact that the *simplicity, uniformity* and *general application of a single schema* were the points against which my criticism was directed.

Was this idea of the tropism theory sufficiently general to justify a criticism of it on that basis? The word tropism has been used in many senses and the theory has taken many forms, as we shall see later; but I believe that any one who has followed the literature of behavior must realize that there was such justification, even though he may himself hold to some other definition of the word tropism. The great movement toward extreme simplification in these matters has certainly been generally identified with the tropism theory; "reduction to simple tropisms" has been the ideal. Doubtless not all investigators have held the tropism theory to be so simple and of such wide applicability, but it is true that there has been a general belief that such was the case—a belief not confined to the uninformed, but shared by workers of high standing. Thus, Bohn, in his recent admirable review[2] of this entire question, after setting forth in detail examples of the tropism theory, says, "It is evident that nothing is simpler than this explanation," and again, "For more than ten years certain biologists have thus explained the actions of animals by tropisms. . . . This had become the *necessary* and *sufficient* explanation of all cases. Whenever it was observed that animals accumulated at a point, without even seeking to determine how they reached that point, a tropism was made to intervene." Bohn makes these statements merely as a presentation of well-known facts, and it would be easy to multiply quotations from biologists of the first rank showing that this idea of tropisms was a general one.

In view of certain passages in Professor Loeb's recent paper,[1] a note of historical character is here required. My criticisms have been directed not against any person or school, but against a prevalent view. I have never considered any single person as the sole author or only proper expositor of the tropism theory, but have taken the theory as I found it commonly presented in biological literature. I have not, therefore, considered it necessary to accompany a statement of my results with an exposition of Loeb's work and views; there are other authors whose work and friendship I value highly whose expressed views are more directly in opposition with what I have pointed out than are Loeb's. Certainly many authors besides Loeb have ventured on inde-

[1] *Journal of Experimental Zoology*, 4, 151–156.

[2] "Les Tropismes, les Réflexes et l'Intelligence," *L'Année Psychologique*, T. 12, 1906, pp. 137–156.

pendent contributions to the tropism theory and on expositions of it; if it was an error to take these into consideration, I am guilty of that error. Here we are seeking to discover whether there is divergence of view as to the facts themselves, and nothing would be more gratifying than to find in Professor Loeb an ally instead of an opponent, in this question of the complexity of behavior. We may, if we desire, call the theory which I criticized the popular tropism theory.

Now, how did this popular tropism theory simplify behavior? There is among investigators an extraordinary diversity of opinion as to what a tropism is. Some use the word as a mere name for certain observed facts. In reading, conversation and correspondence I have met the following definitions, each held by well-known investigators: (1) any reaction of a lower organism is a tropism; (2) any reaction to the chemical or physical agents of the environment is a tropism; (3) any movement toward or away from a source of stimulation is a tropism; (4) a tropism is any reaction in which the organism turns as directly as possible toward or away from the source of stimulation; (5) a tropism is any turning produced by stimulation; (6) a tropism is any reaction in which orientation to a steadily acting external force is the main characteristic. It seems clear that there is no tropism "theory" in any of these views; they merely apply a name to certain facts, leaving the nature of the reaction to be determined by experiment, and permitting different explanations in different cases. I myself at first used the term (or its equivalent "taxis") in some such collective sense, till a paper from the laboratory of one of the leading exponents of the tropism theory set forth with some warmth that the phenomena I described had "nothing to do with the tropisms."

Among those who use the word tropism in a precisely defined sense, implying a theory as to the nature of the reaction,[4] there is likewise diversity of view. The theories held by certain investigators give no ground for considering the tropism a simple, elementary phenomenon, nor one of wide application to lower organisms; they involve a highly developed sensory apparatus and a complex activity of the nervous system. Against such theories my criticism was not directed. On the other hand, there *is* a widely prevalent theory of tropisms which if correct really justifies the common view of the elementary simplicity of these phenomena. This is the "local action theory of tropisms," and it was against this that my criticism was directed.

I wish to emphasize this point, as it gives the key to the entire discussion. I found the fountain head of the commonly held belief in the simplicity and uniformity of the behavior of lower organisms in the "local action theory"—representing the stimulus as producing its reaction in that part of the body on which it directly falls, so that the organism reacts as a bundle of independent parts rather than as a unit. I therefore attacked this theory, and no other, in the chapter of my book which deals with this matter. I believe I made it perfectly clear that this was the theory under criticism; in the title of the chapter the "local action theory of tropisms" is specified; I defined precisely what I meant by it; all through the chapter I took pains to specify it, and in my summing up I expressly

[4] I am uncertain whether Professor Loeb, in his recent paper (*Journ. Exp. Zool.*, 4), wishes to range himself with those for whom the word tropism implies nothing as to the nature of the reaction. In his note on page 156, he says that my statement of the tropism theory on page 94 of my original paper is erroneous. The essential point in my characterization of the theory on that page seems to be the statement that "the theory of tropisms says that certain definite things happen in the change of position undergone by organisms under the influence of stimuli; that the organisms perform certain acts in certain ways." If this is the point which Loeb holds to be erroneous, my criticisms of course do not touch his views in the least. Many authors present the tropism theory as a theory of how reactions occur, and it was as such that I criticized it. If I have anywhere wrongly classified Professor Loeb with these, I regret it, and am delighted to discover my mistake. Any one who holds a theory (or would be a *theory?*) of tropisms that says nothing as to how the reaction occurs will hardly find anything in my discussion to oppose his views.

named the local action theory. I believe there is no ground for misunderstanding the theory that I was criticizing, though this seems to have occurred in certain cases.

My discussion has been attacked from two sides. In one recent number of SCIENCE Parker[5] takes the ground that the local action theory is not held, so that it was not worth while to demolish it; while in another recent number, Torrey[6] expressly defends the local action theory. These mutually destructive criticisms naturally relieve me of some embarrassment in replying to both. Torrey's elaborate defense shows that the theory is still very much alive and I can, therefore, only greet with pleasure Parker's ready support of my main contention, even though this takes the form of Sairey Gamp's crushing retort, "Who deniges of it, Betsey? Who deniges of it?" Parker's work has been mainly with more complex animals than those dealt with in my book, and his interests have lain rather in the field of sense physiology than in the development of activity. I can, therefore, readily understand that he should find it inconceivable that such a view should be held; he has doubtless not met it in opposition at every turn, as have those working with the lowest organisms, and as I now meet it in Torrey's paper. In my book I have given precise statements of the theory in the form of quotations from authors of highest standing. Bohn[7] in his recent exposition adds others. None of the authors quoted has, so far as I am aware, repudiated the local action theory. It would appear, therefore, that a statement of the relation of the observed facts to this theory was much needed.

Before turning to the arguments urged in support of the local action theory, another criticism of my discussion, made or implied by most of my critics, must be dealt with. This may be put as follows. Suppose that the simple, local action theory of tropisms is not satisfactory. Nevertheless, there is another, less precise, less simple, theory of tropisms which is of itself important; a theory in support of which Parker and Torrey cite the circus movements of animals when the sense organs of one side have been obstructed. A theory of such importance, it is contended, should have been dealt with in a general work on the behavior of the lower organisms. Further, the chapter criticizing a theory under the name of tropism gives the impression that this other theory is also condemned, though arguments against it are not advanced.

To this criticism my book is justly open. I should have given an exposition of the theory in question, with an attempt to estimate the part it plays in the behavior of the lower organisms. This unpurposed omission was partly due to the fact that the two groups of whose behavior I gave a detailed exposition—the Protozoa and Cœlenterata—have furnished practically none of the evidence cited by my critics; partly to my attempt to focus attention upon the local action theory as of infinitely greater importance than the other form of the theory. But even though I held that action in accordance with the complex form of the theory plays little part in the behavior of the lower animals, the phenomena and theory should have been set forth, and I regret that this was not done.

We may now return to the criticisms and defense of the local action theory. Regarding the nature of my criticisms, one point must be emphasized—a point that has been much misunderstood, though I believe I expressed myself explicitly on the matter. I made no attempt, and had no desire, to deny the existence of the factors on which the local action theory, or any other existing theory of tropisms, was based. So far as local action is concerned, I emphasized in my book such cases as were established, and gave a list of them on page 306. The question which I tried to answer in my discussion of tropisms could be put thus: After some years of study of the behavior of the lower organisms, what is your impression regarding the extent and importance of the part played by tropisms? A well-known investigator, after one of the most thorough and detailed studies of the behavior of a certain group of invertebrates that have ever been made, in which he watched and ex-

[5] SCIENCE, October 25, 1907.

[6] SCIENCE, September 6, 1907 ("the response to stimulation is local," p. 319, etc.).

[7] *Loc. cit.*

perimented with the animals literally day and night for long periods, remarked to me, in discussing this matter, that he never saw any tropisms. Without going so far as this, my answer to the question asked above was that "the theory of tropisms does not go far in helping us to understand the behavior of the lower organisms." I did not deny the existence of the phenomena which the theory takes into consideration, but it seemed to me that there are so many other factors, playing such important parts, that the tropism factor is of relatively small importance in a general consideration of behavior. In my first paper on this subject[8] I included the more complex forms of the tropisms in this judgment. The remark of the investigator above mentioned illustrates the fact that there are certainly other aspects of behavior so striking and important as to quite mask the existence of tropisms.

Let us attempt a brief characterization of tropisms, their history, and the part they play in behavior.

1. The essential point in the tropism, as originally applied by Loeb to reactions to light was, in a word, the idea that the organism in going toward or away from the light is not trying to go somewhere or to reach something, but is merely taking a certain position or *orientation* in the light. This recognition that the *position* is the essential point was a great step in advance, and its application by Loeb to certain features of the behavior of animals was an achievement of the highest importance.

2. This idea of orientation having proved so helpful in the study of reactions to light, the next step was, very properly, to apply it to other features of behavior, to see if it would not prove equally useful elsewhere. The reactions to chemicals, heat and cold, contact with solids, electricity, light, gravity, etc., were all brought under this point of view; attempts to show that the position is the essential point in each of these have for a long time been made with energy and persistence. Our knowledge has grown till we are in a position to estimate the results. In the main it appears that to most of the behavior the orientation idea has little applicability. To that immense province of behavior comprised in the reactions to chemicals of all sorts (including food reactions, respiratory reactions, etc.) it has shown itself quite inapplicable. The case is the same with the reactions to heat and cold. With regard to the reactions to solid bodies nearly the same may be said, though there are some special cases in which the idea of orientation is applicable. The reaction to the electric current furnishes a typical orientation. In some of the reactions to gravity and to water currents the orientation idea is helpful. Yet the recent work of Lyon and others shows that even in these the movement in a certain direction is an essential part of the reactions; they are essentially compensatory movements, and the taking of a certain orientation is by no means the only important point. In certain reactions to light the orientation idea has been most helpful, yet in an immense proportion of the reactions of organisms to this agent it does not show itself the essential point. The orientation theory is of greatest service in such cases as the going of insects toward a bright light, yet even here such work as that of Holmes on Ranatra shows that the orientation is not the only point; the approach to the light seems after all essential, since if a certain orientation does not bring the animal to the light, it learns by experience to take a different orientation which does have this effect. The work of Cole, of Radl and others, shows that in the lower organisms we have the beginnings of reactions to *objects* perceived visually; the animal is not merely oriented by the strongest light, but goes toward such objects, whether bright or dark, as might be said to be "of interest"[9] to it at the given

[8] "Contributions to the Study of the Behavior of the Lower Organisms," Carnegie Institution, Publication 16, pp. 89–107.

[9] The expression "of interest" of course has some objective equivalent, but to try to use it would be to substitute an unintelligible conjecture for an expression which at least conveys an idea

moment. The reactions to light are bound up with almost every possible aspect of behavior, and the orientation principle plays in them but a relatively small part.

3. In Loeb's original theory nothing was said as to the way in which the position of orientation is reached, and I take it that he does not now consider this matter as belonging to the theory proper. But on this matter a tempting idea presented itself, to the effect that the position of orientation was reached in the simplest possible way—by a local reaction of the part on which the stimulating agent impinges. This gave the "local action theory" which made the tropism a thing of such extreme simplicity; it has been applied, in detail or in general, to all sorts of reactions, by many authors. While it holds in a measure for the effect of the continuous electric current, I believe that it has been demonstrated that in the main this idea was not correct; that the element it deals with plays little part in behavior, aside from the effects of electricity. With this we shall deal in later paragraphs.

Attempts have been made to controvert my position on the tropism theory by the performance of crucial experiments or by the citation of specific observations. These are clearly based on misunderstanding. It is obvious that the relative importance of an admitted single factor in producing a set of complex phenomena can not be settled in this manner. Valuable judgment on such a question can be based only on an extended study of the phenomena. My own opinion derives any worth it may have solely from the fact that I had worked for nine years on the behavior of a large number of organisms, attempting to make a careful analysis, with detailed studies of the different factors involved and the part played by each. My conclusions are of the same character as are drawn from a large mass of statistical data. They can be adequately controverted only by showing that the analysis of this mass of data, or of another equally large or larger, will not yield these conclusions. Single observations are of course important, since they are the material from which the large mass is made, but single observations taken by themselves do not help much in taking off the *facies* of a long series of investigations, which is what I tried to do. My conclusion, like all statistical conclusions, is nothing that will enable one to predict for a given individual case; if it were, it would of course be of much greater value than it is. No single observation whatever is inconsistent with my general conclusion.

Thus, writers who have flown to the defense of the *existence* of tropisms will find themselves in no conflict with my stand on the matter. It was only the prevalent opinion of the wide generality and importance of the phenomena that I called in question. To hear that the actual existence of the tropism was held to require defense came as a real surprise to me. If put forward as merely one factor out of many, with its relative importance subject to discussion, I shall agree most cordially.

In certain quarters there seems to be an impression that observation of the direct turning of an organism toward a source of stimulation is in some way opposed to my views, and that citation of specific cases of this will come to me as a painful surprise. Yet, of course, this is one of the commonest and most evident facts of behavior, and is discussed in detail in my book (see, for example, pp. 306–308). Its existence is required if the theory I suggested is correct. I pointed out that in consequence of the three factors in behavior whose importance I emphasized, this direct turning toward a localized stimulus would occur; if it did not occur, that would tend to disprove the theory. "Innumerable instances of this class of reactions could be given; they include perhaps the greater number of the directed movements of organisms" (p. 307).

Thus the direct turning of animals is not in dispute. A matter that *is* of interest lies in the answer to the question whether the turning is due to the simple local reaction of the region on which the stimulating agent impinges. My own contention was that this is rarely the case. If authors will state clearly whether

of the outward facts. The animals go toward visible things that serve for food, protection, etc.

they conceive the turning to be due to such simple local reaction, and give the evidence on which this opinion is based, that will be a real contribution on a disputed point.

The reaction to the electric current, in which the effect is local and the behavior is uncoordinated and unadaptive, is the type and pattern of the local action style of behavior. Its importance is thus naturally emphasized by Torrey, in his defense of that theory, as against my own contention that this reaction is not typical of the behavior of lower organisms. The question will be cleared most readily by noticing the different objects which guided us in taking our stands. My own purpose, in my topographical survey of behavior, was to give the reader a correct idea of the facts—of what he would see if he examined the phenomena himself. In doing this, one must inevitably come, I believe, to my conclusion that the "action . . . under the electric current is not typical of the behavior under other stimuli." If the reader examined accurately the reaction to the electric current he would see certain phenomena—local action, lack of unity and coordination, different parts of the body opposing each other, etc. The question is—Is this typical of the behavior? Is this what would be seen if the reactions to heat, light, gravity, chemicals, etc., were examined in the same way? Certainly it is not. If the reader should get the impression that the extraordinary series of phenomena seen when an electric current is passed through a collection of infusoria is likewise what is seen when they are subjected to other stimuli, his idea of behavior in the lower organisms would be a ridiculous caricature of the reality. There appears to be no reason for concealing this fact, and I set it forth as clearly as I could.

On the other hand, Torrey holds that in the reaction to the electric current we may have exhibited in a very direct way some of the fundamental changes that occur in living matter when subjected to the action of a stimulus; hence its great importance. Nothing that I have said militates against this opinion. The statements and implications that I hold that "the uniqueness of the electric stimulus . . . vitiates its claim to consideration"; that "the interesting phenomena of galvanic stimulation are to be so lightly put aside," etc., emanate from Torrey, not from myself. So far have I been from "neglecting" it, that I devoted in my book more space to this reaction than to any other. But the importance of the reaction to electricity is of the same sort in the behavior of lower as in that of higher animals; though of the utmost importance, no one would consider the reaction of a muscle to electricity "an adequate type of the behavior of mankind." I believe that it was made plain in my book that this was the point which I was setting forth.

Torrey takes up my account of the reactions of *Euglena* to light, and attempts to show that it agrees with what would be expected from the local action theory of tropisms. It is not possible to take up the details of this matter here. But I may point out the following: In accordance with my general practise, my account in this case was based, not on an attempt to explain an isolated reaction by a preferred theory, but on an extensive analytical investigation of the reactions of the organism, attempting to isolate experimentally the various elements of which the behavior is made up. In this investigation I was not able to find experimentally that element which the tropism theory calls for, while those I did find accounted for the entire behavior. I, therefore, had no ground for asserting the existence of the tropism element. I do not see that Torrey has adduced any additional ground for such assertion; at best he has merely tried to show that interpretation along the line he prefers is not inconsistent with the facts.

One of my figures of the reaction (Fig. 93 in my book) Torrey thinks "perfectly in harmony with the tropic schema," he says: "it is hard for me to conceive how an organism swimming of necessity in a spiral course could react more definitely to a moderate directive stimulus than *Euglena* does here"; and he "can only wonder at my running so boldly and far into the enemy's camp." Surely this last remark does not mean that Dr. Torrey considers it a reputable scientific procedure to manufacture or alter a figure claiming to represent the facts, in order to make it agree with a theory. My figures were made from as precise a study of the facts as I could make, before I had attempted by analysis of all the facts to see what they mean, so that the figures form part of the data for my later conclusions. In my preface I said that my ideal was "to present an account that would include the facts required for a refutation of my own general views, if such refutation is possible," and I should not be without the gratification of having fulfilled that ideal if Torrey should be adjudged to have made out his case. But the reason why I held that the organism does not react as directly as possible is as follows: The oriented organism is swimming toward the light in a spiral course, thus swerving first to the right, then to the left (omitting from consideration the movement in other planes). Now the light is changed, so as to come, say, from the right, as in my Fig. 95. The most direct way in which the organism, swimming in a spiral, could become oriented to the light would be by an increase in the swerving to the right and a decrease in the swerving to the left, and this is what the tropism theory would lead us to expect. But the fact is that there is an *increase* in the swerving both to the left and to the right, the spiral becoming a wider one; the increase to the right being, however, greater than that to the left, the organism becomes gradually pointed to the right. The increased swerving to the left is not accounted for by the tropism theory, and is indeed squarely opposed to it, while it is to be expected if the analysis I gave is correct.

The point becomes quite clear when we compare this reaction with that to the electric current, which with its undoubted local action Torrey considers a typical tropism. Since *Euglena* itself has not been shown to react to electricity, we can not make the comparison here, but Torrey does not maintain his views for *Euglena* alone, and the facts in the reactions of ciliates to light, gravity and water currents are parallel to those in the reactions of *Euglena* to light. In all these reactions the organism swerves, in becoming oriented, only toward a certain side x, never toward the opposite side y, just as in the reaction of *Euglena* to light. But in the reaction to the electric current the organism may be caused by the local action to swerve directly toward the side y, and to become oriented in that way. Local action would cause swerving toward the side y in the reactions to light, gravity, etc., exactly as in the electric current, and the fact that this does not occur seems to be a demonstration that local action is not the explanation in these cases.

It will then be clear, I hope, that my analysis was based on a thorough consideration of the available experimental data, and not on prejudice for or against any given theory. Torrey indeed admits, if I understand him, the existence of all the factors which I set forth, and the correctness of my analysis so far as it deals with positive factors, but believes that there is an additional factor, in virtue of which *Euglena* may turn *directly* toward a light. Thus the behavior of *Euglena* is more complex, according to Torrey's view, than I represented it. There is no doubt but that increase of knowledge tends to reveal increased complexity in the behavior of the lower organisms; of this many recent examples could be given. My own work has had decidedly this tendency, but, as in the present case, I tried to keep the theory as simple as the facts would permit. But my experiments on *Euglena,* while not revealing the power of direct turning, do not disprove its existence. It has always seemed as extraordinary to me as to any one else that the direct turning should not occur. There is little profit in discussing matters which only experiment can settle. At the time my work was done, I had no opportunity to study the reactions of *Euglena* in the stage when it has no flagellum and moves by contractions. Such a study is much needed, and it may reveal the additional factor which Torrey looks for. Many higher organisms show a power of direct localization, in connection with complex activities of other sorts; there is no antecedent improbability of this in *Euglena*.

Related to this matter is Torrey's discussion of the question whether the organism is or is not stimulated after it is oriented, which leads him finally to the extraordinary conclusion that I "insist on an interpretation of organic behavior by means of general changes in internal states that are psychical rather than physical," and to a general condemnation of my analysis on this account. Most of the points made in Dr. Torrey's interesting paper I can appreciate, but at the discussion which leads to this conclusion regarding psychic factors I must confess my astonishment. The conclusion is reached only by the aid of the somewhat desperate assertion that to say that an oriented organism is subjected to no general stimulation "is no more than saying it then possesses no feeling of discomfort." Had I made such a statement, I should have expected much just and severe criticism for "psychologizing"; for "crude anthropomorphism."

The root of the difficulty lies in a misunderstanding of certain of my attempts to avoid the use of indefinite terms not having a precise experimental meaning; it comes finally to a simple matter of definition. Experimentally, it has seemed to me that the study of behavior reduces mainly to a study of two things: (1) the causes of changes in behavior; (2) the nature of the changes themselves. Now these two things correspond nearly to what are commonly called *stimuli* and *reactions,* though the common usage is a little less precise, not always representing experimental concepts. I, therefore, adopted for experimental discussions the word reaction as signifying a *change in behavior;* the word stimulus as meaning the *cause* of a change in behavior, though so far as I could I used the plain phrases in place of the two terms. Unless some such definitions are used there is no experimental method of telling whether an organism is reacting or not; whether it is stimulated or not. On page 283 of my book I took the greatest pains to emphasize the fact that my discussion would not be intelligible unless this meaning of the word reaction were kept in mind. With this, a stimulus, as the cause of a reaction, is likewise clearly defined; this definition I had already given on page 6.

Stimulation and reaction are evidently, as thus used, correlative terms; if there is no reaction, there is no stimulation. I have no desire to insist that these are the only possible definitions; I merely wish to point out that this was my explicitly declared usage. Now, if we apply these definitions, the whole structure of difficulties raised by Torrey falls to the ground. From the definitions it follows that when the movements of an organism are uniform, it is not stimulated. After the infusorian has become oriented to light, it does not change its movements, but swims in the same way it did before; there is then no external evidence that it is stimulated, and if my purely empirical definition is accepted, it is not stimulated.

If it be maintained, as Torrey does, that the organism is nevertheless stimulated at such a time, then evidently some internal condition is taken as a criterion of stimulation. This is precisely the criterion which Torrey incorrectly attributed to me, and on the ground of which he charged me with making "feelings of discomfort" and other psychical phenomena the basis of my analysis. If there were any sound foundation for his argument, I could retort that it is his view that calls for the psychical factors. But, of course, there is no reason for dragging in psychic factors at all; it is perfectly easy to suppose that the organism when oriented is in a differing physico-chemical state, and this assumed state might be considered stimulation, unless the empirical definition of stimulation as correlative with reaction is preferred. To be unable to conceive a change in physiological state otherwise than as psychical would seem to unfit one completely for the objective analysis of behavior; such changes demonstrably occur even in unicellular organisms.

It is evident that the highly objectionable propositions which Torrey deduces from my discussion, to the effect that there can not be "a constant stimulus that does not induce a differential movement," or that I deny the "possibility of symmetrical stimulation for an oriented organism," depend simply on the definition of stimulus and reaction as correlative terms of purely experimental meaning. I certainly believe that many animals, after they have "fixed" a source of light and are swimming toward it, are in a different physiological state from before. If we define stimulation somewhat indefinitely as meaning any such changed physiological state, then we may of course hold that they are then stimulated. There seems to be no real difference of opinion on this matter; but the method of formulation of course depends on the definition of the terms employed.

A further point discussed by Torrey has to do with the relation between selection and adaptation. As an aid to understanding the existence of adaptations in behavior, I accepted certain forms of the selection theory. Torrey emphasizes the existence of unadaptive reactions, like that to the electric current; he points out that there is no ground for supposing that selection has played a part in their production. To this I agree fully. But since Torrey draws therefrom the conclusion that "the hypothesis advanced by Jennings is not sufficiently broad to encompass all the phenomena it is devised to explain," it needs to be pointed out that my view was not "devised to explain" such phenomena. A theory of selection, while directed primarily to the explanation of adaptiveness, requires the existence of raw material from which selection may occur, and this raw material must of course be largely unadaptive, or there would be no ground for selection. Selection can never account for the existence of that from which selection is made. This, I believe, was made plain in my book. "It is clear that natural selection can not account for the origin of anything; only that can be selected which already exists" (p. 326). I stated explicitly that the hypothesis set forth was a theory *of regulation;* my exposition of the matter opens on page 315 as follows: "The question in which we are interested is then the following: How can behavior develop? That is, how can it change so as to become more effective—more regulatory?" The existence of unadaptive reactions not coming under this theory was recognized. "The organism is composed of matter that is subject to the usual laws of physics and chemistry. External agents may of course act on this matter directly, causing changes in movement that are not regulatory" (page 345). The origin of these unadaptive reactions I did not discuss, because I had no light to throw on the matter. But I emphasized my conviction that the study of the laws of matter and energy furnish the main field for investigation, as compared with questions of selection. "Whatever the part assigned to natural selection, the superlative importance of these laws remains; they must continue the chief field for scientific investigation" (p. 326). I might have said "the only field," since of course the study of selection is merely the study of how these laws work under certain complicated conditions.

Torrey evidently overlooked my explicit statements of the object and limitations of the theory in question.

This discussion of theories of development tends to give the impression that these form the important part of my treatment of behavior. It is, therefore, only just to point out that this matter was a side issue from the main purpose of my work, and was explicitly put forward merely as a suggestion as to what may have occurred. The short chapter on this subject begins as follows: "It is not the primary purpose of the present work to treat the problems of development, but rather to give an analysis of behavior as we now find it. But the results of this analysis furnish a certain amount of evidence as to how development may have occurred; this it will be well to set forth briefly." The book is primarily a treatment of behavior as a branch of experimental physiology.

But I believe it to be short-sighted and unfortunate for a physiologist to attempt to set in opposition physiological interpretation, on the one hand, with so-called "historical" interpretation, dealing with selection and evolution, on the other. Selection is not something outside of physiological or physico-chemical action; it is merely a characterization of certain ways in which such action occurs. Some of the relations brought about in such action are lasting, while others are fleeting; those which last are said to be "selected." The study of selection is an examination of the relative permanency of different physico-chemical and physiological relations, and it is eminently a matter for experimentation.

Again, in addition to the rapid processes occurring mainly in the lifetime of individuals, there are slow processes requiring more than a generation to produce evident effects; various aspects of these we call "heredity," "evolution," "genetics," etc. These slow processes belong as much to physiology as do the rapid ones. The existing condition of living things is known to be largely a product of these processes, so that to attempt to exclude them from consideration and to act as if their effects did not exist, when we are trying to understand living things, is a most futile proceeding. These matters are coming rapidly under experimental study, so that attempts to exclude them from consideration in physiology, as "historical," can not endure much longer.

We now come to the matter which seems to underlie most of the criticisms of my discussion. Certain authors seem to identify the "tropism theory" with the view that the behavior of organisms is to be explained by objective, experimentally determinable factors. They feel that an attack on the "tropism theory" is an attack on this view; this comes forth notably in the criticisms made by Loeb and Torrey, and it is evident in the attitude of some other writers.

There is, so far as I can see, nothing in the facts and relations which I have brought out that in any way opposes the principle that behavior is to be explained by objective, experimentally determinable factors—or indeed that bears in any way on the question. I have simply assumed throughout that it *is* to be explained in that way, and I do not see how experimental investigations can proceed on any other basis. Beginning my work in 1896, when the movement led by Loeb against the use of psychic concepts in explaining objective phenomena was in full swing, I considered that battle as fought and won; I have, therefore, ever since proceeded, without discussion or ado of any sort, on that basis. Every one must recognize the tremendous service done by Loeb in championing through thick and thin the necessity for the use of objective, experimental factors in the analysis of behavior. No convinced experimentalist, knowing the previous history of the subject, can reread, as I have just done, Loeb's early work on behavior without being filled with admiration for the clear-cut enunciation, defense and application of the principles on which valuable experimental work has rested since that time, and on which it must continue to rest.

Any differences of opinion between Loeb and myself are then matters of detail; they concern merely the results of the application of the agreed principles of investigation. It has seemed to me that some of the experimentalists have rested content with superficial explanations; that they did not realize the complexity of the problems with which they were dealing. This has been the history of most applications of experiment to biology; the more thorough the work, the deeper are the problems seen to be.

Thus I have not hesitated to bring forth facts tending to show the inadequacy of the physico-chemical factors thus far set forth, and doubtless some have suspected that this was done with the concealed purpose of discrediting the general adequacy of such factors. This is a complete mistake; I did not till lately realize even the existence of such a suspicion. Complete confidence in the experimental method removes anxiety as to the effect of criticizing the details of its application. My objections are only to the adequacy of particular factors; they are based on experimental grounds, and the difficulties they raise are to be resolved only by experimental study. There is a vast difference between holding that behavior is fundamentally explicable on experimental grounds, and holding that we have already so explained it.

In a recent paper Loeb[8] has intimated that even if the behavior of the organisms under consideration were as complex as that of man, the same objective and experimental methods must be used in analyzing it. To this I fully agree, and the behavior of man is of course no more to be excepted from this treatment than is that of any other organism. In some recent writings one finds indications of a curious dualism, as if the behavior of lower organisms were to be analyzed in the objective, experimental way, but the behavior of higher animals and man were not. This takes most often the form of objection to any comparison between the objective features of the behavior of higher and lower animals, or to the use of the same terms in speaking of them, with a tendency toward accusations of vitalism or "psychologizing," against those making such comparisons. Such accusations evidently depend on the premise that the behavior of higher animals is to be explained only by vitalism or by "psychologizing." When one is tempted to accuse an opponent in such ways, it is worth while to first examine whether the tendency to read psychic or vital factors into the phenomena does not lie in the mind of the accuser, rather than in that of the accused. When one has consciously and consistently taken the ground that the behavior of all organisms, including man, is to be analyzed in the objective, experimental way, and that there is no ground for expecting a failure of this method at any point, there is less occasion for anxiety at the use of similar terms for similar objective phenomena throughout the series.

For example, the "method of trial and error" is as much an objective phenomenon, to be explained by experimentally determinable factors, in the dog or man, as in the infusorian. The undoubted great differences between the exemplifications of the "method" at the two extremes are matters for experimental analysis and demonstration, if the experimental method is not to fail. They do not necessarily show that the fundamental principle involved is different, and it is this common fundamental principle to which the common name calls attention. How far we should avoid words that have ever had any psychic connotation whatever is a matter on which there may be divergence of opinion; but it is most important to realize that this is totally distinct from the question whether the psychic connotation is of any use in objective experimental analysis. If this distinction is lost sight of, a divergence in practical details is taken for a conflict in fundamental principles, to the detriment of experimental science. That it is impossible to avoid such words completely is seen when we find in the writings of such men as Loeb the frequent use of such terms as "associative memory." Of course it is to only the objective phenomena that Loeb refers; but this is precisely the case also with other experimentalists accused of similar practises!

To sum up the discussion with the defenders of the tropism theory: We all stand on the same foundation, and the differences of opinion are in matters of detail. In attempting to demonstrate the complexity of the problems of behavior, I have focused attention on a certain precise and narrow form of the tropism theory which seemed to me to have gained undue prominence—in order to show that such narrow schemata are inadequate. In so doing other forms of the theory, more flexible in character, and setting forth the tropism as but one factor out of many, have been thrown into the background; of this the supporters of the theory have justly complained. With my main contention that behavior in the lower organisms is complex, involving many factors, so that no one schema gives an adequate account of it, there seems to be little disagreement. As to the value of the "local action" theory there is still divergence of opinion.

And now a word as to my own positive contributions to the analysis of the matter. It is obvious that conclusions of the "statistical" character that I have attributed to my own, are, from their relative inapplicability to specific cases, of much less value than precise

[8] *Pflüger's Archiv*, 1906, **115**, p. 581.

chemico-physical or physiological ones. It is also obvious that to demonstrate the complexity and difficulty of a field of work is not an achievement to be compared in value with the demonstration that this field is simple and easily explicable on a few known principles. I am under no illusion in regard to this. The clear-cut, narrow tropism theory would be of infinitely greater value for predicting and controlling the behavior of animals than anything I have offered, if only it were true. I am sure I regret that I can make no attempt to put an equally simple schema in place of the one I criticized; if the phenomena of behavior were of elemental simplicity, that would certainly be much more convenient, though perhaps they would then be less interesting. Many of the concepts used in my analysis—"physiological states," "selection," "trial and error," and the like—are collective ones, characterizing varied phenomena of a high degree of complexity. They all require much further analysis; they are programs for future work, not final solutions of the problems. My analysis was mainly an attempt to lay out the field, to point out the principal phenomena with which we have to deal, and to define some of the main problems. If any one attempts to explain all behavior on any one basis, to unlock all its secrets by any catchword whatever, be it "trial and error," "selection," "tropisms" or what not, he lacks a realization of the complexity of his field of investigation. Like other complex fields, that of behavior, even in lower organisms, must be divided up; the various factors must be subjected to long and intense special investigation, with a realization that we have here material for the work of many generations of investigators.

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November 26, 1907

SPECIAL ARTICLES

INTERPRETATION OF THE CHEMICAL COMPOSITION OF THE MINERAL BENITOITE

In July, 1907, Professor G. D. Louderback published an interesting paper on the new mineral benitoite. For a description of the physical properties of the mineral the reader is referred to the original article.[1] The analysis of the mineral, made by W. C. Blasdale, showed the following:

	A	B	Average	Mol. Ratios
SiO_2	43.56	43.79	43.68	0.723
TiO_2	20.18	20.00	20.09	0.250
BaO	36.34	36.31	36.33	0.237
	100.08	100.10		

This yields the empirical formula $BaTiSi_3O_9$. From this Louderback concludes: "Benitoite is then a very acid titano-silicate of barium and stands in a class by itself, both as regards acid silicates and titano-silicates."

Upon reading the paper, immediately after its publication last year, I noticed that there was a very striking similarity to be observed between the composition of benitoite and beryl, for, if benitoite be interpreted as a metasilicate, we have:

Beryl .... $\overset{II}{Be_3}\overset{III}{Al_2}(SiO_3)_6$

Benitoite .... $\overset{II}{Ba_2}\overset{IV}{Ti_2}(SiO_3)_6$.

This similarity in the chemical composition is sufficient to consider the two compounds as isomorphous, for, although titanium with a valency of four replaces aluminium with one of three, the total valences in both compounds are the same. There is, however, a difference of one with respect to the number of atoms. A few examples of well-known isomorphous series will show that the above is not unusual.

In the marcasite group we have:

Marcasite .... $\overset{II}{Fe}\overset{II}{S}S$

Arsenopyrite .... $Fe\overset{III}{As}\overset{II}{S}$

Löllingite .... $Fe\overset{III}{As}\overset{III}{As}$.

Here the number of atoms is constant in all three compounds, but the valences vary. The albite-anorthite group furnishes another illustration.

Albite .... $\overset{I}{Na}\overset{III}{Al}\overset{IV}{Si}Si_2O_8$

[1] "Benitoite, a New California Gem Mineral," University of California Publications, Bulletin of the Department of Geology, Vol. 5, 149–153, 1907.