CONCERNING THE BEHAVIOR OF GONIONEMUS.

BY

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The courtesy of Mr. MORSE in calling my attention to the results of his study of the reactions of *Gonionemus* and in discussing them with me before their publication has made possible the following prompt explanation, on my part, of the apparent differences in our results.

Since Mr. MORSE told me of the results of his study of the reactions of *Gonionemus* to light I have repeated certain of my earlier experiments and made such additional observations concerning the influence of light as the scarcity of material at the time permitted. I wish now to present the results of my recent experiments, in connection with my reply to the criticisms of my work.

As appears from Mr. MORSE's paper,¹ we disagree concerning the following five points:

1. That light is an important factor in the determination of the inversion of the bell when the medusa reaches the surface of the water.
2. That there is at times a temporary gathering in the brighter region when the medusæ are exposed to intense light in a vessel of which one portion is shaded.
3. That sudden decrease in the intensity of illumination temporarily inhibits the movement of an active individual.
4. That intense light may determine the direction of movement.
5. That the influence of light on active individuals is different from its influence on resting individuals.

Mr. MORSE has contradicted all of the above statements of my papers.

¹MORSE. Notes on the Behavior of *Gonionemus*. *Jour. Comp. Neural. Psychol.*, Vol. 16, No. 6, p. 452. 1906.

First, as to the cause of the surface reaction of *Gonionemus*, Mr. MORSE states, incorrectly, that I believe the reaction to be due to light. As a matter of fact, I have said, and have attempted to show that, although light seems to be one of the important conditions for this reaction, it may occur in the absence of light. My view concerning the reaction, together with one of my chief grounds for holding the view, are expressed in the following quotation from one of my papers: "In sunlight the medusæ at first come so forcibly to the surface that half the bell may appear above the water. Usually a bell thus forced out of the water inclines slightly to one side, and thus tends to turn the animal over, so that the observer can never be quite sure whether the turning is due altogether to the action of gravity, or whether it is in part due to some peculiarity in the final contraction of the bell. After having been in sunlight for a few minutes, the animals come to the surface with noticeably less impetus, and soon they fail to reach the surface at all. But even in the latter case they turn over, just as they do in ordinary light after reaching the surface. Under these conditions the turning due to stimulation by light evidently is accomplished by bell contractions."¹ And I further add, in an attempt to account for the inhibitory influence of light, "Light having been one of the most important stimuli for the initiating of the surface reaction; i.e., turning, inhibition of activity, expansion of organs, may finally have come to be the cause of a very similar reaction in the presence of other conditions, so that increase in light intensity now uniformly causes an active *Gonionemus* to expand fully for a few seconds and permit itself to sink passively."²

As Mr. MORSE, without contradicting any of my statements of fact and without offering further facts or suggesting an explanation of the surface reaction of *Gonionemus*, simply questions the correctness of the partial account of the phenomenon which I have given, I can not do otherwise than hold to my earlier view of the matter.

On p. 3 of Mr. MORSE's paper attention is called to certain "paradoxical facts" in my work which demand further investigation. These facts, or better statements, are numbers 2 to 5 of the above list of points in which Mr. MORSE disagrees with me. The

¹*Amer. Jour. Physiol.*, Vol. 9, p. 285, 1903.

²*Amer. Jour. Physiol.*, Vol. 9, p. 288.

first of these apparently paradoxical statements made by me is that, the medusæ under certain conditions at first gather in a region of bright illumination and later come to rest in a shaded region. In his experiments, Mr. MORSE did not observe "a collection of the medusæ in the illuminated portion of the vessel."¹ As I was utterly unable to account for the disagreement in our results I at once repeated my former experiments. Eleven medusæ were placed in a white earthenware dish such as AYER and I used in our experiments with *Gonionemus*. The dish was illuminated by direct sunlight from a southeast window. All of the animals at once began to swim about actively, mostly, however, keeping close to the bottom of the dish as if seeking to move away from the light. After a few seconds one-half of the dish was covered with a piece of black cardboard. Within a minute, ten of the eleven medusæ were in the sunlit portion of the dish, and there they remained for about two and a half minutes, swimming about actively but without moving far in any direction. Then, as quickly as they had gathered in the sunlit portion, they moved to the shaded portion, and in less than a minute all but two were in the shade of the cardboard.

There is no doubt in my mind that the behavior just described is due to a complex of stimuli and internal states of which light, temperature and the condition of the organism are of prime importance. I have always suspected that the temporary gathering of the medusæ in bright light which I have repeatedly observed is due rather to the strong stimulating power of the light than to any definite directive influence. The matter deserves further attention, for AYER and I have done little more than call attention to the fact.

The second paradox appears in my statement that "when an individual, in swimming about, chances to cross from the sunlit region into the shadow, it very quickly ceases swimming and sinks to the bottom. If, later, in swimming about it chances to cross from the shaded region into the sunlight, it in most cases immediately ceases swimming, turns over, and sinks passively to the bottom."²

Perhaps the contrast between "very quickly" and "immediately" in the above description was not sharp enough. At any

¹*Journ. Comp. Neurol. Psychol.*, Vol. 16. 1906.

²*Amer. Jour. Physiol.*, Vol. 9, p. 282. 1903.

rate, Mr. MORSE noted no definite reaction as the medusa passed from light to shadow, but instead merely a gradual cessation of activity due, as he believes, to the absence of stimulation.

I am compelled to disagree with the view that decrease in the intensity of light means absence of stimulation. I have already shown that a rather sudden increase in the intensity of light inhibits the movement of an active *Gonionemus*, in most cases, whereas a considerable decrease causes a more gradual cessation of activity, and I have abundant evidence that change in the intensity of light stimulates the medusa. Whether this change be increase or decrease in intensity, it may either augment or inhibit the activity of a moving individual and it may or it may not bring a resting individual into movement.

According to Mr. MORSE, the third paradoxical statement in my papers is that "the reaction to sunlight is a direct response whereby the medusa turns directly toward the shadow and swims into it."¹ I have never made any such statement, I believe, and I agree with Mr. MORSE that it is false. What I have said is, not that the medusa swims toward the shadow, but instead that, "when it chances to cross from the shaded region into the sunlight, it in most cases immediately ceases swimming, turns over and sinks passively to the bottom. But in this case when it again becomes active, it does not move indifferently in any direction as it does when in the shadow; instead it usually turns in such a way as to move back into the shaded region."² This is precisely what I said and what I meant; I repeat the statement in the light of further observations made during September, 1906.

Mr. MORSE's criticisms have served the good purpose of revealing to me an important omission in the description of the conditions under which Mr. AYER and I observed the behavior described below. We omitted to state that the direct sunlight by which the earthenware dish was illuminated came from a south-east window and was not exactly perpendicular to the surface of the water and the bottom of the dish. From our description, one is led to infer that the line between light and shadow was perpendicular to the bottom of the dish, whereas it inclined slightly toward the shaded region. In the figure given in our paper³ to

¹*Jour. Comp. Neurol. Psychol.*, Vol. 16, P. 452. 1906.

²*Amer. Jour. Physiol.*, Vol. 9, p. 282. 1903.

³*Ibid.*

represent the reaction of the medusa at the transition line between light and shadow the dotted line should incline slightly toward the shaded end of the dish, for the black card which covered the right end of the dish permitted the sunlight to illuminate a larger area at the surface of the water than at the bottom. As a consequence of this condition a *Gonionemus* when it reacted to the sunlight, as it passed into it, by ceasing to swim, turning over and sinking passively, usually came to rest on the bottom of the dish, unless it resumed its swimming before reaching the bottom, partly in the sunlight and partly in the shaded region. In this position it was unequally stimulated on opposite sides, and as a result the bell contracted in such a manner as to turn the animal toward the shaded region.

In my repetition of this experiment the importance of this marked inequality of illumination has been demonstrated for I found that when the animals swam so far into the sunlit region before turning over that they were entirely in the sunlight when they came to rest on the bottom of the dish, they moved away from the region of shadow about as often as toward it. When they came to rest with a part of the body in the shadow they turned back toward the shaded region in about 70 per cent of the cases. With one group of animals there were forty-four movements toward the shade to twenty away.

The effect of suddenly increasing the illumination of a portion of the bell by allowing sunlight to fall upon it was noted. The result apparently depends upon the intensity of light to which the organism happens to be adapted at the moment of the experiment. If it has been in weak light, the brilliant illumination of one side of the bell in more than two cases out of three, according to my recent observations, brings about movement toward the region of lower illumination. Lack of material compelled me to leave this work uncompleted, but in reply to Mr. MORSE I may say that my experiments indicate that *Gonionemus* turns from the region of strong stimulation in as definite a manner as the structure of the organism and method of locomotion permit in the cases of all stimuli which are injurious. Light is not an exception to this rule, nor have I discovered any, although I do not doubt that some such exist.

While repeating my experiments I noticed for the first time another form of local reaction to light. A medusa partly in sunlight and partly in shadow was drawn from the light into the

shadow by the contraction of the tentacles on the portion of the organism which was in the shadow. The effect was a sort of crawling movement. This reaction I saw only three times.

The reasons for certain of the apparent disagreements in the results of Mr. MORSE's experiments and my own are my failure to state that the sunlight was not perpendicular to the bottom of the dish, and his failure to take note of the exact form of my statement of results. With the light perpendicular to the bottom of the vessel I obtained the same results as Mr. MORSE. There was no evidence of the directive influence of light. There is a flat contradiction in our statements, however, so far as the reaction to oblique light is concerned. Possibly this would disappear if the meaning of the term were more fully explained in Mr. MORSE's paper.

Of the fourth paradoxical fact to which attention is called at the beginning of Mr. MORSE's paper—namely, that the reactions of active medusæ when stimulated by light are different from those of resting individuals under the same conditions of stimulation—I find no further mention. Possibly it was his intention to dispute the statement on the basis of the other facts to which he had called attention. I am unable to see anything paradoxical in the statement that the effect of light depends upon the physiological condition of the organism. It would be strange indeed if the active and the quiescent medusa reacted to light in the same manner.

Finally, Mr. MORSE concludes from the results of his study of *Gonionemus* that the behavior of this organism conforms to the theory of trial and error rather than to the theory of the tropisms proposed by VERWORN and LOEB. While partially agreeing with him in this, I still hold that several of the reactions which I have described are in part determined as to the direction of movement by the quality, intensity and location of the stimulus and therefore conform to the theory of the tropisms formulated by LOEB. There is more or less trial in all the reactions of *Gonionemus*, but I fail to see why trial and error and local action should be mutually exclusive. It seems to me that VERWORN and LOEB, in connection with the tropism explanation of certain reactions, have laid emphasis upon the definiteness and uniformity of reactions, while JENNINGS, HOLMES and others have laid all stress upon the variability, complexity and modifiability of the same reactions. Both points of view are important, but they supplement rather than

destroy one another. When *Gonionemus* in swimming from a low intensity of light into a high intensity responds to the sudden increase of light by turning over and sinking to the bottom, its reactions conform to the local action tropism theory in that stronger stimulation of the bell on one side than on the other, causes that side to contract in such a manner as to turn the bell away from the strongly stimulated side. If the organism happens to make a complete circle because of the force of contraction of the stimulated side of the bell, and this often occurs, it is brought into the strong light again and the same reaction may be repeated, with some variation perhaps. Unless this directive influence of the unequal contraction soon brings the medusa into the weak light, other forms of reaction inevitably appear, for the relation of the animal to the stimulus has changed because of the continued action of the light. Is this a series of trial and error reactions or is it merely an instance of the complex relations of local action and the various forms of reaction exhibited by *Gonionemus*? I should say that it is trial and error only from a superficial view, for analysis of the conditions of reaction indicates that local action determines the direction of the medusa's movement in a pronounced way when certain rather unusual conditions exist. Change the conditions—even the repetition of a given photic stimulus may meet with a form of reaction markedly different from the directed movement due to the local action effect of the original stimulus because of the changes in the physiological condition of the organism—and a new form of reaction appears.

At the earliest possible date I shall undertake a thorough study of the light reactions of *Gonionemus* in their relations to other external conditions, as well as to the physiological states of the organism.

Woods Hole, Mass.

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