THE PROCESS OF ORIENTATION IN THE COLONIAL ORGANISM, GONIUM PECTORALE, AND A STUDY OF THE STRUCTURE AND FUNCTION OF THE EYE-SPOT

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SIX FIGURES

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1. INTRODUCTION

Among the most machine-like of the activities in organisms is the process of orientation. It is consequently not surprising that this process, which is common to so many different species, has received much attention in the investigations on behavior, with the result that a mass of highly interesting and important facts regarding it has been collected. These facts seem to show that the process of orientation differs fundamentally in different organisms and that it is far more complicated than has been assumed by some investigators, but that in general it facilitates the life processes in the individuals possessing it, and consequently tends to perpetuate the species. As to the reduction of the process to mechanical principles even in its simplest form, and as to its relation to conscious phenomena, little more can be said than that the field here is still wide open, although prospects are not altogether discouraging.

Among the questions associated with the process of orientation concerning which there is at present much contention is

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that referring to the nature of the orienting stimulus. Loeb and some of his followers hold that this stimulus is, in all organisms, animals as well as plants, dependent, in a specific way, upon the amount of stimulating energy received by the sensitive tissue, in accord with the Bunsen-Roscoe law. That is, that a given amount of stimulating energy (which is the product of the intensity of the agent and the time it acts) always produces the same effect no matter how these two factors may vary. Thus according to this idea a weak agent acting a long time should cause the same response as a strong one acting a short time.

This is one of the essential characteristics of a theory of orientation which will be referred to as the 'continuous-action' theory.

Darwin and others maintain that, in some cases at least, the orienting stimulus is dependent upon the time-rate of change of stimulating energy. That is, that if there is no change in such energy there will be no response, no matter how much energy may be received. Response in accord with this idea constitutes the most important feature of a theory of orientation which will be called the 'change-of-intensity' theory.

Our observations on the process of orientation in Gonium strongly support the latter theory. They also support the contention that the eye-spots function as direction eyes essentially as do the eyes in some of the flat-worms.

The reactions of the colonial organisms have not received much attention. Volvox is the only member of this group that has been extensively studied, and in this form only the responses to light have been thoroughly investigated (Mast '07). It will be expedient to present, in this connection, the essential features of these responses since we desire later to compare them with those observed in Gonium.

Volvox, like most of the simple green organisms, responds very definitely to light. It orients fairly accurately, and is usually positive in light of moderate intensity and negative in that of high intensity. Orientation is direct, that is, if the position of the source of light is changed after the colonies are oriented they always turn at once toward the light again (provided they are positive) never in the opposite direction, as frequently occurs in Euglena, Stentor and the like. The turning of the colonies is due to an increase in the effective stroke of the flagella on the shaded side. So much has been definitely established. As to the cause of the increase in the activity of the flagella on this side we are, however, not in a position to speak with so much assurance, but our evidence seems to indicate that it is dependent upon the time-rate of change of light intensity on the photosensitive tissue in the individual zoöids. Let us briefly consider this evidence.

During the process of locomotion the colonies continuously rotate on the longitudinal axis; consequently, when they are not oriented and opposite sides are unequally illuminated, the zoöids are continuously transferred from a region of higher to one of lower light intensity and vice versa. This results in a decrease of intensity on each zoöid, when it reaches the shaded side of the colony; but there is another factor involved in producing changes of intensity, in all probability of more significance than this. In unoriented colonies the zoöids are not only continuously subjected to a transfer from one intensity of light to another, but during the transfer different surfaces become exposed; for when they are on the more highly illuminated side of the colony the outer surface, and when they are on the opposite side the inner surface is directed toward the source of light. Since the zoöids contain numerous translucent and refractive bodies this change in the surface exposed necessarily results in numerous changes of intensity on the different parts of each zoöid. The eye-spots are the most prominent of the translucent bodies mentioned and they are consequently of greatest importance in producing changes of intensity within the zoöids. The orienting stimuli, in my opinion, depend upon the time-rate of change of intensity thus produced.

This opinion is strongly supported by the reactions to light observed in Gonium. These reactions are essentially like those in Volvox, but before describing them it will be necessary to refer briefly to the structure of the organisms under consideration.

2. STRUCTURE OF GONIUM

Gonium is a thin flat rectangular structure somewhat over 0.1 mm. wide. It consists of 16 cells or zoöids loosely united with protoplasmic strands which penetrate a gelatinous substance found in the intercellular spaces (fig. 1). Each zoöid contains among other things, a relatively large chloroplast, a prominent

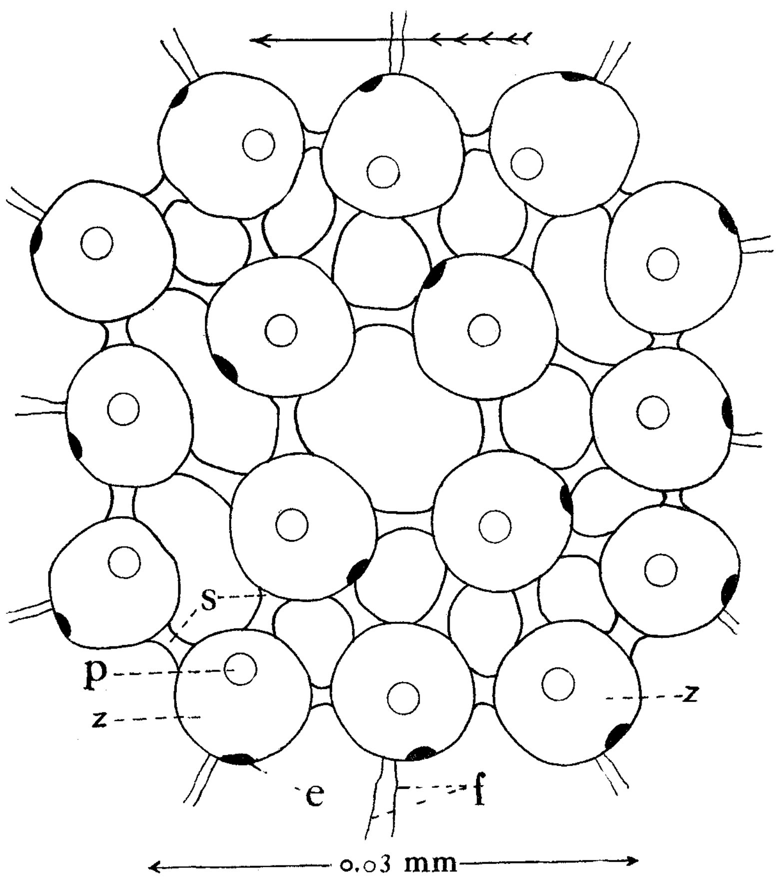

Fig. 1 Camera lucida drawing of Gonium as seen from the posterior surface. Each colony contains 16 zoöids, all situated in the same plane. *z*, zoöids; *e*, eye-spot; *p*, pyrinoid; *s*, strands connecting the zoöids; *f*, flagella; *mm*, projected scale. The arrow indicates the usual direction of rotation. The eye-spots are located at the outer surface near the anterior end of the zoöids. Note that they are a little to one side of the middle of this surface.

eye-spot and two flagella which are about as long as the colonies are wide (fig. 2). The zoöids are slightly elongated and so situated that the longitudinal axes of all are nearly parallel to each other and approximately perpendicular to the flat surfaces of the colonies. The flagella extend from the anterior surface of the colony and the eye-spots are located near their base on the outer surface of the zoöids near the anterior end.

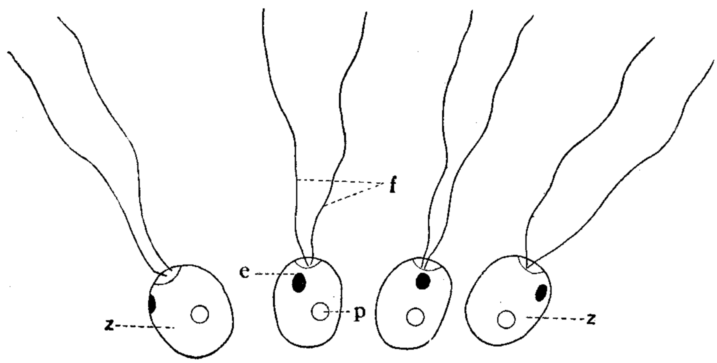

Fig. 2 Free hand sketch of Gonium as seen from one side. *z*, zoöids; *e*, eye-spot; *p*, pyrinoid; *f*, flagella. The eye-spots are situated on the outer surface of the zoöids near the anterior end. For details regarding the structure of the eye-spot, see figure 3.

3. STRUCTURE OF THE EYE-SPOT IN GONIUM, EUDORINA AND OTHER FORMS[1]

Ever since the days of Ehrenberg ('31) the eye-spots or stigmata, as they are frequently called, have been looked upon by many as the most primitive eyes. They have consequently been of great interest especially to those concerned with the evolution of the visual apparatus in the higher forms. They have been described in many different organisms by various investigators. Among these Franzé ('93) probably made the most extensive studies. He investigated them in 31 different species.

Practically all of those who have worked on the eye-spots maintain that they consist of two essentially different substances, a

[1] This section is the result of histological studies made by Caswell Grave. It is a pleasure to acknowledge my great indebtedness to him for his generous assistance.

hyaline substance, globular or lenticular in form and a brownish opaque substance frequently somewhat cup-shaped. The latter, it is held, usually surrounds the former more or less completely.

Thus it appears that these structures resemble, somewhat, the eyes in turbellaria, rotifera and copepoda, and this is largely responsible for the conclusion frequently stated that the former are homologous with the latter. Franzé ('93, p. 162), however, opposes this contention. He says: "Die Augen der Turbellarien und Rotatorien sind keine Homologa der Stigmata, sondern die äusserliche Ähnlichkeit beider Differenzirungen wird durch die gleichen Funktionen bedingt." He, in common with a large proportion of other investigators, holds that the eye-spots function as light recipient organs.

While much of the work on the structure of the stigmata has been thorough, it was our opinion that with the application of modern histological technic it might be possible to discover elements in them that would throw light on their nature and function. With this in view colonies of Gonium and Eudorina were fixed in Bouin's and Fleming's fluids. Some were embedded in paraffin and cut into sections 2μ and 3μ in thickness and stained with iron haematoxylin and safranin. Others were mounted whole, some stained and some not. These preparations were thoroughly studied with a combination of No. 6 Comp. ocular and 2 mm. Apoch. Homog. Immersion objective and briefly with more efficient combinations. It was found that the eye-spots both in Gonium and in Eudorina consist of two parts, an opaque cup-like structure and a lens shaped hyaline structure (figs. 3 and 4) but no further details could be seen in them although the best lens systems made were used. This, of course, does not prove that there is no finer structure present. It merely indicates that if there is, it is ultra microscopic.

By referring to figures 3 and 4 it will be seen that the eye-spots in Eudorina are considerably larger than those in Gonium. These figures indicate that they are situated at the surface of the zoöids with the hyaline portion outside. Careful observations seem to indicate that there is a thin protoplasmic layer, not represented in the figures, which is outside of this structure and extends entirely around the zoöid and is continuous with the strands which connect them with each other (fig. 1). This layer of substance is more distinct in living colonies than in sections. Thus it is highly probable that all of the eye-spots in a colony have protoplasmic interconnections.

Superficially these eye-spots are very much like the primitive eyes in turbellaria and Amphioxus as will readily be seen by comparing figures 3 and 4 with figures 5 a and b. In the latter the

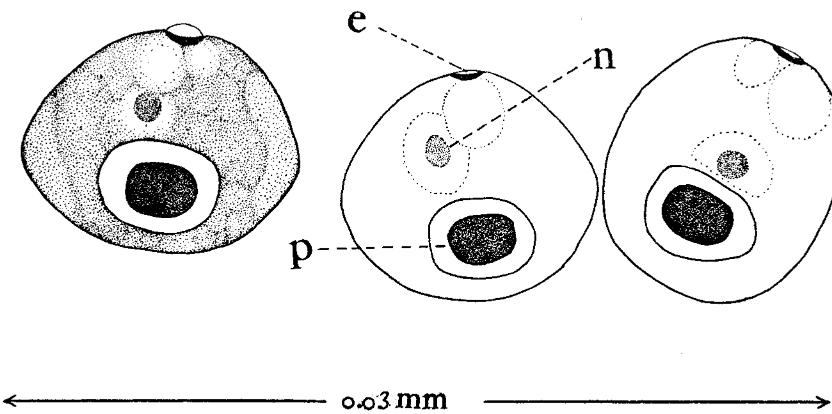

Fig. 3 Camera sketch of a section of Gonium taken perpendicular to the plane of the colony showing three zoöids. Sections 3μ thick. No. 6 compensating ocular and $\frac{1}{12}$ homo. oil immersion objective. Enlarged 4 diameters with pentograph. *e*, eye-spot; *p*, pyrinoid; *n*, nucleus; *mm*, projected scale. The eye-spot consists of an opaque saucer shaped structure and a hyaline lens-shaped body. It is less than 1μ in diameter. In the zoöid to the left the razor passed nearly through the middle of the eye-spot; in the other two zoöids it passed a little to one side of the middle, consequently the hyaline part appears relatively smaller in these. Drawn by Caswell Grave.

opaque part appears to function in restricting to certain areas, the field from which the sensitive hyaline position received light. Thus they seem to function as direction eyes. The eye-spots probably function in the same way. At any rate, these bodies in many species are so well differentiated and so similar in their structure and position in different individuals that they can not be looked upon merely as accumulation of waste products as is maintained by a considerable number of investigators.

4. PROCESS OF ORIENTATION IN GONIUM

The observations on orientation in Gonium were made in essentially the same way as those described in earlier works (Mast '11, pp. 92–96) it will consequently not be necessary to discuss methods here. The results of these observations follow:

Gonium swims in a fairly direct course with the flat surface perpendicular to the direction of motion. The surface with the

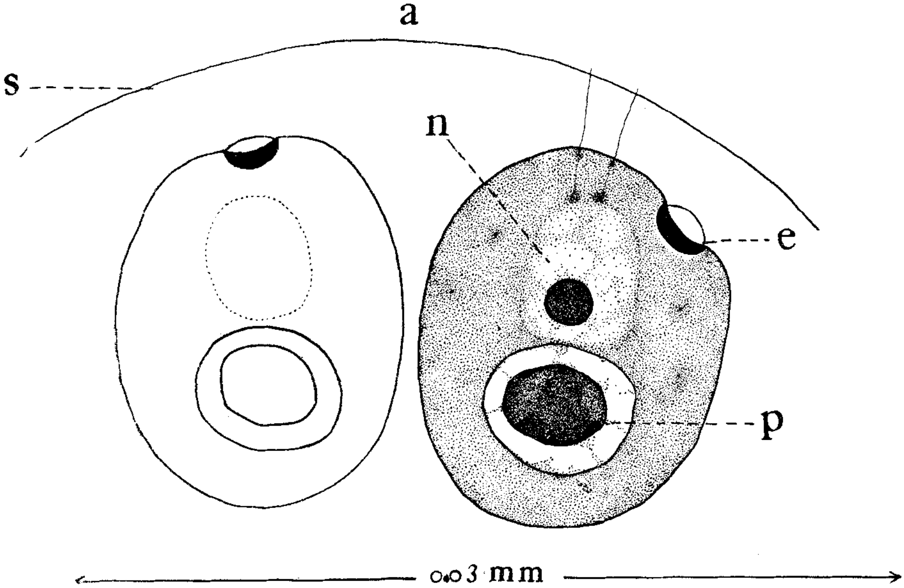

Fig. 4 Camera lucida sketch of a longitudinal section of Eudorina nearly through the middle showing two of the four anterior zoöids. No. 6 comp. ocular; $\frac{1}{12}$ homo. oil immersion objective. *a*, anterior end of colony; *s*, outer surface; *n*, nucleus; *p*, pyrinoid; *e*, eye-spot; *mm*, projected scale. The eye-spot in this form is essentially like that in Gonium but it is much larger and the two parts can be much more distinctly seen. The best lenses available fail, however, to reveal any differentiation in these two parts in either form. Drawn by Caswell Grave.

flagella is always ahead. As it proceeds it continuously rotates, usually counter-clock-wise as seen from the rear, although it reverses frequently and rotates in the opposite direction for short periods of time. It orients fairly accurately in light, being ordinarily positive in moderate and negative in strong illumination.

If the position of the source of light is changed after a colony is oriented so that the rays strike the anterior surface obliquely, it turns at once until the rays are again approximately perpendicular to this surface. The colony as a whole never turns in the wrong direction. Orientation is direct. The process is essentially the same as in Volvox. There is no indication of random movements or trial reactions in the colony as a whole.

The turning of the colony in the process of orientation is due to an increase in the activity of the flagellae of the zoöids farthest from the source of light. The following evidence indicates that

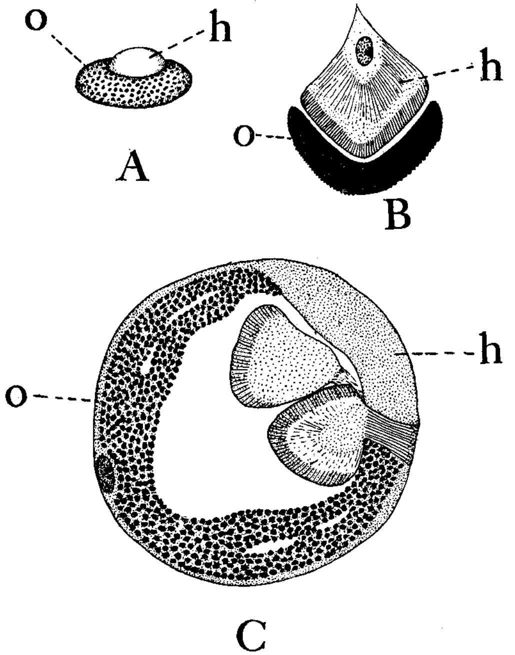

Fig. 5 *A*, sketch of the eye of the turbellarian, Ut. vulgaris prepared by crushing a living specimen. After Wilhelmi (Taf. 15, fig. 4).

B, Sketch of a cross-section of the eye of Amphioxus lanceolatus. After Hesse (Taf. 24, fig. 8).

C, Sketch of a cross-section of the eye of the turbellarian, Sabussowia diocia. After Böhmig (Taf. 12, fig. 15). It can readily be seen that in all of these animals the eyes consist of two essentially different parts, just as do the eye-spots in Gonium and Eudorina, but that there is considerable differentiation in each part in the former while in the latter there is none that can be seen.

this increase in activity is due to a reduction of light energy on the sensitive tissue in the zoöids and that it is dependent upon the time-rate of reduction, not upon the absolute amount of reduction.

If the light intensity in a beam in which positive colonies are oriented is suddenly decreased without in any way changing the direction of the rays, the rate of movement for a short period of time suddenly increases, but if the intensity is suddenly increased there is no response. In negative colonies, however, just the opposite is true. They respond in precisely the same way to a sudden increase but not to a sudden decrease of intensity. This response of the colonies is very striking. It gives one the impression of a very marked forward spring, and seems to be in all essentials like the shock-reactions in Euglena. And just as in Euglena it does not occur if the light-energy is gradually changed. Obviously then, this response is dependent upon the time-rate of change of energy and not upon the absolute change.

The increase in activity in the zoöids farthest from the source of light, during the process of orientation, appears to be of precisely the same nature as the increase in activity of all the zoöids, due to a sudden decrease of the light-intensity in the entire field; consequently it would seem reasonable to conclude that it also is due to a sudden decrease of intensity on the sensitive tissue in the zoöids involved. How can this occur?

In unoriented colonies the light strikes the anterior face obliquely (fig. 6), and as these colonies rotate it is evident, just as in Volvox, that in each zoöid the surface exposed to the light continuously changes. This necessarily causes changes of intensity owing to the movement of the shadows cast by the translucent bodies in the zoöids, particularly the opaque portion of the eye-spots. By referring to figure 6 it will be seen that in the zoöids on the side of the colony nearest the sources of light the hyaline portion of the eye-spot is fully exposed, while in those on the opposite side this structure is shaded by the opaque portion. There is consequently a great reduction in the intensity of the light on it as the zoöids, owing to the rotation of the colony, are transferred from the former to the latter position and an equally great increase as they are brought back to the original position again. If, then, the photo-sensitive tissue is largely confined to this hyaline substance as it seems to be in Euglena, we should

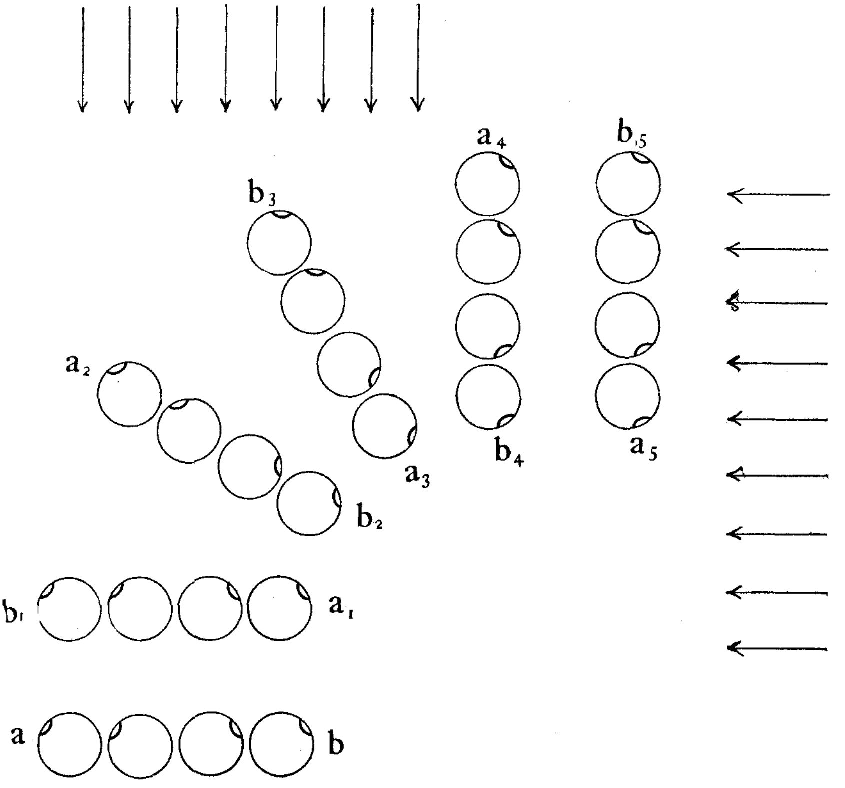

Fig. 6 Diagrammatic sketch representing the process of orientation in a colony of Gonium as seen from the side. Each circle represents a zoöid; the small arcs represent the eye-spots, the arrows the direction of the rays of light, and *a*-*b*, a_1-b_1, a_2-b_2, etc., different positions assumed by the colony during the process of orientation. Only 4 of the 16 zoöids in the colony are shown. The colony rotates on its anterio-posterior axis as it proceeds. This causes the hyaline portion of the eye-spot to become alternately fully exposed to the light and shaded. The turning of the colony is due to an increase in activity of the zoöids as they are transferred to a position in which the hyaline part of the eye-spots is shaded, that is, the positions represented by a, b_1, a_2, b_3, etc. The hyaline part is probably highly sensitive to light, and the increase in activity mentioned is probably dependent upon the time-rate of reduction in illumination on this part.

expect in positive specimens a shock-reaction in the zoöids on the side of the colony farthest from the source of light, owing to the shading of this substance, but none on the opposite side where this substance becomes exposed to the light. This is precisely what is observed in the process of orientation. In colonies in the negative state, on the other hand, we should expect just the reverse and this is also in accord with our observations. Moreover, as the colony turns toward the light the change of intensity on the hyaline portion of the eye-spot becomes gradually less and when it has turned enough so that it directly faces the light, that is, when it is oriented, there is no longer any change, and consequently on the basis of our assumption no more shock-reactions and no further turning would be expected. This is again in accord with our observations. If, then, the photo-sensitive substance is confined to the hyaline portion of the eye-spot, or largely so, and if the orienting stimulus is dependent upon the time-rate of change of light-intensity on this substance, we can account for the observed reactions in the process of orientation, in Gonium, and this is in full accord with our explanation of orientation in Stentor, Euglena, and a number of other organisms (Mast, '11, pp. 80–135). Moreover, if our assumptions are correct, it is no longer necessary to hold, as in earlier publications (Mast, '11, p. 133), that the function of the eye-spot is not the same in all organisms. But how on the basis of these assumptions is it possible to explain the fact that after the colony is oriented it continues in a fairly direct course toward the light?

This question has already been answered, in part, in the statement that after the colonies are oriented changes of light intensity on the hyaline substance in the eye-spots cease, and consequently, if our explanation of orientation holds, no further turning would be expected, and the colonies should therefore remain oriented, unless some factors other than the light in which they are oriented cause them to turn. And if this should occur the orienting stimulus would, in accord with our explanation, again act, and result in reorientation. This explanation is based upon the well known principle that organisms not subjected to lateral stimulation tend to move in direct paths. To account for continued orientation; it is consequently not necessary to assume that the orienting stimulus continues to act after orientation as well as during the process of orientation, as is demanded by the continuous-action theory. Organisms are partially isolated dynamic systems and much that they do is dependent upon changes within, quite independent of immediate environmental factors.

5. DISCUSSION

We have in this and in previous publications presented a considerable amount of evidence in favor of the change-of-intensity theory of orientation. Let us now briefly consider the evidence that favors the continuous-action theory.

In the reactions of the unicellular and the colonial forms very little has been discovered that supports this theory. In fact practically all of the favorable evidence is found in Bancroft's work on Euglena ('13). Bancroft maintains that he has demonstrated that in this form orientation occurs in accord with Loeb's continuous-action theory; at any rate that the change-of-intensity theory does not hold. I need not here enter upon a discussion of Bancroft's interesting observations, for I have elsewhere shown ('14) that his results must be confirmed under conditions more thoroughly controlled before much dependence can be placed upon them and that if his contentions are valid they actually oppose the theory that he substitutes for the one he claims to have overthrown; that is, they oppose the continuous-action theory.

Thus we see that the evidence in support of the continuous-action theory found in the reactions of the forms mentioned is exceedingly weak. In the reactions of some of the more complex organisms there is, however, some evidence indicating that this theory holds at least in part. Blaauw ('08), Fröschel ('08 and '10), Arisz ('11), and Clark ('13) have demonstrated that photic orientations, in a number of different seedlings, is within certain limits, dependent upon the amount of light energy received; that is, that long exposure in weak light produces the same effect as short exposure in strong light. Mast ('11, p. 163) reached conclusions regarding the orientation of Eudendrium which are in harmony with the work just mentioned, and Loeb and Ewald ('14) support these conclusions. Ewald ('14) also maintains that certain responses in Daphnia are proportional to the amount of stimulating energy; at any rate that they are not dependent upon the time-rate-of-change of such energy. Patten ('14) comes to the same conclusion regarding orientation in blow-fly larvae. He says (p. 272): "Orientation in the blow-fly larva depends to a large extent on the stimulating effect of constant intensity. The reaction to light of constant intensity follows the Bunsen-Roscoe law."

Both Ewald and Patten base their conclusions upon the fact that the reactions observed at the intersection of two beams of light were the same when the light in one beam was intermittent, as they were when it was constant in both, provided the relative amount of energy in the two beams was the same under both conditions, and provided that the intermission was relatively frequent and continuous.

It seems to me that these results do not show that the reactions referred to in Daphnia and the process of orientation in the blow-fly larvae are necessarily dependent upon the continuous action of the light as maintained by Ewald and Patten. All that they actually demonstrate is that if the intermission is of sufficient frequency, periodic illumination acts the same as continuous illumination. This is true for the human eye and yet no one holds that this in itself precludes the possibility that stimulation is dependent upon time-rate of change of energy. Moreover, Patten in his work on the fly larvae did not eliminate changes of intensity on the sensitive tissues in the larvae due to the alternate extension and retraction of the anterior end, consequently the reactions observed in the process of orientation in these animals may have been due to these changes without reference to the amount of light energy received.

Patten's conclusion (p. 272) that "orientation to light from two source depends on the relative amount of stimulation received by symmetrically located sensitive areas" is equally precarious. As a matter of fact, all of the responses which he maintains favor this conclusion could be accounted for on the basis of the change-of-intensity theory, even if the photo-sensitive tissue were confined to a single median spot such that there could be no balancing of effects on symmetrically located tissues.

This author, moreover, comes to another conclusion that seems to be supported by neither logic nor fact. He says (p. 271): "Bancroft's ('13) work, in which he showed not only that there was a distinct reaction to constant intensity present in Euglena but that it was largely the reaction to constant intensity which determined its orientation, shows the untenability of Mast's sweeping statement in one of the forms on which Mast himself worked." What is this sweeping statement? Our author quotes it as follows (p. 270):

> Mast ('11, p. 234) says: There is no conclusive evidence, except perhaps in animals with image forming eyes, showing that light acts continuously as a directive stimulus, that symmetrically located sides are continuously stimulated . . . . (p. 235). Light no doubt acts on organisms without a change of intensity much as constant temperature does, making them more or less active and inducing changes in the sense of orientation; but there is no conclusive evidence showing that light acting thus ever functions in the process of orientation.

Is it not perfectly obvious that the results of Bancroft's investigations presented in 1913, assuming that they are as quoted above, do not have the slightest bearing on the validity of this statement, made in 1911? Does the discovery of a certain response at a given time make untenable the statement that it had not previously been discovered?

Whatever the final conclusion may be regarding the two theories of orientation in question the fact that many reactions in animate systems depend upon the time-rate-of-change of stimulating energy is well established. These reactions are of great interest, partly because they are exceedingly rare in inanimate systems, and a thorough study of them cannot fail to yield interesting results.

6. SUMMARY

1) The eye-spots in both Gonium and Eudorina consist of an opaque cup-shaped part and a hyaline lens-shaped part. The latter is partially surrounded by the former and it is probably relatively very sensitive to changes in light-intensity. These changes are probably largely due to shadows produced by the opaque part.

2) Orientation in Gonium is direct. The colonies never turn in the wrong direction, as often occurs in Euglena, Stentor, and many other forms. The turning which results in orientation is due to an increase in the activity of the flagella on the zoöids farthest from the sources of light. In these zoöids the hyaline part of the eye-spot is shaded by the opaque part at the time the activity of the flagella increases.

3) If the light-intensity of the field is suddenly decreased, the rate of locomotion, in positive colonies, suddenly increases. But if it is slowly decreased or if it is increased there is no response. In negative colonies, however, just the reverse is true. They respond to a sudden increase in rate of locomotion if the illumination is decreased but not if it is increased.

4) The increase in the activity of the zoöids on one side of the colony during the process of orientation is apparently of the same nature as the increase in the activity of the whole colony when the illumination is changed. This indicates that orientation in these organisms is dependent upon the time-rate of change of light energy on the photo-sensitive substance, probably the hyaline portion of the eye-spots, and not upon the absolute change or the continuous-action of light.

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