tretenen Außenfaktoren: Alkali und Äthylalkohol aufgefunden werden.

Zum Schluss will ich nicht versäumen, Herrn Geheimrat Klebs meinen herzlichsten Dank auch hier auszusprechen. Bei einer mündlichen Besprechung dieser Arbeit hat Herr Geheimrat Klebs mir vielfach Anregung und Anhaltspunkte gegeben, die zum großen Teil in obiger Untersuchung verwertet und festgehalten worden sind.

Orientation in Euglena with some Remarks on Tropisms.

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In two very interesting papers Bancroft (1913) and Torrey have taken exception to some of the conclusions reached by Jennings and myself regarding the process of orientation, especially in *Euglena*. The points of controversy raised by these authors refer however only to matters of interpretation. Bancroft says (p. 414), "The facts of light reactions of Euglena described by Jennings and Mast have been confirmed in all cases in which they were reinvestigated. No differences of opinion exist as regards these facts"; and Torrey does not question the accuracy of our observations. We may then assume that the processes of orientation in so far as they have been actually observed occur as we have described them (Jennings 1904, p. 49—59; 1906, p. 134—141; Mast 1911, p. 80—112).

The points at issue may be treated unter three heads: A. The nature of the stimulating agent which induces orientation; B. The trial and error theory; C. The definition of tropism.

A. The Nature of the Stimulating Agent which induces Orientation.

Jennings and the writer maintain that the orienting stimulus in *Euglena* is dependent upon the time ratte of change of the intensity of light on the sensitive tissue. Bancroft asserts that he has proved that this is not true, and he holds that all of the evidence at hand favors the idea that the stimulus in question is dependent upon the continuous action of light in accord with the Bunsen-Roscoe law. I shall demonstrate that if the experimental evidence which Bancroft brings forth against our theory is valid, it completely overthrows his own theory in so far as it has any bearing on the process of orientation in *Euglena*. Before entering upon this demonstration it will be necessary, however, to present the chief characteristics of the theories in question.

Concerning merely the nature of the stimulus, there are three essentially different theories of orientation.

These may be designated as follows: (a) Relative-intensity theory; (b) Ray-direction theory; and (c) Change-of-intensity theory.

(a) The Relative-intensity Theory: The relative-intensity theory teaches that orientation is regulated by the relation in the intensity of the stimulating agent on opposite sides of the reacting organ or organism. If the intensity is unequal it is supposed that the two sides move at different rates until such a change in position is brought about that it becomes equal i. e. until the organism becomes oriented. The stimulating agent is supposed to act continuously after orientation, as well as during the process of orientation, the only difference being that in the former case it acts equally on both sides and in the latter unequally.

This theory may be divided into two sub-theories, which are, however essentially the same, (1) the local-action theory and (2) the reflex-action theory.

(1) The local-action theory was formulated by Ray in 1693. It is as far as I have been able to learn the first theory of orientation recorded. Ray maintained that plants turn toward the window because the surface facing the window is cooler than the opposite surface, and consequently the cells on that side grow more slowly than those on the other side, thereby causing the structure to bend toward the light. Each element in the process of orientation was supposed to be directly stimulated. This theory demands no separation of tissues into sensory and motor, and no transmission of impulses, at least to any appreciable extent. De Candolle in 1832 made use of essentially the same theory to account for the orientation of plants in light. He held in accord with Ray that the bending of the plant toward the light is due to difference in the rate of growth on opposite sides, but he maintained that this difference is due to the action of light, not to that of heat as Ray asserted. The explanation of orientation given by Verworn (1899, p. 499), Holt and Lee (1901) and Davenport (1897, p. 209), and some of those given by Loeb (1906, p. 118)[1]), are in full accord with De Candolle's theory, the opinion

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[1] "How can light bring about heliotropic curvatures? Let us suppose that light strikes a plant on one side only, or more strongly on one side than on the opposite side, and that it be absorbed in the superficial layers of tissue of that side. In this case we assume that on that side certain chemical reactions occur with greater velocity than on the opposite side. What these reactions are is unknown; we may think provisionally of oxidations. This change in the velocity of chemical reactions either produces a tendency of soft elements on that side to contract a little more than on the opposite side, or creates otherwise a greater resistance

of Bancroft to the contrary, concerning Loeb, notwithstanding. Bancroft says (p. 387), "Loeb certainly never thought . . . that 'orientation is produced by the direct action of the stimulating agent on the motor organs of that side of the body on which it impinges' (1906, p. 266), . . . and has never written anything of the kind so far as I have been able an discover"; and yet no clearer or more direct statement of the theory has ever been made than will be found in the quotation given above. In this case Loeb does refer to orientation of plants but I assume he would apply the same to animals, for he repeatedly says the process of orientation in plants and animals is identical.

Certain statements made by Torrey also indicate adherence to this theory. He says, referring to *Euglena* (1907, p. 319), „In heliotropism . . . the oriented organism is in a condition of physiological stimulation, and . . . the response to stimulation is local". Judging from this statement I concluded that he was an advocate of the local-action theory, and made a statement to that effect; but in a recent paper (1913, p. 874) Torrey by way of criticism maintains that he never believed in this theory.

(2) The reflex-action theory is similar to the local-action theory. The essential difference lies in the fact that it teaches that the motor elements are stimulated indirectly through a reflex arc, not directly as maintained in the local-action theory. This is the theory most frequently advocated by Loeb in recent years.

He says (1912, p. 38), "Two factors govern the progressive movements of animals [in light] . . .; one is the symmetrical structure of the animal, and the second is the photochemical action of light". In the words of Loeb (1906, p. 135), the orienting reaction is, according to this theory, "a function of the constant intensity". Formerly I assumed that Loeb meant by the phrase "function of the constant intensity" that the stimulating agent necessarily must act continuously, i. e. without intermission. But now I find (1910, p. 465) that he holds that this theory, in so far as the nature of the stimulating agent is concerned, covers all orienting reactions which are in accord wit the Bunsen-Roscoe

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to those forces which have a tendency to elongate or stretch the plant, e. g., hydrostatic pressure inside the cells, or imbibition of certain tissue elements. The otucome will be that one side of the stem will be stretched more than the opposite side, and this will bring about a curvature of the stem. Where the latter is soft at the tip, the bending will occur only, or chiefly, in that region; and as the degree of softness decreases rapidly from the tip downward, the result will be that the tip will bend toward the source of light. This result may possibly be aided by a greater photosensitiveness of the extreme tip of the stem, although I am not aware that this is an established fact".

law, that is, all orienting reactions which bear a definite relation to the product of the intensity of the stimulation agent and the time it acts, no matter whether it acts continuously or intermittently. Stated in other words this means that the reaction is proportional to, or at least bears some definite relation to the absolute amount of energy receive by the sensitive tissue from the stimulating agent. Thus according to Loeb there are two factors involved in the process of orientation, bilateral symmetry and photochemical changes which bear some specific relation to the absolute amount of energy received by the sensitive tissue.

Bancroft says that all of the evidence accumulated favors Loeb's theory, but as a matter of fact his arguments from beginning to end show that he is considering only one feature of this theory, namely, that which refers to the nature of the stimulating agent. This new theory of orientation advocated by Bancroft which in reality is merely a segment of Loeb's theories, we shall call the continuous-action theory.

All processes of orientation which bear a specific relation to the absolute amount of energy received by the sensitive tissue from the stimulating agent are in accord with this theory, regardless as to whether it is received continuously or intermittently; regardless as to whether the organism is symmetrical or asymmetrical; regardless as to whether in the process of orientation both or only one of two symmetrically located sensitive areas are functional. This theory refers only to the process of orientation. It has nothing to do with tropism as defined by Bancroft, Loeb, or any one else.

(b) The Ray-direction Theory. In accord with the ray-direction theory formulated by Sachs in 1876 orientation in some unknown way is regulated by the direction in which the lines of force from the stimulating agent penetrate the tissue of the reacting organism. The stimulating agent is supposed to act continuously during the process of orientation, but there is no necessary relation implied between the reaction and the amount of energy received; and the theory expressly states that orientation is not the result of difference in the intensity of stimulation on opposite sides of the reacting organ or organism. This was the first theory advocated by Loeb. He says (1888, p. 2), „Die Orientierung der Tiere gegen eine Lichtquelle wird wie bei den Pflanzen (J. v. Sachs) bedingt durch die Richtung, in welcher die Lichtstrahlen die tierischen Gewebe durchsetzen, und nicht durch die Unterschiede in der Lichtintensität auf den verschiedenen Seiten des Tieres". Later however he gave up the idea that the direction of penetration is vital in the process of orientation and substituted the notion that the angle between the sensitive tissue and the direction of force

in the stimulating agent is the controlling factor, thus still retaining the central feature of Sachs's theory, that is, that the direction auf the rays of force is all important. This theory has always been "pure theory"; it has never had any positive experimental support. I mention it here because I wish to refer to it later.

(c) Change-of-Intensity Theory. The kernel of this theory consists of the conception that the stimulus resulting in orientation is dependent upon the time rate of change of energy received by the sensitive tissue, not upon the absolute amount as is true for Bancroft's continuous-action theory. That there are reactions which are thus dependent upon the time rate of change has long been known, but Darwin seems to have been the first to hold that orientation may result from reactions thus produced. He says (1880. p. 566), "We believe that this case [referring to an experiment of Wiesner on orientation in plants], as well as our own [observations on orientation], may be explained by the excitement from light being due not so much to its actual amount, as to the difference in amount from that previously received". As to how in the process of orientation the stimulus, caused by change of intensity, acts, and as to the nature of the mechanism involved, Darwin does not express an opinion.

Engelmann (1882, p. 395) foreshadows the application of this principle to account for orientation in motile forms, especially *Euglena*. Jennings (1904, p 43, 59—63) was however the first to analyse thoroughly by direct observation the process of orientation in unicellular organisms, and to present evidence which seemed to prove that in certain cases this process is the result of stimuli produced by change of intensity; that is, that orientation is dependent upon the time rate of change of energy on the sensitive tissue. Jennings also at the same time (1904) concluded that orientation in these forms is indirect; i. e. that it results from the successive assumptions of several different axial positions and the retention of one of these.

The results of my extensive studies of the process of orientation in unicellular organisms, especially *Euglena*, colonial forms and others, support Jennings's conclusions regarding the nature of the process of orientation and the character of the stimulus — particularly the latter.

It is the two conclusions stated by Jennings that Bancroft and Torrey claim to have overthrown in so far as they apply to the process of orientation in Euglena. What is the evidence upon which this is based? We shall concider the question as to the nature of the stimulus first.

In swimming *Euglena* deflects continuously toward the surface near which the eye-spot is located, but at the same time it rotates on the longitudinal axis. This results in a spiral course the axis of which is fairly straight regardless of the degree of deflection. A slight deflection merely results in a narrow spiral course while a greater deflection results in a wider course. The general direction of the course is usually changed by an increase in deflection on one side of the spiral and a decrease on the opposite side. Only slight changes can occur by changes in deflection on but one side of the spiral. It is manifestly impossible to obtain a change in the general direction of motion without either a decrease or an increase in deflection. This is an important point of which we shall make use later.

If, when a given *Euglena* is proceeding toward a source of light, the direction of its rays, without any alteration in the intensity, is suddenly so changed that it becomes perpendicular to the axis of the spiral, the deflection is usually increased on the side of the spiral facing the light and decreased on the opposite side. Ordinarily the increase in deflection is greater than the decrease and the spiral becomes momentarily somewhat wider. Whether or not the decrease in deflection is ever precisely the same as the increase so that there is no change in the diameter of the spiral, as Bancroft maintains, I am unable to say. However that may be, this change in the deflection results in a gradual turning in the axis of the spiral until it is directed toward the source of light and the *Euglena* is oriented.

One further point should be noted here. An unoriented *Euglena* as it rotates on its long axis is successively illuminated from all sides. In one position in the spiral the surface containing the eye-spot faces the light, in another position this surface is shaded and the opposite surface becomes illuminated. Since this creature, though relatively translucent, contains structures (the eye-spot in particular) which are relatively opaque, it is evident that shadows are produced which, as it rotates, travel over different parts of the body, and this results in changes in the intensity of light in all parts. The amount of these changes in illumination decreases as orientation proceeds, and disappears entirely when the axis of the spiral comes to be directed toward the light no matter what its diameter may be.

Concerning the process of orientation as described, there is, as previously stated, no contention. The point at issue concerns the cause of the changes in deflection resulting in orientation. Both schools hold that owing to the shadows mentioned above, the sensitive tissue in *Euglena* receives different quantities of light

energy in different positions of the spiral, least when the dorsal and most when the ventral surface is exposed. Thus it is assumed that the unoriented organism not only receives different quantities of light energy in different positions, but that the amount received changes continuously. Bancroft holds that orientation is dependent upon the difference in the amount received in different positions of the spiral. Jenning's and the writer hold that it is dependent upon the time rate of change in the amount received (shock-reactions). This is the main point of difference in the two theories which primarily concerns us. Both schools, let me repeat, hold that during the process of orientation in positive specimens there is an increase in deflection on the side of the spiral toward the light, i. e., toward the surface bearing the eye-spot.

There is however another point of difference that may be presented here. Bancroft holds that the degree of deflection depends upon the amount of light energy received regardless of the surface illuminated. He says (p. 421) that in negative euglenae, after orientation, the spiral course is narrower, (the deflection less) in low than it is in high intensity, and that in positive euglenae just the opposite is true. In positive euglenae then, according to Bancroft, the deflection, as previously, stated, is greatest when the energy received is least, i. e., when the unoriented organism is in such a position in the spiral that the surface bearing the eye-spot faces the light, and, he maintains, this results in orientation. But after orientation the sensitive tissue still receives light energy. Thus Bancroft holds that the degree of deflection continues to be regulated, after orientation as well as during the process of orientation, that light acts continuously in accord with the Bunsen-Roscoe law, and that thus the organisms are held upon their course after orientation by the same factors which cause orientation. The amount of energy received, however, as stated above, does not, after orientation, vary in different positions of the spiral. According to the change-of-intensity theory, therefore, the condition of illumination which induced orientation no longer exists; the stimulus which causes orientation acts only during the process of orientation, not after the organism has become oriented. Light may, however, according to this theory, continue to act on the organism, much as heat does, making it more or less active, causing changes in the sense of orientation, producing photosynthesis, etc. Organisms in general tend to proceed in fairly direct courses if there is nothing in the environment to prevent this. Thus after orientation, according to our theory, they tend to remain oriented owing to internal factors, i. e. structure, and physiological processes.

Our conclusion as to the nature of the orienting stimulus is founded upon the following facts concerning which there is no contention: 1. A sudden decrease in illumination of the field induces in positive euglenae an increase in swerving toward the eye-spot. This may be marked or only very slight. (See Bancroft, p. 395.) It is known to depend upon the time rate of change, for if the decrease in illumination is gradual enough this phenomenon does not occur. We shall refer to it as a shock-movement or reaction. 2. The orienting deflections are, as far as can be observed, of precisely the same nature as weak shock-movements. 3. There is no response under certain conditions if the ventral surface of a *Euglena* faces the light after the direction of the rays has been changed, until in the process of rotation the surface containing the eye-spot comes to face the light; then there is a sudden turning toward this surface, i. e., toward the source of light. In many instances the turning is so sharp immediately after the dorsal surface becomes illuminated that it may appropriately be designated as a jerk or a twitch. This is in opposition to the demands of the continuous-action theory, as we shall see later. 4. After orientation fire-flies may continue for considerable distances on a direct course in darkness. The same is true for *Euglena*, according to Bancroft (p. 411), and it is probably also true for other organisms. It is therefore not necessary to postulate continuous action of the orienting stimulus to account for the direct movement toward the source of stimulation after orientation.

If I understand the matter correctly our critics do not deny that shock-reactions may sometimes function in orientation. Torrey says (1914, p. 111), "[In *Euglena*] the 'motor reflex' [shock-reaction] plays an important part in its orientation to light". Bancroft however maintains that he has proved that orientation is not in all cases due to shock-reactions. But while he admits that he was unable to prove that it is in such cases due to continuous action of light in accord with the continuous-action theory of orientation, he concludes (p. 425), "In the case of *Euglena* we have seen that what evidence we have is all in favor of the view advocated by Loeb that the heliotropism [orientation] is a function of the continuous action of the light".

Let us examine the evidence. This Bancroft has presented under eight heads. According to our theory (change-of-intensity theory) orientation in *Euglena*, as previously stated consists of a series of shock-reactions. In positive individuals these reactions are supposed to be due to sudden decrease and in negative ones to sudden increase of light intensity caused in unoriented individuals by rotation on the long axis. Bancroft therefore maintains that if a positive *Euglena* orients in a given condition of illumination,

it ought to give the shock-reaction if the light intensity in the field is suddenly reduced, but not if it is increased. If the organism is negative precisely the opposite should occur. There should, in other words, be a strict correspondence in every condition of illumination and physiological state between orientation and shock-reactions. When individuals orient negatively they ought to respond with the shock-reaction if the light intensity in the field is suddenly increased, not if it is decreased. When they orient positively, on the other hand, they ought to respond with the shock-reaction if the intensity is suddenly decreased not if it is increased; and when they do not orient at all they ought not give the shock-reaction to either an increase or a decrease in intensity.

The subject matter under four of the eight headings mentioned (A, B, C and F) deals with this correspondence.

As a general result of his observations Bancroft maintains that in a number of instances the agreement between shock-reactions and orientation demanded by the change-of-intensity theory as described above was not found. His most important results regarding this matter are visualised in the following diagrams.

Culture.

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A	H E L. O O O O O O O O O — — — — — — — — — — —	
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A	H E L. — — — — — — — — — —	
	S. M. S S S S S O I I I F	
C	H E L. + + + + +	
	S. M. I I I I I I	

(From Bancroft, p. 400, Fig. 4.) "Diagram to show the correlation between the sign of the heliotropism and the character of the shock-movements. Distances along the horizontal line indicate distances from the light. On the left, then, we have a weak light and on the right a strong light. Above the line is indicated the sign of the heliotropism (Hel.). Below the line is indicated the character of the shock-movements (S. M.). S = shock-movements produced by sudden shading, and not by sudden illumination; I = shock-movements produced by sudden illumination, and not by sudden shading; F = shock-movement mechanism becomes fatigued if light lasts for half an hour or an hour; O = absence of reaction; B = correlation in Culture B; A = correlation in ordinary individuals of Culture A; Lower A = correlation in exceptional samples of Culture A in which the shading reaction appeared; C = correlation in exceptional sample from Culture B."

These diagrams indicate that in addition to what the change-of-intensity theory demands, he obtained (1) shock-reaction when there was no orientation, (2) negative orientation in individuals which gave shock-reactions to decrease of intensity; (3) negative orientation in individuals which did not respond either to sudden

increase or to sudden decrease of intensity; and (4) positive orientation in individuals which responded with shock-reactions to increase instead of to decrease of intensity. All of these reactions he maintains are contrary to expectations based on the change-of-intensity theory of orientation. He consequently concludes that this theory fails to account for the observed phenomena and that the continuous-action theory must be valid. He says (p. 425), "We have no evidence against the view that in *Euglena* the gradual orientation is a function of the continuous action of the light".

To what extent do Bancroft's results actually warrant these conclusions? Let us consider first the results recorded in diagram B together with the methods used in obtaining them.

According to this diagram the expected correspondence between orientation and shock-reaction holds in the lower light intensity, but as the intensity increases, Bancroft maintains, there is no orientation although there is still a shock-reaction. Is this result necessarily in opposition to the change-of-intensity theory? It would be if the shock-reactions had been induced by changes in illumination in the field, of the same nature and degree as were produced on the sensitive tissue within the unoriented organism due to its rotation, for only such changes could function in the process of orientation; but this was in all probability not true. In these tests Bancroft placed an opaque screen in front of the light practically cutting it entirely off. Thus the reduction of intensity was no doubt very much greater than that caused by the rotation on the axis. If this is correct then all of the reactions described in this diagram with the possible exception of the last, may be, for all that is known to the contrary, in full accord with the change-of-intensity theory; and the same may be said with reference to the reactions represented in the two succeeding diagrams. In all of the experiments in which the results given in these diagrams were obtained there is every indication that changes of intensity of such a degree were used in testing for the shock-reaction as could not possibly have been produced in the process of rotation by the movement of the shadows of the translucent bodies in the organism. The change-of-intensity theory demands shock-movements in negative *Euglena* only when the intensity of the field is increased, but if the intensity is greatly decreased the negative individuals may become positive, and respond with the shock-reaction. This is especially probable if they are near the neutral region as was true according to the diagrams in Bancroft's experiments.

I consider it inexpedient to attempt further analysis of these results, for, strange as it may seem, if they are fatal to the change-of-intensity theory, as Bancroft holds, they are equally fatal to

the theory upon which he relies to explain them, i. e., the continuous-action theory.

According to both of these theories, as I have previously stated, orientation is accomplished by increase in deflection on the side of the spiral course facing the light, i. e., toward the dorsal surface of the organism, the surface containing the eye-spot. In an unoriented *Euglena*, as it proceeds on the spiral course rotating on its long axis, the dorsal and ventral surfaces alternately face the light. According to both theories the sensitive tissue in the organism receives least light energy when the dorsal surface, the surface bearing the eye-spot, is fully illuminated. In case of positive orientation it is only when the organism is in this position that the increase in swerving resulting in orientation occurs. According to the change-of-intensity theory the increase in swerving is dependent upon the time rate of change in the energy received by the sensitive tissue; and according to the continuous-action theory it is dependent upon the absolute difference in the amount of energy received in different positions of the spiral. A change in the amount of light energy in the field which necessarily would result in a change of light energy on the sensitive tissue should then, in positive organisms, result in increase in swerving; i. e., in a wider spiral, on the basis of Bancroft's theory as well as on the basis of ours.

Bancroft says (p. 421) that in negative euglenae the spiral becomes narrower, the deflection toward the dorsal surface diminishes when the light is decreased, and that it becomes wider when it is increased, i. e., the deflection increases. According to Bancroft's theory then there ought to be the same correspondence between orientation and reactions to changes of intensity in the field as is demanded by the change-of-intensity theory. In case of positive orientation a decrease in the intensity of the field ought to result in an increase in swerving toward the dorsal surface; and in case of negative orientation an increase in the intensity ought to induce the same response; and of course orientation ought never occur under conditions in which a change of intensity in the field will produce no increase in swerving. Moreover in positive organisms an increase of intensity ought to cause a decrease in swerving, and in negative organisms a decrease ought to produce the same response. But this is precisely what Bancroft maintains he has proved does not occur. Thus he has, if his results are valid, overthrown his own theory. Even the assumption that the lack of correspondence between orientation and shock-reactions is due to the dominance of the latter over swerving due to "continuous action" would not save his theory, for this would in no way answer all those cases in which individuals that oriented gave no shock-

reactions (increase in swerving) to changes of intensity in the field.

Aside from that concerning the lack of correlation between orientation and shock-movement, Bancroft presents five lines of evidence, some against the change-of-intensity theory, others for the continuous-action theory.

1. Bancroft found that if the position of the source of illumination is very gradually changed after euglenae are oriented, they gradually change their direction of motion and he concludes (p. 407) that "In this way the most convincing demonstrations of gradual orientation without any shock-movements or widening of the spiral were possible." Is this demonstration really convincing? A shock-reaction consists of an increase in swerving toward the dorsal surface dependent upon the time rate of change of energy received by the sensitive tissue. Bancroft admits that this increase in swerving may be very slight. He says (p. 395): "In the weakest shock-movements merely a slight temporary widening of the spiral is seen", i. e. a slight increase in swerving toward the dorsal surface. But this is precisely what occurred in Bancroft's experiments when the euglenae changed their direction of motion (oriented) after the position of the light was changed; for as I have previously shown, change in the axial direction of the spiral course, no matter how gradual it may be, can not occur to any appreciable extent without increase in swerving toward the dorsal surface. It is obvious then that the evidence presented by Bancroft in this connection has no bearing whatever on the question as to whether or not orientation is the result of shock-reactions.

2. Bancroft asserts (p. 408) that the time between increase and decrease of illumination in the sensitive tissue in unoriented euglenae (due to rotation on the long axis) is much shorter than that required for a shock-movement, increase in swerving toward the dorsal side due to change of intensity in the field; and that consequently orientation cannot be due to the time rate of change of intensity, but must be due to the continuous action of light. But his theory as well as ours demands change of illumination on the sensitive tissue due to rotation, and increase in swerving owing to this change. It likewise demands increase in swerving if the intensity of light in the field is decreased. Thus it is evident that if the time between increase and decrease of illumination on the sensitive tissue due to rotation on the axis is too short to induce increase in swerving resulting in orientation in accord with the change of intensity theory, it is also too short to produce increase in swerving in accord with the continuous action theory.

3. It is maintained by Bancroft (p. 411) that if, under certain conditions, there are particles of the proper size in suspension

euglenae give the shock-reaction provided the light is so weak that they do not orient; but if the illumination is increased until they orient they no longer respond to contact with the particles. He holds that the change of intensity theory can not account for this, since, according to this theory, the orienting stimulus is supposed to cease after the organisms is oriented. Consequently he thinks, if this theory is valid, the euglenae ought to respond to contact with particles after orientation quite as freely as before.

These results would be very serious indeed for the change-of-intensity theory if this theory maintained that light acts only in producing shock-reactions. I am, however, not aware that anyone ever held such a view. Engelmann (1882 and 1883), more than thirty years ago showed very clearly that the activity of *Euglena*, and particularly of Bacterium photometricum, depends upon the amount of light energy received, and that this is in all probability not dependent upon the time rate of change of energy. And long before this it was fairly well known that photosynthesis is related to light in the same way. The change in the sign of orientation also appears to be independent of the time rate of change of energy. Light, as I have repeatedly stated (1907 and 1911), in all probability has an effect on physiological processes (activity, etc.) in organisms, an effect which bears a definite relation to the amount of energy received, which is somewhat like the relation between such processes and heat energy. This the advocates of the change-of-intensity theory do not deny. They merely hold that orientation is not due to such effects of light.

The fact that Bancroft obtained reactions to contact with particles in light of low intensity and none in light of high intensity was probably due to changes in the physiological state of the organism and not to differences in orientation, as he assumed. This phenomenon is in full accord with the wellknown fact that when organisms are simultaneously subjected to stimuli of different sorts they may respond to any given one very differently than when they are acted upon by that stimulus alone. The reactions in question, consequently do not militate against the change-of-intensity theory.

4. In his very interesting experiments on galvanic reactions Bancroft states that he found that orientation in an electric current occurs precisely as does orientation in light as described by the present writer; and he holds that there is no contrast between these reactions in *Euglena* such as Jenning's maintains there is for other infusoria.

I agree with him in this conclusion. He assumes however that orientation in the electric current is regulated by continuous

action and concludes that orientation in light must consequently also be a function of its continuous action. I do not agree with him in this conclusion, for I hold that the assumption upon which it rests is unwarranted. In the case of *Euglena*, contrary to what holds under certain conditions for some other organisms, the galvanic orienting stimuli may be due for all that is known to the contrary, to the time rate of change of electric energy received by the sensitive tissue as the unoriented organism revolves on its axis, and if this is true it does not support Bancroft's conclusion regarding the action of light.

5. As a final argument in favor of Loeb's continuous-action theory, Bancroft attempts to controvert the evidence which I have presented to demonstrate that this theory will not account for orientation in fire-flies. I found (1912, pp. 270, 271) that the flashes of light produced by certain fire-flies serve as signals by means of which the opposite sexes are brought together for the purpose of copulation. If a male is anywhere between one and six hundred centimeters from a female when she produces as flash of light, he usually turns and flies directly toward her. This flash of light is very short and it usually if not always disappears entirely before the male starts to turn. Thus in total darkness he turns through the proper angle and proceeds sometimes as far as several meters, directly toward the point where the female produced the glow.

There are three points in connection with this process of orientation that I wish to emphasize. (1) The male fire-fly will not orient in continuous illumination. To induce orientation it is necessary to produce a light, leave it a certain definite period of time, and then extinguish it. If it is not extinguished or if it is left too long there is no response. (2) The length of the period of illumination necessary to induce orientation is approximately the same regardless of the distance between the male and the female. (3) The male fire-fly not only orients in total darkness, but after orientation he continues on a direct course.

In agreement with Loeb, Bancroft holds that the Bunsen-Roscoe law affords the best criterion for testing the validity of the continuous-action theory. He holds that the results of my experiments on fire-flies are in harmony with this law, and he consequently maintains that they do not militate against the continuous-action theory.

It has been found that the plumules of certain plants (Avena, etc.) orient if exposed to a strong light for only a very short period — 1/800 of a second or even less, and that these reactions are at least superficially in accord with the Bunsen-Roscoe law, i. e.,

the reaction is approximately proportional to the product of the time and the intensity no matter how either of these factors may vary. In other words, the reaction bears a specific relation to the amount of energy received. This means that a given amount of energy, other things being equal, produces the same reaction no matter whether this energy is applied intermittently or continuously, whether it is received during the period of a second or a day. Since these plant structures can orient in the dark after exposure in intense light for a very short time, and the reactions are apparently in accord with the Bunsen-Roscoe law, Bancroft sees no reason why this law may not hold for fire-flies which also orient in the dark.

He fails entirely to grasp the fact that the very essence of the law is violated in that the period of illumination necessary for stimulation in the fire-fly cannot be altered. According to this law we should get the reaction if this period is increased provided the intensity is proportionally diminished, as seems to be true within certain limits for plants, but this is not true.

There is however even a more striking contradiction between the law in question and the orienting reactions of these insects. If the male is one centimeter from the female it requires, for stimulation, the same length of illumination of the same intensity as it does when he is 600 centimeters distant. Thus under the former conditions it requires to produce a given reaction 360,000 times as much energy as it does under the latter. How can this be squared with the continuous-action theory if the Bunsen-Roscoe law is to be accepted as a criterion? Moreover the male fire-fly, as stated above, not only orients after the flash of light from the female disappears, but he also remains oriented. How can it be maintained that this animal in the total absence of light is held on his course by the "continuous-action of light" as Loeb's theory demands? On the basis of the continuous-action theory, then, no matter how it be interpreted, I can account neither for the process of orientation in fire-flies nor for the direct course after orientation.

Bancroft admits that he has been unable to demonstrate that orientation in *Euglena* is in accord with the continuous-action theory. He was not able to show that the Bunsen-Roscoe law holds for this response. But this theory has failed not only to receive direct support; it does not account for what actually occurs in the process of orientation. As previously stated, if the dorsal surface of a positive *Euglena* does not face the light after the direction of the rays is changed, there is no response until in the process of rotation this surface comes to be fully illuminated. According to the continuous-action theory the greater the amount

of light energy received the less the deflection. Bancroft admits that *Euglena* receives least energy when its dorsal and most when its ventral surface is illuminated; therefore if the ventral surface is illuminated after the direction of the rays is changed there should be, according to this theory, an immediate response consisting of a decrease in deflection. Failure to get such a response can not be accounted for on the basis of time, for if the dorsal surface becomes fully illuminated when the direction of the rays is changed there is an immediate response. The same difficulty is encountered in attempting to account for the orienting reactions in *Stentor* (Mast, 1911, p. 117) on the basis of the continuous-action theory. And in *Volvox* the discrepancy between the reactions observed during the process of orientation and those demanded by this theory is even more serious. In this organism in the positive state it is found that an increase in light energy causes an increase in the activity of the zoöids, but in unoriented individuals it causes, contrary to expectations on the basis of the theory in question, the greater activity on the shaded side of the colonies. This results in orientation. These phenomena together with others seem to show that in *Volvox* activity is dependent upon the absolute amount of light received, and orientation upon the time rate of change of light. (See Mast, 1907, pp. 151—154; 1911, pp. 140—143.)

I have elsewhere given the experimental results which directly support the change-of-intensity theory of orientation in *Euglena*. In my opinion if there is any evidence whatever which militates against this theory it is found in certain cases presented by Bancroft in regard to the correspondence between orientation and shock-reactions; but as has been shown this evidence militates against his own theory quite as seriously. If this evidence should be confirmed under carefully controlled conditions, both theories of orientation would have to be abandoned, and it might be necessary to return to Sachs's very vague ray-direction theory.

Let me state in concluding this section that I have never maintained that the stimulating agent does not function in the process of orientation in animals in accord with the continous-action theory. In fact I believe that it does so function in some animals. I have however persistently maintained and I still affirm that there is no conclusive evidence in support of this conviction. It has never been proved that this theory holds for the orientation of any animals, with the possible exception of *Eudendrium*. Regarding this organism, after making some very careful observations on the process of orientation, I came to the following conclusion (1911, p. 163): "In the orientation of *Eudendrium* it seems probable that light acts as a constant directive stimulation." Loeb and Ewald

have also recently (1914) obtained results which seem to indicate that orientation in *Eudendrium* is, within certain limits of intensity, in accord with the Bunsen-Roscoe law. But this surely does not warrant their conclusion that the process of orientation in plants and animals in general is "identical" and that the Bunsen-Roscoe law holds for all.

B. Trial and Error.

Both Bancroft (p. 415) and Torrey (1913, p. 875) maintain that they have proved that orientation in *Euglena* is direct; that it is not due to the assumption of various axial positions and the retention of that axial position in which the animal is directed toward or from the source of stimulation in accord with the "trial-and error" theory as applied by Jennings. And if I understand Torrey correctly (1913, p. 875) he concludes that this demonstrates that overproduced, random, or trial movements are not primitive reactions from which, as Jennings holds, "the definitely directive reactions of bilateral animals to light have . . . been developed by any process of selection based on such movements."

Bancroft bases his conclusions largely upon my description of the process of orientation in which it is stated (1911, p. 104) that orientation may occur without any increase in the diameter of the spiral. I am inclined to believe that this statement holds literally under certain conditions, although I established by direct observation, only that when *Euglena*, as it proceeds on its spiral course, is illuminated from the side, it swerves farther toward the light than in the opposite direction, and that the swerving from the light does not carry the animal as far in that direction as it was in the same relative position of the spiral on preceding turns. All this could evidently occur with or without an increase in the diameter of the spiral. Bancroft holds that if it occurs without an increase in the diameter of the spiral. *Euglena* orients "as directly as its locomotor mechanism allows", and consequently orientation contains nothing of the nature of a "trial-and-error" reaction. This is a good point; but the question remains: does orientation actually ever occur thus?

Without pausing to analyse Torrey's evidence (1913) against indirect orientation, evidence which in my estimation is far less conclusive than Bancroft's, let us grant that *Euglena* actually does orient directly, that is, without trial, and see what bearing this has on the idea that "trial-and-error" reactions are more primitive than responses which have a more direct relation to the location of the stimulus. Any one who has studied the reactions of *Euglena* knows that under certain conditions a very large majority

of its reactions bear no observable specific relation to the localization
of the stimulus, that is, they are of the "trial" type. Moreover it
is undoubtedly true that this type of reaction plays a large rôle
in the process of orientation in general. That is, if orientation
occurs at all without an increase in the diameter of the spiral, it
is probably certain that such occurrences are, under natural con-
ditions, in the minority.

I am consequently unable to understand how, even if orien-
tation in *Euglena* were found to be direct in all cases, this would
prove that the "trial" reactions are not primitive, and that "differ-
ential response to localised stimulation" has not been evolved from
such reactions, as Jennings maintains.

C. The Definition of Tropism.

The term tropism has been applied by different authors to
almost every conceivable sort of response. There is so little
unanimity in the interpretation of its meaning as applied to reac-
tions in animals that practically every one who uses it finds it
necessary first to state what sort of reactions he proposes to group
under it. In my book "Light and the Behavior of Organisms" I
have collected some seventeen different definitions of this term
(1911, pp. 53—57). (A number of new ours have appeared since.)
Bancroft (p. 384) maintains that in this collection I have "inex-
tricably mingled definitions of the term and theories to account
for the reactions". He intimates that the confusion in the use of
the term is due largely if not entirely to such mingling, and pro-
poses to settle the whole matter by distinguishing definition from
theory. "Heliotropism", he says (p. 384), "will be used here as it is
used by Loeb, and most authors who use the word, to indicate
a certain kind of reaction, entirely apart from the theory which
may be adopted to explain the way in which the reaction takes
place". He maintains that "Loeb makes his use of the term clear
in many places", and gives in support of his contention the follow-
ing quotation (Loeb, 1910, p. 452); "Unter den Tropismen der
Tiere verstehen wir die zwangsmäßige Orientierung gegen resp. die
zwangsmäßige Progressivbewegung zu oder von einer Energiequelle".
Finally he gives his own definition which is supposed to be in
accord with Loeb's and which he asserts merely "indicates a certain
kind of reaction, entirely apart from the theory which may be
adopted to explain the way in which the reaction takes place".
He writes (p. 384), "In this paper, then, Heliotropism includes
those reactions in which there is a compulsory orientation with
respect to the light, no matter how that orientation may have been
brought about". Is this definition in accord with Loeb's? Is it
in reality free from theory? Does it eliminate confusion regard-

ing the use of the term in question? Is it practicable and serviceable?

Bancroft's definition of tropism is no doubt in harmony with the ideas expressed by Loeb in the statement quoted above, but this statement contains only a part of Loeb's ideas concerning the use of this term and in presenting only this isolated selection it seems to me that Bancroft has unjustly misrepresented Loeb's views. Loeb says (1912, p. 38), "Two factors govern the progressive movements of animals (in light) . . .; one is the symmetrical structure of the animal, and the second is the photochemical action of light". If an animal is illuminated laterally, the light intensity received by the two eyes differs. Thus it is supposed to cause, through direct nervous connection, a difference in the tension of the muscles of the locomotor appendages on the two sides resulting in unequal rates of movement on these sides and eventually in orientation. The stimulating agent is supposed to act continuously, after orientation as well as during the process of orientation. Only those processes of orientation which are brought about in this way are considered to be tropisms. Bancroft maintains that Loeb does not exclude from tropisms orientations due to stimuli dependent upon the time rate of change of energy received by the sensitive tissue. He says (p. 418) "Loeb does not think, as has been assumed by some writers, that if a tropism is shown to be due to differential sensibility that by definition it ceases to be a tropism". Loeb however has stated in unequivocal terms that he does exclude such reactions. He says (1903, p. 135), "Heliotropism covers only those cases where turning to the light is compulsory and irresistible, and is brought about automatically or mechanically by the light itself. On the other hand, there are compulsory and mechanical reactions to light which are not cases of heliotropism; namely, the reaction to sudden changes in the intensity of light . . . In the former case the results are a function of the constant intensity, in the latter a function of the quotient of the change of intensity over time". Thus, according to these statements, Loeb considers as tropisms only those processes of orientation which are due to the continuous action of the stimulating agent on the sensitive tissue, symmetrically located on opposite sides of the body. He excludes all those processes of orientation which are due to stimuli dependent upon the time rate of change of energy in the sensitive tissue and all those which may be due to differential response to localised stimulation. Bancroft does not exclude these. His definition is in harmony with only one of the various features found in Loeb's.

The definitions of both of these authors however appear to me to involve, contrary to Bancroft's opinion, an explanation of

how orientation occurs. For is not the statement by Loeb that orientation must be a function of the constant intensity in order to be a tropism an attempt to explain the way in which the reaction takes place? As a matter of fact Loeb's writings on reactions are full of such attempts[2]). And does not Bancroft's idea that only "compulsory" orientations are tropisms imply a theoretical explanation? Every limiting adjective of this sort if it means anything at all necessarily implies explanation of some sort for if it did not how would it be possible to distinguish between compulsory orientation (tropisms), and orientations which are not compulsory. It is evident that both Bancroft and Loeb hold there are such, for if they did not the adjective "zwangsmäßig" and "compulsory" would mean nothing. Orientation and tropism would become synonymous and the phrase "heliotropic orientation" used so much by Bancroft (pp. 413, 414, etc.) would become "helio-orienting orientation", — a senseless combination.

In order to ascertain then whether or not a given orientation is a tropism it is necessary, in accord with these definitions, to ascertain among other things whether or not it is compulsory. How is this to be accomplished without theory and explanation? Unfortunately Bancroft does not tell us. Loeb, however, if I correctly, understand him holds that conscious orientation is not compulsory i. e. that psychic phenomena are involved as causal agents in such processes; and if this be true he must believe in free will and material indeterminism. Thus we find that these definitions, supposedly free from theory, involve a question literally steeped in theory, a question which has been discussed for ages and is still being discussed, a question which all experimental methods have failed to solve for any case even under the most favorable circumstances; and yet Bancroft would persuade us that "compulsory orientations" are certain kinds of reactions, that, without theory or explanation, can be separated from orientations which are not compulsory.

No more convincing illustration of the futility of this definition can be desired than is found in the fact, as I shall show presently, that Ewald, who accepts this definition, does not agree with Bancroft in classifying the orienting reactions of *Euglena*, in spite of the fact that he was his colleague and worked in the same laboratory.

There are, in my opinion, only two definitions of tropism that avoid theory. In one this term is used synonymously with orien-

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2) A number of examples may be found in my book (1911, pp. 28—35). See also Loeb (1912, pp. 38—46).

tation, in the other synonymously with reaction; and if this be
true, it would be a simple matter to extricate them, no matter
how much they may be mingled with others in my collection of
definitions. Accordingly the "inextricable mingling" to which Ban-
croft refers is of no serious consequence.

If, then, it is impossible do distinguish between compulsory
and non-compulsory orientation, Bancroft's definition of tropism
is impracticable, and there are many others of the same nature,
for example, the most recent one by Torrey (1914, p. 120) in
which he proposes to make predictability the criterion of tropisms.
Thus he would call all processes of orientation which can be
predicted tropisms. The impracticability of such a criterion is
evident to anyone who is familiar with the activity of animals. I
suppose the rational reactions of man can be as accurately predicted
as any, and yet the strongest advocates of tropisms have always
attempted to exclude such reactions. Is it not true that all responses
in all organisms can be predicted within a certain degree of pro-
bability, and is it not equally true that none, except in a very
general sense can be predicted with certainty? How then is one
to know precisely which, in accord with this criterion, are to be
considered elect and which not? And what probability is there
that two different investigators would select the same? The follow-
ing sentence from Parker is apt in this connection (1914, p. 384):
"Woe be to him if he begins to tell what a given animal at a
given moment will do!"

Many seem to think that tropisms[3]) are a specific sort of reac-
tions, elementary in character and quite different from those
heretofore marshalled under the familiar terms, reflex action, random
movement, trial reactions, orientation, etc., and yet every attempt
to bring together under a specific definition a group of reactions
having these characteristics and differing from others already known
has signally failed. The term is in fact, as previously stated, at
present used in so many different senses that everyone finds it
necessary to indicate in which sense he proposes to use it. Thus
it has become a burden rather than a help and it would seem
advisable to drop it altogether. There is no more necessity for
it in the study of the reactions of lower organisms than there
is in the study of the higher forms, and in the study of these we
succeed very well without it. If "tropism" is to be used synonym-
ously with "orientation" or "reaction", — and these senses are the
only ones regarding which there is any considerable amount of
agreement — why not use in place of it these terms which have

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3) Warren (1914, p. 96) classifies reactions as follows: "tropisms, reflexes in-
stincts, intelligent action, and rational volition."

a fairly definite meaning? Thus in place of tropism we would have orientation or reaction, in place of positive or negative phototropism, geotropism, etc., we might use positive or negative orientation or reaction to light, gravity, etc.; and in place of positively or negatively phototropic, geotropic, etc., we might use photo-, geo-, negative or positive, etc., or merely negative or positive reaction to light, gravity, etc. These terms are purely descriptive, and there could be no confusion as to their meaning. Thus the controversy regarding the definition of "tropisms" would end and attention would be focussed on the various processes involved in orientation and reactions.

The desirability of this is made strikingly evident by the contents of a recent paper by Ewald (1913) referred to above. In this article Ewald, like Bancroft, throws to the wind most of Loeb's ideas regarding "tropisms". He says (p. 583), „Es ist ein Irrtum, wenn von verschiedenen Autoren die Tropismentheorie selbst mit den angeführten Argumenten Loeb's identifiziert wird." And, like Bancroft, he defines tropisms (p. 584) as compulsory orientation: „Tropismus ist (ohne Rücksicht auf den Mechanismus der Reaktion), der Ausdruck für eine zwangsweise Richtungsbewegung in bezug auf eine Energiequelle." He closes the article with the following startling statement (p. 597): „Nachdem kürzlich Bancroft auch die von Jennings und Mast auf Grund ihrer Versuche an *Euglena* erhobenen Einwände gegen die Tropismenlehre durch exaktere Experimente widerlegt hat, dürfte die Bahn nunmehr wieder auf einige Zeit für die rein experimentelle Arbeit frei sein."

Thus it is evident that Ewald holds that orientation due to a series of shock-reactions as described by us for *Euglena* opposes his tropism theory (compulsory orientation) for all that we have shown is that orientation in *Euglena* is due, at least at times, to shock-reactions. Bancroft, however holds that they are in full harmony with this theory. He says (p. 385), "Does *Euglena* become oriented to light as directly as its method of orientation admits; or does it orient indirectly, by the method of trial and error? In either case the reaction will be heliotropic, but the method of orientation will be different?" (Italics are mine).

If these two investigators, closely associated in the same laboratory as they were, differ so radically in the interpretation of their own definition of the term tropisms, what might be expected of others? Could anyone desire a more striking illustration of the futility of attempting under present conditions to convey by the use of this term, anything but the vaguest sort of an idea.

It may be said, however, if Ewald means by compulsory orientation merely that there are no psychic phenomena involved in

the process there is nothing in the writings of either Jennings on myself that in any way opposes his theory. As a matter of fact our work has no direct bearing on this question.

But the most surprising statement I have yet seen is that found in the quotation given above, in which Ewald implies that it was necessary to refute our conclusions in order to put the study of behavior on an experimental basis. Is it really possible for anyone at all familiar with the searching and ingenious experimental work of Jennings on behavior to hold such an opinion!

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Dysteleologen in der Natur.
(Zur Psychobiologie der Hummeln II.)[1]
Von Prof. Dr. H. v. Buttel-Reepen, Oldenburg i. Gr.

Die nachstehenden Ausführungen sollten im baldigen Anschluss
an die unten bezeichnete Veröffentlichung, die sich insonderheit
mit dem großen Werke Wladimir Wagner's (1907) über die
Hummeln beschäftigte, erfolgen. Sie liegen auch seit dem Jahre
1908 druckfertig da, aber die biologische Nachuntersuchung eines
besonderen Falles, die nicht gerade notwendig aber doch wünschens-
wert erschien, verzögerte die Herausgabe. Nun kann der Biologe
aber, sofern es sich um Beobachtungen in der freien Natur handelt,
die Tatsachen nicht zwingen. Es ist manchmal reine Glückssache,
ob es ihm gelingt, das Gewollte zu beobachten, und oft vergehen
Jahre geduldigen Wartens, ehe er zum Ziele gelangt. Eine neuer-
liche Durchsicht nachstehender Erörterungen zeigte mir aber, so
glaube ich, eine genügende Geschlossenheit der Beweisführung, so
dass sie hiermit unverändert erfolgen, zumal die gewünschte Be-
obachtung in genügender Weise inzwischen gemacht werden konnte.

Es lag mir vor allem auch daran, den Nachweis zu führen,
dass die *Apis mellifica* nicht unter die primären Dysteleologen zu
rechnen ist, wie das häufig geschieht. Meine Beobachtungen seit
1908 haben mich weiter in dieser Auffassung bestärkt.

Die wunderbaren Wechselbeziehungen zwischen Blumen und
Insekten, die uns eine erstaunliche Gesetzmäßigkeit enthüllen, haben
seit Sprengel's Zeiten eine große Anzahl von Beobachtern gefesselt
und die Tatsache, dass viele Blumen hinsichtlich der Befruchtung
auf Insekten mehr oder minder ausschließlich angewiesen sind,
steht gefestigt da.

Diese auch aus ästhetischen Gründen so überaus reizvollen, in
gesetzmäßigen Bahnen verlaufenden Beziehungen finden sich nun
in befremdender Weise durchbrochen. Diese „Ungesetzlichkeit",
die sich als eine Unzweckmäßigkeit ergibt, besteht darin, dass ge-
wisse Insekten, anstatt die Erlangung des Nektars auf dem gewöhn-
lichen Wege vorzunehmen und damit zugleich — durch Übertragung
des Pollens die Befruchtung zu erzielen, von außen in die Röhre
(Korolle) der Blumenkrone einbrechen und so den Nektar „stehlen",
ohne sich durch eine Gegenleistung erkenntlich gezeigt zu haben.

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1) Vgl. Biol. Centralbl. 27. Bd., Nr. 18 u. 19, 1907.