strike. I was at a window in the university building, looking westward toward a valley, at the center of which, about a quarter of a mile away, there was a field with a few iso-A thunderstorm coming up lated trees. slowly from the southwest gave me hopes of seeing the lightning strike. I saw it strike one of these trees. The flash appeared to me as a superb column or shaft of light, about four or five hundred feet high, and about eight or twelve inches in diameter, perfectly straight, vertical and steady. The shaft was white, the base, however, was distinctly red, like the fire of a conflagration, and tinged probably with a little orange. This column of light seemed to stand between the two diverging stems of the tree. It lasted for The thunder was loud, about two seconds. but not the loudest I have ever heard. Α light rain was falling at the time.

The effects of the flash seemed to be none whatever. The tree was not shattered and was not set on fire. Some cows grazing about a hundred feet away paid no attention to the discharge, except one which walked toward the tree, as if interested in something there, and then turned around and continued to graze.

The next morning I examined the spot closely. The tree was a cottonwood and stood in moist ground. It consisted of two trunks, about eight and twelve inches in diameter, diverging from a common base towards the north and south. The southern or smaller one had the bark stripped off its western side, in the shape of a broad ribbon, about two yards long and six inches wide. The east side showed two furrows starting from above the same branch, about ten feet above the ground, and running downward in irregular paths. These furrows seemed to have been plowed by a piece of steel and the bark torn off by violence, because there was no sign of scorching or any change of natural color. There was absolutely no other noticeable ef-I was told that a horse standing near fect. the tree had been thrown over a fence, badly stunned but not otherwise injured.

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## SPECIAL ARTICLES

# THE METHOD OF TRIAL AND THE TROPISM HYPOTHESIS

In his recent book entitled "Behavior of the Lower Organisms" Professor Jennings has drawn attention to the existence of an issue between two attitudes assumed by investigators in attempts to interpret the behavior of organisms. His own position is made sufficiently clear. He is frankly hostile to what he conceives to be the essentials of the tropism hypothesis, and is equally devoted to what he has called the "method of trial" as a means of explaining facts for whose interpretation he believes the tropism hypothesis to be entirely inadequate.

My reason for venturing upon the present discussion of the issue thus emphasized lies in the fact that, while I have been much impressed by the admirable plea which Professor Jennings has made for the method of trial, I do not quite see the force of his main contentions, as applied either to the destruction of the tropism hypothesis or to the support of its successor.

The value of any hypothesis may be estimated according as it does or does not (1) accord with the facts, (2) simplify the problem to be solved, (3) suggest a new line of advance. These tests may be applied to the hypotheses that at present concern us. The views of Professor Jennings will be considered first.

Professor Jennings attempts to account for the phenomena of organic behavior on the basis of two principles. According to one, "behavior is based fundamentally on the selection of varied movements." According to the other, "the resolution of one physiological state into another becomes readier and more rapid through repetition." These are the "primary facts for the development of behavior." Given organisms that react to changes in their environment, given a variety of responses to the same conditions, and the material is provided for the development of all types and grades of organic behavior in accordance with the two principles just stated. This is obviously a strict application to the

phenomena of behavior of that variant of the Darwinian doctrine known by the name of organic selection. It is a view that lends itself with especial facility to the interpretation of physiological evolution. It distinguishes between adaptations that are relatively unstable, resulting from the capacity of given individuals to accommodate themselves to changing conditions, and adaptations that are relatively stable, such as the inherited adaptations characteristic of races. Its chief contribution to the present discussion lies in the recognition that acquired characters, such as habits, cultivated aptitudes, advantages obtained over competitors by larger experience, may be approved by natural selection, even though heredity decline to place them on a permanent footing. Fortunate individual adaptations of the unstable variety come then to play important rôles in the preservation of the species, and in one sense actually determine the course of its evolution. Such, at least, is the claim of the organic selectionists with whom Jenings allies himself, and I have no wish to deny the hypothesis.

How the organism comes into accord with its environment to the extent that it is able to persist is determined, according to Jennings, primarily by application of the method of trial. The individual itself selects those reactions which are favorable for its existence from a number of random or trial reactions. Let us consider a typical case. Whenever the protozoon Paramecium, swimming along its narrowly spiral path by means of the vibratile hair-like cilia that clothe its body, chances to come in contact with an impediment, whether it be in the shape of a sand grain, a droplet of some chemical solution or a sudden change in temperature, the beat of its cilia may be reversed and it may back off for a distance varying with the strength of the stimulation. Another reversal of the cilia then sends it forward again, but not quite in the direction it had previously taken. Owing to the peculiar beating of its cilia, its progress is along a spiral path, with the primitive gullet (hence a structurally defined side) always towards the axis of the spiral. On resuming a forward

movement, the creature swerves toward the side away from the mouth. This has been described as an avoiding reaction, since it provides a method of passing obstacles. The method is said to be a method of trial. *Paramecium* backs and fills until it chances to hit upon an unobstructed pathway. No cause of a reversing reaction being offered, it keeps on its way. Its final appropriate reaction is said to be selected from a number of inappropriate trials or errors.

How far the facts obtained from an analysis of the behavior of *Paramecium* are applicable to the analysis of behavior in general may best be considered after an examination of Jennings's scheme according to which behavior develops, that is, becomes more effective:

The behavior of any organism may become more effective through an increased tendency for the first weak effects of injurious or beneficial agents to cause the appropriate reaction; in other words, through increased delicacy of perception and discrimination on the part of the organism. Such a change would be brought about through the law of the readier resolution of physiological states after repetition. When the organism is subjected to a slight stimulus, this changes its physiological state, though perhaps not sufficiently to cause a reaction. Such a slight stimulus would be produced by a very weak solution of a chemical, or by a slight increase in temperature. Now, suppose that this weak stimulus, causing no reaction, is regularly followed by a stronger one, as would be the case if the weak chemical or slight warmth were the outer boundary of a strong chemical solution, or of a region of high temperature toward which the organism is moving. This stronger stimulus would produce an intense physiological state, corresponding to a marked negative reaction. That is, the first (weak) physiological state is regularly resolved by the action of the stimulating agent into the second (intense) one, inducing reaction. In time, the first state would come to resolve itself into the second one even before the intense stimulus had come into action. As a result, the organism would react now to the weak stimulus, as it had before reacted to the strong one. It would thus be prevented from entering the region of the chemical or the heat, even before any injury had arisen.

2. In the same way the organism may come to react positively or negatively to a stimulus that is in itself not beneficial nor injurious, but which serves as a sign of a beneficial or injurious agent, because it regularly precedes such an agent.

This proposition is illustrated by the approach of an enemy which casts first a faint, later a deeper shadow. The organism comes to react to the faint stimulus.

3. Progress takes place through increase in the complexity and permanence of physiological states, and in the tendency to react to these derived and complex states instead of to the primitive and simple ones....

4. Progress in behavior may take place through increased variety and precision of the movements brought about by stimulation.

New movements, even new organs, such as flagella, might be acquired by the selection of overproduced movements and of overdeveloped structures whose movements become advantageous.

Thus through development in accordance with the two principles mentioned, the organism comes to react no longer by trial, by the overproduction of movements—but by a single fixed response, appropriate to the occasion.... Such fixed responses are the general rule in the behavior of higher organisms, and are found to a certain extent in all organisms. In the higher organisms we speak of some of these fixed responses as reflexes, tropisms, habits, instincts.

This is, in brief, the general course of the development of the behavior of single individuals.

Recognizing the dangers in attempting to state adequately the position of an author in this fragmentary fashion, I feel confident I do him no injustice (1) in calling attention to his assertion that fixed responses, such as reflexes, tropisms, habits, instincts, are developed through selection from overproduced random movements by means of the method of trial; (2) in noting that the substances suggested as agents of stimulation all initiate reactions of the tactual type. Reaction takes place on contact, the essential stimulus being the abrupt change produced by the contact and depending qualitatively not at all on the character of the object touched.

No one, I am sure, would doubt that the behavior of an organism rests somewhere on a

basis of physiological change. Such changes, however, may be of various kinds, involving various groups of factors and giving rise to various types of reaction. That definitely directive reactions are reducible to the motor reaction type, as seen in its essential features in Paramecium, is a conclusion that does not appear to follow from the present accessible facts of behavior. Though the selection of overproduced movements by trial may account for certain types of behavior, I do not see how it accounts also for definitely directive or tropic reactions. It is not clear that the latter belong in the category of secondary, rather than primary reactions, notwithstanding Professor Jennings's vigorous endeavors to put them there. My difficulties are soon stated.

Any one who has stimulated excised muscle from a freshly killed animal by means of a galvanic current, is aware that its behavior at the moment the current is made or broken is quite different from its behavior during the continuous passage of the current. It is well known that this difference is to be referred first of all to the fact that the make and break responses are caused by sudden changes in electrical potential, which changes do not accompany the passage of the constant current. Further, the reactions of many organisms without muscles to galvanic stimulation exhibit parallel differences. Indeed, it has been determined that the behavior, under galvanic stimulation, of such an organism as Paramecium, accords in many essential details with the laws and theories originally formulated with reference to the reactions of the muscles of vertebrates. The passage of the constant current through a muscle may produce a tonic contraction at the kathode, not, however, at the anode. In Paramecium, a similar condition expresses itself in the behavior of the cilia. Paramecium can be made to turn with the utmost definiteness and directness until its anterior end is toward the kathode. When finally oriented, it is still clearly affected by the stimulus. For the behavior of the cilia at opposite ends of the body, normally uniform, is in this case different.

In this brief résumé of some phenomena

connected with galvanic stimulation, the following facts should be noted: (1) that the phenomena of galvanic stimulation present certain important correspondences with respect both to vertebrate muscle and freeswimming unicellular organisms; (2) that galvanic stimulation is of two kinds and produces two different effects, the constant current producing a definitely directive orientation effect (galvanotropism); (3) that the stimulating effect of the constant current does not cease with the establishment of the per-A further fact should manent orientation. be added, namely, that galvanic stimulation is practically unknown in nature.

These facts would appear to lend support to the tropism hypothesis. Professor Jennings, however, believes that the very uniqueness of the electric stimulus in producing its peculiar local effects upon the organism, and its practical absence from nature, vitiate its claims to consideration in any attempt to formulate a universal explanation of the behavior of organisms.

It is not easy to see how, on such grounds, the interesting phenomena of galvanic stimulation are to be so lightly put aside. That a stimulus is unique in any respect is hardly ground for neglecting it. And that it does not occur in nature is for the candid analyst one of its most valuable assets. He thereby gets rid of the selection hypothesis and the mass of unestablished inferences which it has gathered to itself. He is free to examine types of animal behavior which never could have been produced by selection. He comes so much the nearer the fundamental responses of organized matter to at least one stimulus. And he finds, instead of the varied, haphazard reactions which are the only primary reactions for Jennings, two sorts of reactions, one of which is as definitely directive as any class of reactions in the organic world.

If organisms, without the aid of selection, respond definitely and directively to one sort of stimulation, whether in or out of nature, does that not at least raise a suspicion that definite directive reactions, wherever they occur, may also be interpreted without such aid ? With such a suspicion in mind, we may examine some of the evidence from nature which has been counted for the trial and error schema.

From galvanic stimuli, then, we may turn to a consideration of the reactions of organisms to light.

In this field numerous investigators have been accustomed to distinguish between two types of reactions which parallel the two types of responses to galvanic stimulation. The first type depends upon rapid changes in the intensity of light and has been called Unterschiedsempfindlichkeit by Professor Loeb. Many years ago, he distinguished this type of reaction from the second or tropic reaction, finding it well exemplified among certain annelid worms that dwell in tubes from which the anterior ends of their bodies project. When the intensity of the light falling upon one of these projecting ends is rapidly diminished beyond a certain degree, the worm suddenly responds by contracting its longitudinal muscles and withdrawing into its tube. It is a significant fact that a corresponding increase in the intensity of the light falling upon an extended worm does not cause a contraction. Similarly, the unicellular Stentor passes from a brightly illuminated field into shadow without reaction. but reacts when it reaches the edge of the shadow in passing in the reverse direction.

Whether this difference in the response is directly comparable with certain observed differences in the effects produced by making and breaking the galvanic current we are not yet in a position to determine. That there is an obvious resemblance, however, between the reactions produced in organisms by a constant current and by continuous exposure to light can not be denied. Numerous animals orient themselves with the utmost definiteness and directness so that they may move toward or away from the source of light. Two cases may be examined, both of which Jennings places in the category of trial and error responses.

1. Euglena is a chlorophyll-bearing protist, with an asymmetrical body, a long flagellum arising from one end and a spot of pigment

near the base of the flagellum, which appears to be particularly sensitive to light. Like Paramecium, Euglena swims in spirals, and possesses a similar avoiding reaction, which follows not only upon stimulation by chemical and mechanical agents, but upon sudden changes in the intensity of light as well. Depending on the strength of the stimulation, the response may be a reduction of the speed of locomotion, a total stoppage, or, rarely, a reversal. Then there is a swerve toward a certain structurally defined side of the organism so that the spiral in which it swims becomes wider than before. It thus comes into a number of new positions with reference to the source of the stimulus. These, according to Jennings, are trial positions or orientations. and which one of them may be selected for the forward movement will depend upon the degree to which it lessens the stimulation which is inducing the trial movements. Continuous selections, based upon a continuous series of new trials, bring the organism finally into such an orientation that it proceeds toward the light around an axis of progression that passes through the latter.

The second case need but be mentioned. The rotifer Anuræa is a very small but very different organism from Euglena. Nevertheless, it moves also upon a spiral path and its reactions in the presence of light differ in no essential respect from the reactions of Euglena, except that the animals experimented upon by Jennings moved away from rather than toward the light. With this difference in mind, the same figure will serve admirably for both organisms (Jennings, Fig. 93, p. 137).

My analysis of their responses, based upon the figure which Jennings himself has drawn, with text description, leads to quite a different conclusion from his. The figure indicates that *Euglena* is both unterschiedsempfindlich and heliotropic. At a, the reversal in the direction of the light which has been coming from the direction in which the creature has been swimming produces a sudden change in intensity of stimulation, a shock which results in the swerving from the previous course as indicated between a and c. The organism recovers rapidly, only to be subjected to the constant stimulus of a steady light from one direction to the end of the experiment. The result of the action of the constant stimulus is a path, from c to 5, so perfectly in harmony with the tropic schema, that, in spite of Jennings's descriptions and elucidations, I can only wonder at his running so boldly and so far into the enemy's camp. 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 does *Euglena* here.

It will be noticed that orientation by the method of trial depends, according to Jennings, upon the selection of trial orientations that subject the organism to less and less effective stimulation; that when the final orientation is adopted, the organism is in an unstimulated condition with reference to the stimulus which had been acting up to this point. This is clearly the application in the field of light stimulation of the facts obtained by the observation of the reactions of such an organism as Paramecium to contacts. It is assumed (1) that the locomotion of Paramecium is a necessary result of its peculiar metabolism, and (2) that in the absence of perturbing influences in the environment, it may swim along a spiral course with a straight axis. These assumptions may be granted without, however, admitting thereby the converse, namely, that when the axis of progression is a straight line Paramecium is necessarily free from the influence of external It does not appear self-evident that stimuli. as soon as Euglena becomes oriented so that its axis of progression passes straight toward the source of light it ceases to be stimulated, to be again stimulated only when it chances to swerve out of that course.

For Jennings there is nothing comparable to symmetrical stimulation in the field of organic behavior. There is likewise nothing comparable to a constant stimulus that does not induce a differential movement. This is as much as to say that an object which is subjected to equal degrees of pressure from diametrically opposite directions is not being affected thereby until perchance the pressure on one side becomes less than the pressure on the other. Or, to draw a parallel from the field of organic behavior itself, it has been determined by many investigators that when, instead of a single source of light, two sources of equal intensity, such as two incandescent lights, are placed symmetrically before phototropic organisms, the latter may move toward or away from them along the perpendicular, passing through a point midway between them. When one light is cut out, the organisms may change their direction at once, moving toward or away from the remaining light. According to Jennings, they are not in a condition of stimulation while moving toward or away from the two lights, but only during the period between the removal of one light and their orientation to the light remaining. Jennings denies emphatically the possibility

of symmetrical stimulation in such a case. Now it has been shown already that the constant galvanic current does produce observable constant effects in organisms which are moving directly toward one pole. It is also well known that certain organisms (e. g., newly hatched barnacle larvæ) after exposure to light for a time, during which they may move toward the light, may change the sense of their response, moving in the opposite direc-There is no doubt that we are dealing tion. here with a physiological effect produced by a constant stimulus that occurs commonly in nature, and that this effect conditions a definitely directive response. Yet, though this sort of behavior is cited in another connection by Jennings, its significance in the present connection is not considered.

But let us consider briefly one other class of facts which receive no consideration in Jennings's book. It is well known that certain phototropic crustacea and insects, when robbed of the use of one eye by a coat of opaque varnish, perform what have been called circus movements. They move in circles in the presence of light, toward or away from the functioning eye according as they are negatively or positively phototropic. These movements are just what would be expected from

a phototropic animal that can receive light stimulation only through its eyes, when one eye is kept constantly in the shade. They are in entire accord with the tropic schema. Now it happens that hemisection of the brain causes the phototropic reaction to disappear in certain Amphipods on which the operation has been performed, although unilateral injury of the brain does not interfere with the phototropic response. That these facts are to be explained on the assumption of a reflex of some sort between eyes and locomotor mechanism, and that one eye is connected with that part of the mechanism which operates one side of the body, while the other eve is similarly associated with the mechanism for the other side of the body, seems clear. The reactions of the leg muscles of Ranatra, when that animal is subjected to light stimulation alternately on the two sides of the body, change with the utmost definiteness, according to the position of the light with respect to the The response is unquestionably reflex eyes. and singularly definite and local.

To consider just one more case that will bring out still more clearly the difference between Jennings's conception of a stimulus and my own. When the semicircular canals on one side of the head of an animal are removed or injured, or the nerve supplying them is cut, the normal response to gravity will be disturbed. In man, sensations of unbalance would result, general sensations or feelings, such as discomfort, even distress. These are obviously psychical facts. So far as the injured man is concerned, reflex responses to gravity by way of the semicircular canals have never been noted. He has never suspected any mechanism in his body devoted to the task of keeping him physically upright. Accordingly, in the absence of the feeling of discomfort resulting from operation or injury, he may be said to be in a non-stimulated condition, but only so far as the facts of consciousness are concerned. Some such case is what Jennings appears to have in mind when he insists that a stimulus depends essentially on a change in condition. When an organism moves in a straight line toward or away from

a point midway between two lights of equal intensity that are equidistant from the organism itself, it does so, he believes, because in such an orientation it is subjected to no general stimulation, which is no more than saying it then possesses no feeling of discomfort. In the face of the facts which have been presented to show that light induces definite reactions of definite muscles, just as definite as the complex but unconscious reactions of a decapitated frog to, let us say, acetic acid applied to the skin of its back, he insists upon an interpretation of organic behavior by means of general changes in internal states that are psychical rather than physiological. Here, as it seems to me, he has abandoned one attempt at explanation for an alleged explanation which itself assumes the facts most in need of elucidation.

It will not be necessary to delay further by examining the phenomena of geotropism. Organisms respond to the stimulus of gravity by reactions essentially similar to those which characterize their reactions to light. No new elements are introduced. It may be well, however, to summarize the discussion up to this point before entering upon a somewhat different line of criticism.

Jennings has applied to the facts of behavior a general explanation in the form of two principles. According to these principles, no definitely directive or fixed reactions, such as reflexes, tropisms, habits and instincts are primary, but result from the selection from random movements of such as are advantageous to the organism, and the gradual development of these advantageous reactions in the individual by the law of the readier resolution of physiological states, in the race by the operation of organic selection. The primary type of reaction is non-directive, and is illustrated by some such response as the motor reaction of Paramecium. The necessary condition of stimulation is an abrupt change in the environment, which leads to a general reaction of the whole organism. What the adherents of the tropism theory call a condition of symmetrical stimulation is, therefore, in reality a condition of no stimulation at all.

The existence of constantly acting directive stimuli after orientation is explicitly denied.

In our examination of this general view and the propositions on which it is based, we have arrived at the following preliminary conclusions:

I. That the essential facts of galvanic stimulation are identical in widely different organisms, which suggests their fundamental character; that there exist among the phenomena of galvanic stimulation two types of reaction, (1) non-directive, dependent on sudden changes of current potential, and (2) directive, dependent upon the action of a constant current which, it was shown, produces, after orientation an observable effect on locomotion; further, that the very fact of the pronounced absence of galvanic stimuli in nature greatly increases the value of galvanic stimulation as an aid to analysis.

II. That organisms exhibit toward light (gravity as well) two types of reaction comparable with those typical of galvanic stimulation; that certain responses, in Euglena and Anuræa, which are readily analyzed on the basis of these two kinds of stimulation, afford no support for the trial and error schema; that in heliotropism as well as in galvanotropism, the oriented organism is in a condition of physiological stimulation, and that the response to stimulation is local; finally, that the interpretation of the behavior of heliotropic organisms on the basis of general changes concerning the whole organism, not only does not accord with the known facts, but is rather psychical than physiological in character.

If these conclusions be sound, it follows that the method of trial, however useful it may be in the interpretation of certain classes of facts relative to the behavior of organisms, lends no aid toward the analysis of certain other classes of facts in the same field; that it not only does not simplify the general problem which these facts present; but that it actually tends to divert inquiry from a line of investigation which has been shown by recent achievements to be not only promising but fertile. To these conclusions I believe we may justly add another that has not yet been formulated in the discussion.

If all definite directive responses to stimuli have been produced by the selection of responses "that favor the normal life processes" as Jennings appears to believe, then such directive responses must be adaptive, must be of distinct advantage to the organism possessing them in the struggle for existence. There are, however, among certain organisms and in connection with certain classes of stimuli definite reactions which do not appear to serve the organism in any way.

In the first place, the phenomena of galvanotropism are obviously not in any way related to a possible adaptive value. In the second place, Professor Loeb mentioned long ago the caterpillar of the willow borer, and Diastylis (Cuma) rathkii, as two animals that live away from the light, the one buried in the wood of trees, the other in the mud of bays and lagoons, that yet react positively when exposed to light. Such instances are brushed aside as insignificant by Jennings, because few have been recorded. I feel confident, however, that instances of this sort will multiply. And far from being insignificant, it is most fortunate for the analysis of behavior that, in a world where the struggle for existence is so intense, even a few organisms have been found whose behavior has remained unaffected by it.

I do not think it is necessary to go farther into the facts to make it clear that the hypothesis advanced by Jennings is not sufficiently broad to encompass all the phenomena it is devised to explain. As a method of analysis, it is essentially historical. It seeks to derive all forms of organic behavior from a simple type or unit assumed to be funda-We have seen, however, that the mental. assumed fundamental unit is really not fundamental physiologically, since it is based squarely upon a psychological conception. The method, therefore, prescribes the interpretation of purely physiological phenomena, such as reflexes and tropisms, in terms of psychology. From the standpoint of effective analysis, this is surely putting the cart before the horse. The trial and error program looks very much like a modern recrudescence of the attitude toward the problems of behavior that could tolerate the interpretation of the behavior of a moth toward a flame as an exhibition of curiosity.

We may now examine somewhat more closely than has been possible so far, another interpretation, known by the name of "tropism hypothesis," which has been applied to certain aspects of the behavior of organisms and has been sharply attacked by Jennings. Far from pretending to be a universal formula, it has been suggested in various forms by various investigators for the purpose of testing the applicability to the problems of organic behavior of the data of physics and chemistry. It is a guide for analysis along experimental rather than historical lines, and in accord with its reason for being, is dependent upon no psychological data of any sort.

It has appeared from the preceding discussion that there is ground for believing in the existence of two classes of stimuli in nature, and that according to the tropism hypothesis both may elicit primary responses.

The view that the definitely directive responses known as tropisms are primary does not rest, however, merely on whatever presumptive evidence the curtailment of the trial and error program may admit. There are numerous examples in nature of the dependence of the tropic reaction upon the physiological condition of the organism. The larvæ of Polygordius, a marine annelid worm, when taken, are negatively heliotropic. Two hours later, they may be positively heliotropic. This change may be obtained immediately by cooling them down to a temperature of 7° C. The response may again be reversed by suddenly diluting the salt water containing the larvæ with one third to two thirds its volume The sense of the resulting of fresh water. response may in turn be reversed by increasing the concentration of the water. I have already referred to the barnacle larvæ that are positively heliotropic immediately after hatching, but, after a certain limited exposure to light, become negative. Terrestrial amphipods which are positive, change the sense of their response when thrown into water. Many animals change the sense of their response to light with age and sexual condition. The larvæ of the king crab react positively in their earlier stages, negatively later. Maggots of the house-fly respond negatively at the end of their larval period, but are quite indifferent to light both before and after this stage in their existence. At the time of sexual maturity, both ants and bees have exhibited positive responses to light.

Further, it is a highly interesting fact that certain caterpillars, notably Porthesia chrysorrhæa, are positively heliotropic when starved, unresponsive when well fed. The suggestion at once arises that the diffusion of chemical substances into the body from the digestive canal may cause the modification of the reaction. Acting on the hint here given, Professor Loeb initiated a series of experiments to see whether the immediate effect of the light in causing the heliotropic reaction is of a chemical nature. Such a supposition could be put to the test by placing heliotropic organisms in an artificial chemical environment. The results of experimentation in this direction have been productive of the most important results. Gammarus, Daphnia and Cyclops, all freshwater crustacea, were used. Gammarus pulex is, if anything, negatively heliotropic. By the addition to the water containing a number of individuals of this species of slight amounts of various chemical substances-esters, hydrochloric, acetic, oxalic and carbonic acids (the last itself a product of the metabolism of the animal), alcohol, paraldehyde and ammonium salts-in each case the animals become positively heliotropic. Similarly, Cyclops, either negative or indifferent, may be made positive by the addition of hydrochloric acid or carbon dioxide.

It is clear from the facts just recited that the heliotropic reaction of an animal is not necessarily constant, but that it may vary widely and suddenly in sense, or disappear altogether, in accordance with internal changes which are immediately chemical in character. There is little in such phenomena to suggest that tropic reactions are products of carefully selected trial movements. On the contrary, they suggest most strongly the possibility of identifying such reactions with de Vriesian mutations.

With the demonstration that chemical changes are connected in an important way with the reactions of organisms to light, the analysis of the tropic reaction has only begun. Recent experiments have achieved further results. I may quote, in translation, from a recent paper by Professor Loeb:

It might be assumed that acids call forth positive heliotropism among fresh water organisms because they accelerate the formation of a certain substance upon which the positive heliotropism depends. This conjecture, however, can be disproved. We know, namely, that reaction velocity increases with the temperature, and that the temperature coefficient is in these cases very high, namely, in general for each 10° rise in temperature  $\geq 2$ . Now I determined for freshwater copepods how large the minimal amount of carbonic or acetic acid is that is necessary to make indifferent animals positively heliotropic. It became apparent that for temperatures of about 10°-15°, not more but actually less acid is required to call forth positive heliotropism than at 20°-25°. That shows that the acid in this case can not act through the formation of a substance that conditions positive heliotropism. A similar experiment resulted even more strikingly for Daphnia. Here a fall in temperature below that of the room lessened in the clearest way the amount of acid necessary for the production of positive heliotropism. Now it appears to be generally the case, that when the temperature influences especially the sense of heliotropism in animals, this, so far as at present known, always happens in the sense of making it more positively heliotropic. We can accordingly draw the conclusion with absolute safety that the production of positive heliotropism is not due to an acceleration in the formation of a positive heliotropic substance-to use an expression which may be permitted for the sake of brevity. Rather are we forced by all these facts to the conclusion that the production of positive heliotropism in animals by means of acids rests upon the inhibition of the formation or action of an antipositive substance. It is conceivable that the conditions of positive heliotropism (therefore the positive heliotropic substance) are present in the organisms that here interest us, that, however, their (photochemic?) activity is inhibited by the continuous formation of certain stuffs in the body, e. g., in the eyes. If, now, we assume that acid inhibits the formation of these latter antibodies, then the positive effect of the acid is intelligible. Just so is the positive effect of the fall in temperature intelligible, since thereby the rapidity of the formation of the inhibitive antibodies is diminished.

Though the nature of the substances connected with the heliotropic reaction is not definitely known at present, experiments have suggested strongly that they may be of the nature of oxidases. Researches soon to be published confirm this view in a striking manner.

These facts still further emphasize the improbability of the production of tropic reactions as the result of the selection of a series of trial movements; while they further emphasize the probability that such reactions, dependent upon the presence of definite chemical substances, have sprung suddenly into existence in the manner of the mutations of de Vries. As such, they provide material for natural selection, along with every other variation, whenever they tend to preserve the life of any organism in its struggle for existence.

It has already been said that both Unterschiedsempfindlichkeit and heliotropism (or some other tropism) may be associated in the same organism. Such cases are common, and in every one of them the possibility of confusing the two reactions (as shown for Euglena) exists. To cite but a single instance, certain positively heliotropic butterflies will not move toward the brightest light when their bodies chance to be in contact with a pane of glass under which they have crept. Furthermore, a weak light may produce no reaction upon organisms where a light of greater intensity would. It often happens that under a light stimulus too weak to produce its appropriate definite directive effect, an organism may waver about, swinging now toward, now away from the source of the stimulus. These have been called trial movements. I do not believe they belong in that category, for two reasons. In the first place, when the organism comes into a proper orientation for an

organism whose line of least resistance runs toward the light, it does not stay so oriented. In the second place, when the light is sufficiently strengthened, the organism may make for it with the utmost directness.

The earthworm, a much used and abused animal in this connection, has recently afforded a case in point. *Perichæta* is an unusually active worm, and reacts, as all earthworms do, negatively to light. To quote from Harper:

2. The body is less sensitive to light when contracted than when extended, owing to the fact that when extended the sensitive elements are spread out over a greater surface and become more susceptible.

3. In locomotion, as there are alternate extensions and contractions, there is an alternation of the condition of lower and higher sensibility. This is important particularly in the sensitive anterior end.

4. As the worm begins each extension in a condition of lower sensibility, it may project its anterior end toward the source of light. This movement is checked as soon as the increased sensibility of the extended anterior end appreciates the stimulus. Movements away from the light do not meet such a check and so are prolonged farther. Orientation is the result of a trial and error method.

Up to this point the reaction comes under the head of Unterschiedsempfindlichkeit.

5. In strong enough light, random movements toward the light are suppressed altogether, and the worm appears to move directly away from the light without noticeable trial movements. This applies to worms which have been kept in the dark and are in a perfectly fresh condition, as after a time they lose their discrimination and begin to make random movements.

This section should be noted, especially the last sentence. Just as it has been seen that larvæ of barnacles may change their response when exposed for a time to light, so *Perichæta* becomes, after a certain exposure, indifferent to stimulation that produces a typical heliotropic reaction in the fresh worm. The animal remains, however, unterschiedsempfindlich. It contracts whenever, by extension of the anterior end, a sufficiently large sensitive area is exposed to the light. In *Perichæta*, therefore, not only do the two types of response occur, but prolonged exposure to light eliminates the possibility of one without interfering with the other. It is difficult to see how responses that are not different in kind could be distinguished in this manner.

In closing, it will not be necessary to summarize again the elements of the schema that Jennings has proposed for the interpretation of the behavior of organisms nor the objections which it has seemed to me could be urged against it. There is no doubt that by his very serious discussion of the problems of behavior, Professor Jennings has done the great service of focusing attention upon the essentials and the unessentials, understandings and misunderstandings in this field of investigation. And I offer the foregoing discussion, originally prepared for a non-biological audience of scientific men, in response to the invitation which is implied on many pages HARRY BEAL TORREY of his book.

ZOOLOGICAL LABORATORY,

UNIVERSITY OF CALIFORNIA, April 8, 1907

#### BOTANICAL NOTES

#### WOOD-STAINING FUNGI

In the September number of the Journal of Mycology George G. Hedgcock publishes a descriptive list of twenty fungi which stain different kinds of woods, in some cases so injuring the appearance as to cause much damage. Eight species of Ceratostomella, seven of Graphium, one of Fusarium, two of Hormodendron, one of Hormiscium and one of Penicillium are listed and described. The woods are species of pines, beech, sweet gum, oak, Rubus and elm, and in large part the staining takes place in the lumber piles after the trees have been sawn into boards, planks, etc.

NEW METHOD OF MOUNTING FUNGI

A NEW method of mounting culture-grown fungi for preservation in the herbarium is described in the July number (1906) of the *Journal of Mycology* by George G. Hedgcock and Perley Spaulding. Pure cultures on rather stiff agar supply the specimens, which are taken out in little blocks with a layer of agar adhering, dried on stiff cards, and then protected by pasting on perforated pieces of thick cardboard of the proper size, the specimens occupying the opening. These cards may be attached to herbarium sheets, and preserved in the usual way, or they may be kept for easy reference in the manner of library cards in ordinary card cases.

## ELEMENTARY BOTANY OF FLOWERING PLANTS

PROFESSOR MAST has published in a booklet of 54 pages a series of "experiments" intended to cover the essentials as to the structure and physiology of flowering plants in an elementary course in high schools and colleges. Dr. Mast having had "unsatisfactory results in beginning the study of plants and animals with such forms as Amoeba. Paramecium and Spirogyra," he prepared a set of directions for his students (in Hope College), beginning the work with the flowering plants, and taking up in succession, seeds, stems, roots, protoplasm, leaves, modified plant structures (tubers, tendrils, spines, aerial roots, etc.) and flowers. The subjects for these studies are well selected, and the directions are clear. For those who believe in beginning with the higher plants (which we do not) the book must prove helpful, as indeed it will be suggestive to those who prefer the more natural sequence from the simple structures to the more complex.

### FOREST TREES OF NEW JERSEY

DR. B. D. HALSTED in a recent bulletin (No. 202) of the New Jersey Experiment Station publishes a useful annotated list of the forest trees of New Jersey. He enumerates 104 species, of which 98 are natives, the others being exotics which have become pretty well established. Of the native species 13 are conifers, leaving 85 broad-leaved species. The largest genus is Quercus, the oaks, with 16 species, followed by *Pinus* (pines), Acer (maples) and Salix (willows) with 6 each, Populus (poplars) with 5 native and 2 ad-Of the ashes (Fraxinus) and hickventive. ories (*Hicoria*) there are 4 species each.  $\mathbf{It}$