

## EXPERIMENTS ON THE BEHAVIOR OF TUBICOLOUS ANNELIDS

BY

CHAS. W. HARGITT

WITH THREE FIGURES.

During the past summer it came in my way to collect numerous colonies of the serpulid annelid, *Hydroides dianthus*, which is very abundant in the waters about Woods Hole. Finding them to be well adapted to aquarium life I kept colonies under observations upon my laboratory table during almost the entire summer, and made such experiments and observations on their reactions and various forms of behavior as suggested themselves from time to time.

In connection with the observations upon *Hydroides*, at the suggestion of Dr. J. P. Moore, I also included species of *Potamilla* and *Sabella*, though they were very much less numerous than the former species. I am under obligations to Dr. Moore for identifying the several species.

As is well known, many of these annelids are remarkably sensitive to the slightest disturbances of various sorts, such as vibrations, the intervention of shadows, etc. In connection with interesting observations concerning the habits of various tubicolous worms Dalyell,<sup>1</sup> remarked concerning *Amphitrite bombyx* that "it is impatient of light," withdrawing into its tube instantly upon the interception of the light.

<sup>1</sup>The Powers of the Creator Revealed. London, 1853. Quoted from *Andrews' Jour Morph.*, vol. v, p. 287.

Claparède,<sup>1</sup> has also called attention to a similar feature in *Branchiommæ köllikeri*, stating that "it is very sensitive to changes in the amount of illumination, for a slight movement of the hand at a distance of a meter from the aquarium, causes all the animals to withdraw into their tubes as soon as the shadow falls upon them. Yet *Sabellas*, having no eyes, remained immobile and unaffected."

It will be seen from some of the following observations that the reference to *Sabella* is more or less incorrect, since our species of *Sabella*, at least, are quite well provided with eyes, and are also subject to the same stimuli as are others, differing only in degree.

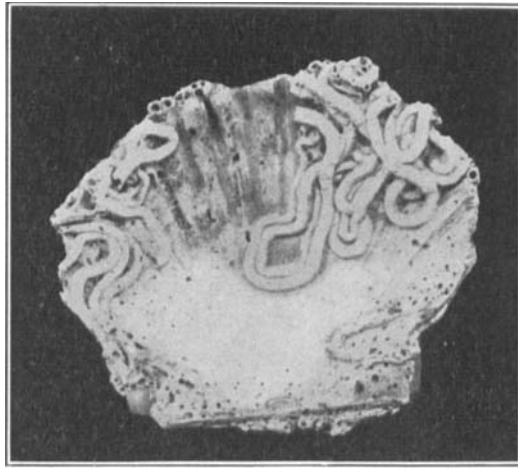


Fig. 1. Several individual tubes of *Hydroides dianthus*, showing general aspects when growing freely upon shells or similar substratum. (Somewhat less than natural size.)

Similar observations have been made also by Darwin<sup>2</sup> and others upon earthworms, the significance of which is probably of the same general character as the former. Still later observations upon species of *Tubicolidæ* have been made by Andrews, Loeb, Nagel, and others, which will be considered in detail in a later connection.

<sup>1</sup>*Annelides Chetopodes du Golfes de Naples*, 1868. Quoted from Andrews *Jour Morph.*, vol. v, p. 287.

<sup>2</sup>*The Formation of Vegetable Mould through the Actions of Worms*. 1881.

My observations extended to the following named species: *Hydroides dianthus*, *Potamilla oculifera*, and *Sabella microphthalmia*, chiefly the first. These were available in considerable numbers, and collected from various shells about the docks of the United States Fish Commission, from shells, various bivalves, *Venus*, *Pecten*, etc., from rocks dredged from depths varying from two or three fathoms to fifteen to twenty in Vineyard Sound and Buzzards Bay. The other species were obtained in part from among colonies of *Cynthia* collected from the docks, and in part among colonies of *Hydroides*. Their numbers were smaller than those of *Hydroides* and the observations correspondingly

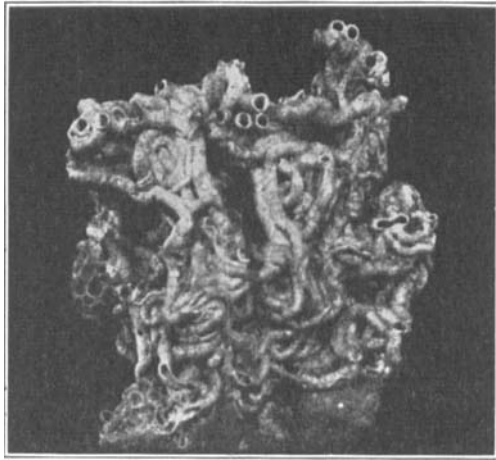


Fig. 2. Colony of *Hydroides dianthus* growing in complex mass from flat rock base. The various aspects of the mouth of the tubes may be easily distinguished, showing vertical, lateral and downward relations referred to in the paper. (Somewhat less than natural size.)

less extended. As will be observed in a later connection the limitations of experiments on species of *Potamilla* and *Sabella* were due in part to their comparative indifference to the various tests applied.

#### EXPERIMENTS ON *HYDROIDES DIANTHUS*

The general character of these annelids is so well known that no particular account is necessary. The photographs of several typi-

cal conditions will show quite enough to make clear the habitat and modes of growth. Colonies growing upon shells are seldom large, while those growing upon rocks are frequently quite large, often including from thirty to fifty, or even more, distinct specimens, each inhabiting its own tube, but forming inextricable masses variously intertwined, and among which are usually various other annelids, corals, hydroids, etc., the whole comprising a most interesting ecological community, as well as a most beautiful display of richly varied form and color, rarely surpassed among the almost infinite variety of marine life. It may be noted in passing that most of this richness and variety of coloration is to be found in the

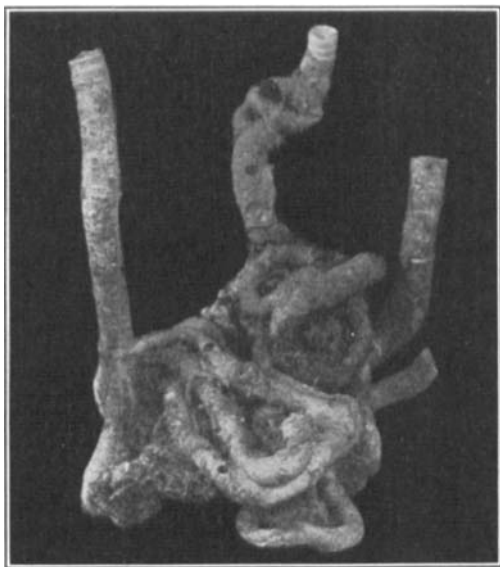


Fig. 3. Colony of *Protula intestinum*, from Bay of Naples. The serpentine aspects of the tubes referred to in the paper are easily recognized. The coiled tubes to be seen upon the central tube of the colony is particularly interesting as clearly indicating the indifference of the creature to the influence of gravity. (Somewhat less than the natural size.)

annelids themselves, a fact which has been long known and commented upon, but little understood. This feature will be further considered in connection with the several accounts in which it may be involved.

Though I had often observed the general sensitiveness of these creatures to sudden intervention of shadows of various sorts, my attention was particularly attracted to the matter in the present instance by the observation that shadows of even the slightest degree, such as those produced by a strip of white paper, or even a glass rod, seemed quite as effective a stimulus as those produced by the hand or other opaque screen. And this was the more noticeable in that the specimens were before a north window, and thus in diffused light.

Having determined upon a series of observations and experiments, the colonies were arranged in several aquaria, certain of which were placed upon a table before a window facing south, the others upon a table facing northwest, the latter also in such a position that a sixteen candle-power incandescent lamp was available for certain experiments at night.

#### *First Series*

The first series of experiments was made to determine exactly the character of the stimulus to which the reactions of the worms were due; that is, whether they were the result of differences of the intensity of light, or whether to the suddenness of the stimulus, or the apparently negative effects of shadow stimulus. Loeb ('93) had pointed out, in a simple experiment made by opening and closing the shutter of a window before which specimens of *Hydroides uncinata* were living in an aquarium, that "only the decrease in the intensity of light acts as a stimulus upon the animals."

This experiment I repeated many times and under variously modified conditions. The general fact that only the decrease of light, or in other words the shadow, is effective was abundantly confirmed. Drawing the shade before the window, interposing the hand or a sheet of paper, always sufficed to insure the prompt retraction of the animals. Now by continuing the presence of the shadow, the worms extended themselves quite as before. When thus extended the curtain, or other intervening object, may be removed, allowing the increase of light to its former intensity.

This was variously done, in the case of the curtain, vertically; in the case of the hand, screen or cardboard, etc., by either lateral, downward, or vertical withdrawal; but in every case the added increment of light produced no effect whatsoever upon the behavior of the animals.

The experiment was further varied by employing artificial light, an incandescent electric light of sixteen candle-power, hung just over the table upon which the aquarium was placed. Allowing the specimens to become fully extended, which was quite as common by night as by day, in darkness as in light, the light was suddenly flashed directly in their faces, so to speak, but in no case was there evidence of any specific reaction. On the other hand, the sudden extinction of the light almost always gave the same response as the shadow, as could be seen by immediately turning on the light again.

Again the experiment was made in bright sunlight. Allowing the specimens to fully expand under an appropriate screen they were then subjected to the sudden increment of full sunlight but without the slightest reaction. This was varied by covering the aquarium with a dark box; leaving them in total darkness until fully expanded, then quickly removing the box and allowing the full sunlight to fall directly upon them gave the same negative result as in the former.

There can be no doubt, therefore, that the reaction is not due to simply a difference of light-intensity alone. For whether in diffused or direct sunlight, whether in natural or artificial light, the response is to the shadow, sudden diminution of light, a purely negative condition. But it may well be doubted whether this can be properly designated as simply negative phototropism or heliotropism. The phenomena are much too complex to be explained by any single factor. Details on this point will be taken up in a later connection, however.

The experiments were varied by interposing the screens at a distance of from a very few inches, perhaps two or three, to five, ten, fifteen, twenty, etc., up to forty or fifty, but without materially affecting the results. In the diffused light before a north window the shadows from the greater distances were not always equally

effective, but before a south window when the light was bright, even though diffused, the results were as certain and effective as at the shorter distances. No attempt was made to determine the limits beyond which the shadows might become too indefinite to act as a stimulus.

Furthermore, the experiments were still varied by varying the *time* or *rate* of the shadow movements. It was found that ordinarily little difference could be detected as to the reactions under a swift and a slow motion as ordinarily made by the movement of the hand. But if pains were taken to insure a very rapid movement, as by propelling an object before the aquarium by mechanical means, such as a spring, it was possible to pass the shadow of a small object before the specimens without producing sufficient effect to act as a stimulus. Likewise it was possible to interpose a screen by such very slow degrees as to avoid any direct reaction on the part of the specimens.

Another experiment was tried to test the effects of a constantly recurring, or rhythmic shadow. This was effected by arranging a pendulum so adjustable as to secure a rhythm of from about a quarter of a second to a full second. With the full second movement there was more or less constant reaction with each passing shadow. With the half second movement it was found that, after the first few beats, a considerable portion of the worms failed to respond at all; and with the quarter second beats almost all the colonies became indifferent to the presence of the passing shadows.

These results are extremely interesting as indicating the possible relations of the reactions to protective or adaptive ends. May it not be possible that in these rhythmic shadows we have a simulation of the more or less rhythmic shadows resulting from the ripples or wave action, which are phenomena of more or less constancy and of course affecting in much the same way specimens living in the shallower waters?

In connection with this matter of rhythmic shadows it was observed that where experiments were repeated with any considerable frequency specimens sooner or later became somewhat irresponsive, often failing entirely to react to any of the usual tests.

This I am inclined to regard as the result of fatigue. But it may naturally be asked if this might not be equally well explained as the result of a condition similar to that induced by the rhythm just considered?

That it is a matter of fatigue, or a closely related phenomenon, rather than the latter, seems to me strongly indicated by the fact that it results from any form of shadow stimulus which may be applied, such as a vertical or lateral; slow or rapid; made by the hand, by a small rod or broad screen; in short, by any or all of the various tests applied successively or in any order whatsoever. These tests applied singly and at irregular intervals rarely failed to produce the appropriate reaction. It was only when repeated at such rapidly recurring intervals as to leave insufficient time for readjustment that the animals gradually became irregular and indefinite in their behavior. At almost every point the results simulated so intimately the fatigue phenomena of higher organisms as to leave a very strong impression of its similarity, or even identity, differing, if at all, chiefly in degree rather than in character.

### *Second Series*

The second series of experiments was directed to a determination of the exact localized areas involved in the various reactions. The first step toward a solution was the observation that when the crown of gill filaments was directed away from the source of light, as would be the case when the opening of the tube, and consequently the direction of the head was turned from the light, it frequently happened that the worm failed to respond to the usual shadow stimulus. This was variously repeated and with cumulative evidence to the effect that the outer, or under surface of the gills was distinctly less sensitive to these stimuli than the inner surface. This is only what might naturally be expected, since it is the inner surface which in expansion sustains direct relations to sources of contact or approach from the surrounding medium, while on the other hand the outer surface in the unfolding and expansion of the plumose filaments would be least exposed.



Furthermore, it was found by close observation that the terminal portions of the filaments were likewise more sensitive than the basal portions, which is again what might naturally be anticipated. If one watched carefully the behavior of a specimen following a retraction of the gills it would be seen that the following protrusion was a very cautious process, so to speak. The tips of the gills would be gradually extended, barely protruding beyond the margin of the tube, and in this position the creature would wait for a time, the filaments in the meantime actively vibrating, as if searching for any source of danger. Next they would be protruded somewhat farther, with another pause, and finally the entire crown would be protruded and gradually expanded. The same process was frequently observed, but in reverse order, in a contraction following a very slight stimulus.

Following an unusually vigorous stimulus, as a very dense shadow or a mechanical disturbance, the worms would frequently remain for some time deeply withdrawn, and in again expanding would do so with unusual caution.

This was most strikingly demonstrated in the following experiment of further attempting to locate the sensitive areas by a process of graduated excision of the gill filaments. This was attempted by a quick snip with scissors as the specimens were quietly expanded near the surface of the water. The operation was found, however, to be an exceedingly difficult one, owing to the lightning-like rapidity of the contraction of the worm at the slightest disturbance. I succeeded in several cases in clipping off about one fourth of the terminal portion of the filaments, and found in every case that there followed an appreciable loss in the acuteness of the sensory reaction, though as will be seen in the later discussion of "mixed stimuli," it is not beyond doubt that this apparent loss was due to the interposition just here of another stimulus, that resulting from the mutilation, which for the time being superseded that of the light. This is further suggested in the fact that immediately following such an excision the creature seemed to go through various maneuvers, rubbing the filaments over each other in the most curious fashion, protruding and withdrawing them in very unusual ways. And it was further ob-

served that within perhaps a dozen hours the worm behaved in quite a normal fashion, and seemed to have regained much of its former sensitiveness, though its responses were less definite or exact than before.

Attempts to excise further portions of the same gills upon a following day showed the operation to be a much more difficult matter than in the first instance. This was not only due to the same extremely rapid reaction mentioned before, but also to the fact that the creature had apparently acquired a degree of caution in protruding far beyond the tube, and had likewise apparently become much more easily disturbed than before. This became even more marked upon a third or fourth attempt. It was as if it had acquired an experience which served much as in higher animals, and will have a peculiar significance in some of the later discussions.

I finally succeeded in excising entirely the gills down to the base of the palps in the case of several specimens by substantially the same process, except that it was necessary, in order to secure this result to place the scissors about a quarter of an inch below the orifice of the tube, and then to cut off that much of the tube, and in the process "catch" the crown of the retreating worm. In a few other cases I forced the worms out of the tubes by thrusting a bristle into the smaller portion of the tube, posterior to the worm, and then gradually irritating it till it emerged entirely, or so far as to allow careful excision of the entire gill area, after which the worm was allowed to readjust itself in the tube.

This last expedient was found, however, to give less satisfactory results than the former, as a rule, since it often happened that by the process of forcing the worm from the tube there was great liability of injuring it sufficiently to seriously interfere with the subsequent experiments, or to so modify the reactions as to give inconclusive results.

As a result of these several experiments it was clearly demonstrated that the sensory centers are within the gill areas, and chiefly the more distal portions, though with the basal third of the gills intact the creature still retains more or less of sensory activity. But with the entire gill area removed close to the palps, the sensory

power is wholly lost for the time being. It must be stated incidentally that the capacity of regeneration is well developed in these worms, and new tissue begins to make its appearance within about two days, and with this regeneration there is recovered in a more than proportional measure, the sensory function. The entire gill is regenerated in about two weeks, or in some cases perhaps less.

It will be evident, I think, from these several experiments, that the sensory area is quite definitely circumscribed in this species, and it may also be stated in this connection, that it is equally so in the other species included within the present account. But it remains to consider the further question, whether there be any special sensory organ, answering the structural or functional purposes of an eye? In reply it may be said that such organs, the so-called eyes, have long been known in many of these worms, and that they have been generally regarded as having a visual function. The citation from Claparede in an earlier section of this paper is one of many which might be given in support of the view.

On the other hand it is likewise equally well known that there are not lacking many species, not only among worms, but cœlenterates, molluscs, etc., which are totally devoid of anything of the sort and are nevertheless, quite as sensitive as species having an abundant supply of these "eyes." Such is the case, for example, with species of Hydroides. So far as known the gills are wholly devoid of anything like the "eyes" of *Potamilla* or *Sabella*; and yet the latter are, so far as my observations go, much less sensitive than the former.

Andrews several years ago made a critical study of the eyes of annelids, comparing them with similar organs of molluscs. Commenting on points of the comparisons, he remarks, "In both cases the animals respond very quickly to slight sudden changes in the intensity of illumination, bivalves seeking safety by retreat within the hard shell, the annelid withdrawing into firm tubes." But he continues, "The great number and position of these organs suggests doubts as to their usefulness as eyes, the same that have been made to the like organs of *Arca*" (op. cit., p. 287.)

This author found no structure which was in any degree comparable to the "eyes" in the other species investigated, including *Potamilla* and *Sabella*. Yet he found that "the seat of sensation is also in the branchiæ; when these are cut off more and more, the animal still reacts till nothing but the bases of the branchial stems remain." This last point differs slightly from my own observations as just given above, though it would seem to be rather a difference of degree than of kind.

It may be mentioned in passing that Dr. A. L. Treadwell, who has carefully studied the histology of the branchiæ of Hydroides, assured me that he was not able to distinguish anything comparable with the eye-like organs found in other species of annelids.

It seems fairly certain, therefore, that we have in these annelids a condition of highly sensory activity, more or less definitely localized, yet without any specialized organs, as sensory centers, or media of photic coördination. Whether it shall be found upon further investigation that there exists in these annelids certain specialized cells, similar to those found by Langdon<sup>1</sup> in the earth-worm, which may be regarded as having a similar function must be left for the future to determine, though the probability of such sensory cells may be confidently anticipated.

### *Third Series*

A third series of experiments was conducted in relation to the effects of colored light upon the reactions of these worms.

The general influences of various parts of the spectrum on organic processes are too well known to call for special details. It will be sufficient to refer to the observations of Lubbock,<sup>2</sup> Graber,<sup>3</sup> and Engelmann,<sup>4</sup> as examples of many who have given attention to the matter. Others will be cited in connection with particular phases to be considered later.

My experiments with colored light were made with dark ruby glass such as is commonly used in photographic dark rooms, and

<sup>1</sup>Langdon, F. E.: Jour. Morph., vol. xi, 1895, p. 193, etc.

<sup>2</sup>Lubbock: Ants, Bees and Wasps, 1882, p. 186, *et seq.*

<sup>3</sup>Graber, V.: Grundlinien des Helligkeits- u. Farbensinnes der Tiere, 1884.

<sup>4</sup>Engelmann, Th. W.: Ueber Licht- u. Farbenperception niederster Organismen, Arch f. d. gesam. Physiol., Bd. xxix, 1882.

with deep blue cobalt glass. No attempt was made to determine whether the glass was approximately monochromatic. However, for the purposes involved, it answered fairly well.

The first experiment consisted in the very simple process of interposing a plate of colored glass between the aquarium and window, with no attempt to protect other portions of the aquarium from the diffused light of the room. As might have been anticipated, under the circumstances no definite results were distinguishable.

The next experiment was made by enclosing the entire aquarium under a dark box, one end of which was fitted with a colored glass. The specimens were left here for about a half hour before observations were attempted, and then no differences could be distinguished. After another half hour further tests were made, but with no appreciable differences as compared with those under natural light. In this instance the red glass was used. The experiment was varied by interposing blue glass, and again the aquarium was left for about the same time, and no differences being apparent, the apparatus was left for another hour before testing, and again with negative results. Finally it was left over the entire night and tested about 8 A. M. the next day, but again with negative results. As will be seen by the later experiments the apparent failures were due to the fact that immediate attention was not given to the matter of tests and observations.

At 8.15 the aquarium was placed under the red glass and testing immediately, it was observed that there were no responses to any of the former tests, even perfectly opaque screens like a thick pasteboard, gave only negative results. That is, reactions were wholly inhibited. After an hour, further tests showed that specimens were quite recovered and reacted to any of the usual tests quite promptly and energetically. Repeating the tests at intervals during another hour they gave the same positive reaction which had been shown under normal conditions. Removing the red screen entirely, in order to repeat the tests under blue glass, it was found that the entire colony was strangely irresponsive; none of the usual tests making any impression whatever upon them. Repeating the tests in every way possible failed

to secure any reaction for at least two minutes, when it was noted that the specimens were apparently recovering from a sort of dazed condition, and within five minutes all were reacting quite as promptly as under normal conditions.

The specimens were left for about forty minutes under natural conditions and were then placed under the red light again and carefully observed, and with the same results as in the last experiment except that it was found that after the first effects of inhibition due to the red light, they were found to gradually recover sensitiveness in from five to ten minutes. Testing as before at intervals of from five to ten minutes during half an hour they reacted quite as under normal conditions. Then again the red screen was removed and the animals carefully watched and tested as before with the same results, namely, that immediately following the removal of the screen they were found to be quite indifferent to any of the usual tests but that in from two to five minutes they had quite recovered and reacted as under normal conditions. By actual count the reactions were as follows: At the end of one half minute none; end of one minute one specimen; end of one and one-half minutes four specimens; end of two minutes ten specimens; end of two and one-half minutes all but five of the colony of twenty-five specimens. These did not fully recover normal activity until some six minutes had elapsed.

At two o'clock they were placed under the blue screen and carefully watched as before. There was at first the same inhibition of reaction as in the former case. At the end of two minutes the first indication of recovery of sensory activity was noticed. Repeated at intervals of one minute it was found that in four minutes apparently the entire colony became normally responsive. Tests made at intervals of about five minutes for nearly half an hour seemed to show that there was a higher average of response than under the red light. At 2.25 the screen was carefully removed and tests showed specimens to be acutely sensitive, responding to the slightest shadow.

The experiment was repeated, after adding a new and fresh colony to the aquarium, and with almost identical results.

Again at four o'clock the same experiment was repeated, and with the same results, the creatures losing for about five minutes any sensory discrimination, but quickly recovering it with apparently greater acuteness than under natural light. This was likewise the case at the conclusion of the experiment at six o'clock, when the screen was removed, every specimen reacting with great promptness and vigor.

These experiments were repeated again and again, under varying conditions of light, temperature, etc., but with so large a measure of constancy as to preclude the possibility of the operation of merely accidental or incidental causes.

As has been noted in an earlier section, the coloration of these creatures is very variable, ranging from orange-red on through yellow, dull brown, blue and purple of all degrees of combination to almost pure in some cases. In connection with the experiments on colored light occurred the query, whether there might be any possible relations between the various colors of the worms and the exposure to varying intensities of light? While their arrangement in the colonies gave no apparent support to an affirmative probability, still it seemed well to carefully test the individual reactions of the more conspicuously colored specimens. This was accordingly done in repeated instances but with entirely negative results. Whether in natural light or under the influences of artificial and colored light; whether among a group of bright orange-colored specimens, or in deep purple colored specimens, not the slightest individual difference could be distinguished. And the same was equally true whether the experiments were made with colonies just taken from the natural habitat or those long in the aquarium. It may be assumed therefore that these rather remarkable colors have little or no adaptive relations to light, any more than to selective protection. It seems most remarkable that in a single colony of these worms numbering perhaps thirty or more specimens, and probably arising from a single brood or generation, all this range of color variation should be found, and that without any apparent significance in relation to their habits or life history, yet such seems to be the case here as in many other equally well known instances among this and other phyla or classes.

In this connection may be mentioned an illustration of observations cited by the writer in an earlier paper,<sup>1</sup> namely, the decline of color brilliance under the artificial conditions of the aquarium. In *Hydroides* this was quite marked, as was also the case with *Protula*. The colors in which this was first noticeable were the reds, orange and yellow, though it was not lacking in the bluish tints. These changes were less evident in *Potamilla* and *Sabella*, the colors of which are less striking.

It might be inferred from what has gone before that these color changes would have little effect upon the sensory responses of the specimens, and such was the case. While as already shown, any evident decline in vigor was likely to involve a corresponding decline in sensory qualities, but there was nothing to indicate that there was any necessary relation between these phenomena and that of decline of color.

#### EXPERIMENTS ON OTHER ANNELIDS

Reference has been made repeatedly to *Potamilla* and *Sabella*, but no special account has been given of definite experiments made upon them. As already stated, the numbers of these specimens obtained were comparatively few, and the experiments much less extensive than upon *Hydroides*. But one species of each was found, namely, *Potamilla oculifera*, and *Sabella micropthalmia*. In size and habit they are very similar. Their tubes are not calcareous and rigid as with *Hydroides*, they are much smaller in size, with a habitat among sponges, ascidians, etc. Their general behavior is similar to that of *Hydroides*, but very much less striking. The experiments made upon them were the same as have been already described for the other species. In various experiments with light of varying intensities—to electric and colored light, to touch, etc., they gave no reaction which was not much more clear and convincing in the former. To colored light their behavior was almost uniformly negative, as was also the case with that of the electric lamp. Furthermore, their reaction time was much more sluggish and uncertain than in the case of *Hydroides*. Their

<sup>1</sup>Science, vol. xix, 132, 1904.



reaction to shadow stimuli, while similar to that of *Hydroides*, was as before very much less striking. It was frequently the case that only after some two or three more or less dense shadows had been cast over them that a reaction followed, and then comparatively slow, and so to speak, deliberate-like. Tactile stimuli, and excision of portions of the gills induced, as in *Hydroides*, apparent caution and more promptness of reaction.

Concerning the behavior of *Protula intestinum* a brief reference has already been made in another section. It may be worth while to cite a few additional observations which serve to confirm and accentuate those of the other species. *Protula* is a large tubicolous annelid, quite common in the Bay of Naples which like *Hydroides* secretes dense calcareous tubes curiously coiled in serpentine aspects, as shown in Fig. 3. These tubes are often 180 mm. or more in length and from 5 to 8 mm. in diameter at the opening. The color is usually of a more or less uniformly bright orange red, and a colony of these creatures fully expanded forms a most brilliant picture.

Their reactions to the various stimuli already mentioned are very similar to those of *Hydroides*, though somewhat more erratic. Thus it frequently happens that while at one time responses to shadows are very prompt and decisive, at another time they may be apparently quite indifferent. Perhaps on the following day this may all be changed and the colony acutely sensitive to the slightest variation in the intensity of light. Furthermore, they seem less adapted to continuous aquarium conditions than do species of *Hydroides*, a lowering of vital tone being more or less evident after about a fortnight. This is also associated with a decline in the color tone of a more marked degree than is the case with the former species. And with these changes the reactions to various stimuli, especially light, become very uncertain or even entirely lacking.

#### GENERAL DISCUSSION

The foregoing experiments and observations bring before us certain clearly defined facts which call for further consideration and explanation. This may be facilitated, perhaps, by a com-

parison with similar facts from other sources, some of which have already been referred to. Patten,<sup>1</sup> whose somewhat extended observations and study of the eyes of molluscs is well known, has offered suggestive comments concerning their reactions to varying intensity of light. For example, he has observed that in *Arca*, whose sensory organs are very numerous and highly complex, the reaction is much less marked than in species of *Avicula* in which the slightest shadows, such as that of a pencil, causes instant response. He makes a similar comparison between *Cardium* and *Pecten*, the former of which is extremely sensitive to varying light intensity but only slightly so in reference to mechanical disturbances like a jar of the aquarium or the action of waves; while the latter is highly sensitive to mechanical stimuli but much less so to shadows, though in this case again the sensory organs are both numerous and complex.

Hence he concludes that "We are led to suspect the presence of some other factor which must, when known, account for the apparent agreement in functional powers between two organs so widely different in structure."

Concerning *Pecten*, Patten also observed the phenomenon of fatigue, to which reference has been made previously, finding that specimens experimented upon frequently become erratic in responses, "so that finally, even quite deep and sudden shadows may produce only restless or uneasy movements, or perhaps no effects at all" (*ibid.*, p. 614).

Darwin's observations concerning the reactions of earthworms to light are too well known to call for more than passing notice, except to point out that this critical observer expressed no hesitation in ascribing to these creatures definite light perceptions, nor did he hesitate to suggest the coöperation and coördination of other factors in bringing about the varying results obtained in his experiments. For example, he observed that, under the conditions of feeding, mating, etc., or where they were otherwise preoccupied, they either failed entirely to react to the light stimulus, or did so in very different degrees of promptness or directness. He even

<sup>1</sup>Mitt. Zool. Sta. Neapel, Bd. vi, p. 608, *et seq.*

suggests that at times their behavior indicated changes of nervous states, "as if their attention were aroused or as if surprise were felt."<sup>1</sup>

Under the later development of the theory of tropisms, and its extension to the phenomena of animal behavior, its dominance has relegated the earlier views to the limbo of discarded anthropomorphisms so called. Without essaying any review of the *pros* and *cons* of this problem, it may be said that already a reaction has taken place and frankness compels a reconsideration of some of these discarded and discredited views. Such a review has already been made by Jennings<sup>2</sup> so far as it relates to the lower organisms, and his conclusions must, it seems to me, be equally true for many if not most higher animals as well.

Among those who have given especial attention to the behavior of annelids, the most important are Loeb,<sup>3</sup> and Nagel,<sup>4</sup> and to a less extent Rádl.<sup>5</sup>

As is well known, Loeb maintains without hesitation that the behavior of these annelids in their relations to light is governed by the same laws as is that of plants. Indeed, concerning the general orientation of these creatures he contends that they are governed by two fundamental influences, namely, gravity and light, and in support of this view describes various experiments, and gives illustrations as to various details.

Concerning the influences of gravity as a factor in the case of the species I am unable to find any adequate confirmation of Loeb's views. An examination of the several photographs presented herewith will, it seems to me, show that neither in the case of single individuals nor in that of colonies is there any such uniformity as to position or relation as would indicate the predominant influence of any single factor or force. Where single specimens are found growing either upon a shell, or upon a solid and fixed

<sup>1</sup>The Formation of Vegetable Mould. London, 1881.

<sup>2</sup>Contributions to the Study of the Behavior of Lower Organisms. Washington, 1904.

<sup>3</sup>Der Heliotropismus der Tiere und seine Ueberlinstimmung mit dem Heliotropismus der Pflanzen. Würzburg, 1890.

<sup>4</sup>Der Lichtsinn augenloser Tiere. Jena, 1896.

<sup>5</sup>Untersuchungen über den Phototropismus der Tiere. Leipzig, 1903.

support, as a rock, the general position is more or less prone, with a varying serpentine aspect, as shown in Fig. 1. In certain cases the mouth of the tube would be found in one direction, and in others quite otherwise. Sometimes the head projected upward, often downward. This is better shown in some measure in the case of colonies. While here the general tendency of the tubes is vertical in growth, many are found diverging laterally, and in not a few cases directly downward, as may be seen in Fig. 2. In this figure the open mouths of several tubes may be observed near the top. This colony is attached to a flat stone, whose center of gravity would serve to maintain a constant position, hence the variously coiled tubes are evidence of a correspondingly shifting behavior on the part of the worms during their growth. This is perhaps still better seen in Fig. 3, a colony of *Protula*, several of which I studied at Naples. While here as in the former figure, the general aspect of the tubes is toward the vertical, still their lower serpentine coils show the varying conditions of orientation at different periods of growth. But if further evidence be needed it is found in the tube coiled about the larger central one the mouth of which opens almost directly downward. But furthermore, colonies kept in the aquaria for nearly two months, during which time the tubes had grown almost half an inch, showed not the slightest evidence of any response to gravity. They did, however, show unmistakable evidence of adjustment to conditions favorable for respiration, and for the capture of food; and these I regard as of far more importance in determining orientation than either gravity or light.

Zeleny,<sup>1</sup> who has reared the larvæ of these serpulids in connection with his investigations upon their regeneration and regulation, has incidentally recorded brief, but very interesting observations concerning the behavior of the young worms in relation to "gravity, light and food, but was able to find no general rule, although some groups seem to be arranged with respect either to maximum food-obtaining ability, or with respect to a lateral stimulus of unknown character."

<sup>1</sup>Biol. Bull., vol. viii, p. 309.

While not sufficiently extended to warrant definite conclusions, these observations go to corroborate my own as to the importance of adjustments in reference to respiration and obtaining food.

Concerning the reactions to light Loeb<sup>1</sup> holds very decided views, and has taken Nagel sharply to task concerning a suggestion that the behavior of such creatures as responded to the stimulus of shadows might be due to something akin to a sense of apprehension as to the approach of an enemy or other threatening danger. In opposition to this he undertakes to show the necessity for the existence of some organ of perception similar to a cerebrum in order to enable the creature to possess any instinct, or sense of self-preservation, such as Nagel's suggestion implies. Loeb suggests, on the other hand, that the effect of light may tend to induce a muscular expansion or stretching so that the worm emerges from the tube. If now, a sudden diminution of light follows, as in the case of a shadow, an opposite muscular reaction is set up, and consequently the worm rapidly withdraws into the tube, and the sudden retraction of the worm is only the expression of the rapid extension of the contraction wave of the worm's musculature.

Of the relations of light to many of the phenomena of life there is not the slightest doubt. That in many cases these relations may be so intimate as to warrant designating them by such terms as phototropism, heliotropism, etc. But that there is any such correlations involved in the aspects of behavior under review as to warrant regarding them in the light of cause and effect seems not only doubtful, but wholly inadequate. As Ràdl has remarked, "Diese Erklärung Loebes ist vielleicht ebenso einfach wie unrichtig" (*op. cit.*, p. 78).

In the present case there are many difficulties in the way of the rigid application of any theory of tropisms. In the first place the widely differing degrees of responsiveness among closely related species of slightly differing habitat is difficult to explain by this means. Again, the varying behavior under slightly differing

<sup>1</sup>Archiv f. d. gesam. Physiol., Bd. lxvi, 1897, p. 461.

conditions, as for instance, where specimens have been rendered wary under attempts to excise the gills, or where a given specimen has been placed for a time so near the surface of the water that it has been compelled to extend itself in an unusual manner to bathe its gills at all, under which circumstances it often fails entirely to react to the ordinary stimulus. In this case we have apparently what Jennings has designated as "physiological states" namely, conditions in which the internal changes involved in respiration perhaps, have served to render the animal indifferent for the time to stimuli which under normal conditions are very constant and effective in their action, or perhaps as suggested above, complex or *mixed stimuli*.

That light of itself is not a determining factor in impelling the worms to emerge from the tubes is evident in that this attitude occurs in darkness as well as in light, by night as well as by day.

Furthermore, it must be recalled in this connection that the particular stimulus involved in these observations, as previously pointed out, is not light at all directly, but the lack of light, or the shadow. The response is, therefore, induced by a negative stimulus, if such an apparent paradox be tolerable in relation to phenomena of behavior. Of course, it is not overlooked that Loeb has designated these and similar reactions as due to "negative heliotropism." At the same time it is not clear that in the present case we are dealing with phenomena at all comparable with those associated with negative heliotropism as ordinarily understood. For as already observed, the phenomena are not in themselves negative. They are not dependent upon any given degree of light, or rather darkness, but to the suddenness of the change.

Rawitz<sup>1</sup> long ago called attention to exactly this peculiarity in describing the reactions of species of *acalephs*. Referring to the suggestion of Drost concerning the effect of shadows as stimuli, he says "Ein Reiz kann immer nur von etwas positivem, also in diesem Falle vom Lichte, ausgeübt werden, niemals aber von

<sup>1</sup>Der Mantelrand der Acalephen. Jenaische Zeit. f. Naturwiss, Bd. xxii, xxiv, xxvii.

einer Negation. Und Schatten ist eine Negation, die des Lichtes namlich," etc.

But it will be asked, if we are not to regard these reactions as due to some form of light stimulus, whether it be positive or negative, nor perhaps even to photokinesis, how then shall they be interpreted? For myself they seem much better explained as activities concerned with protective adaptation than by any merely mechanical or mechanico-chemical adjustments. If the tubes in which these creatures have their homes have been acquired as protective adaptations, and if it be granted that they, in common with other annelids, have some sensory capacities, including light perceptions, then it would not seem a far call to interpret the phenomena in question as sensory reflexes which have become instinctive through multiplied generations of struggle with various predatory enemies, whose approach cast fateful "shadows before."

It only remains to consider, briefly, the reactions involving the influence of colored light. In a general way the principal features concerned under this head have long been known. Experiments, have shown that violet rays have a definitely higher phototropic quality than have those of lower refrangibility, such as orange and red.

Nagel<sup>1</sup> has called attention to the same facts in relation to molluscs, though he enters into few details, and frankly admits the desirability of additional observations. He believes that all the colors of the spectrum, except red, have a measure of stimulus for such organisms as show, like his mussels, sensory reactions to the presence of light.

Loeb<sup>2</sup> has also made similar observations, and concludes that "since the heliotropic phenomena appear only weakly or not at all behind dark red glass, while they occur just as in diffuse daylight behind dark-blue glass, the few red rays which penetrate the dark-blue glass cannot be responsible for the heliotropic phenomena which take place so energetically behind this screen but can be due only to the activity of the more refrangible rays."

<sup>1</sup>Der Lichtsinn augenloser Tiere, Jena, 1896, p. 53.

<sup>2</sup>Physiological Studies, vol. i, p. 18.

A comparison of these views with the facts cited in connection with my observations will show that in several particulars there are obvious differences. In the first place, my observations show that, though there is an inhibitory quality in the dark-red rays when first brought into relation with the worms, it is only temporary. Within some ten minutes, or after time has allowed the specimens to become adjusted in their sensory activities to the new conditions, they become almost if not quite as responsive to the shadows as under normal light. And, moreover, the same thing happens under the influence of the dark-blue rays. Here there is a brief period of inhibition, as in the case of the red rays though the adjustment is more rapid. Usually within five minutes the animals have become accustomed to the new light and behave quite as under normal light. I have pointed out in the earlier connection that it was not certain that the red glass with which my experiments was made was monochromatic, but since it was sufficiently so to render the light passing through it nonactinic, it may be assumed that it was sufficiently so to prevent the passage of the essentially blue or violet rays, at any rate in sufficient measure to act as a stimulus. It seems not improbable that the apparent discrepancy concerning the effects of the red rays may be due to the fact that a longer time is required in adjustment to these rays than to the blue.

In the next place, and here I have seen no similar records, the most striking difference appears in the fact, previously mentioned, that following the removal of the red screen there was a most remarkable inhibition of all sensory responses under the effects of normal light. For several minutes, not more than five, the animals behaved in the most striking manner, much as if asleep, and recovered sensory activity in much the same way as if awakening. Nothing of this sort was apparent when suddenly brought from under the influences of the blue rays. Here if anything their sensory activities seemed even more than normally alert.

However, while this behavior seems more or less peculiar and singular, I am inclined to believe its explanation may be found along the same line of influence which has already been cited, namely, the inhibitory effects of the colored light when first applied.



Under both the blue and red there was a period of inhibition for some time varying in the two cases, as pointed out above, but most effective in the case of the red. Recovery of sensory activity under these changed conditions involved, of course, some physiological change in the sensory apparatus in response to the changed conditions. Now in the sudden emergence from the low refrangibility of the red rays which had involved the preceding adjustment there was involved likewise another physiological change but in the reverse order.

#### SUMMARY

1. Under the varying degrees of light intensity furnished by the sixteen candle-power incandescent lamp, the diffuse light from north and south windows, and direct sunlight, the results of all experiments involving increased intensity of light were uniformly negative. On the other hand, experiments involving a sudden decrease of light intensity gave results as uniformly positive. However, the behavior does not seem to be essentially comparable with that usually designated as negative heliotropism.

2. Experiments continued without interruption for some time gave rise to behavior analogous to that of fatigue.

3. Various experiments involving the direction of light contact, the excision of branchiæ, etc., showed that the sensory areas are located in the branchial filaments, chiefly the inner and terminal portions.

4. When the animals are brought under the influence of red and blue light sensory activities are for a time inhibited. This is more marked under the red than the blue. On the other hand, when brought suddenly from the colored light into normal white light there is apparently an intensified sensory acuteness due to the blue light, while the effects of the red seem to have been just the opposite, namely, to positively inhibit sensory response for a period of from two to five minutes.

5. Species of *Potamilla* and *Sabella* behave in essentially the same manner as do those of *Hydroides*, though with less acuteness, promptness and certainty. This is somewhat remarkable since

these species are abundantly supplied with "eyes," which are entirely lacking in Hydroides.

6. Species of *Protula* likewise behave in essentially the same manner as do the others, though apparently somewhat more erratic and uncertain in their reactions.

7. The experiments tend to discredit the theory of tropisms, since no single factor, such as light or gravity, furnishes an adequate explanation.

8. The experiments strongly suggest the presence in the gill filaments of these creatures of sensory cells and nerve endings through which are coördinated by means of nervous centers the various aspects of behavior toward protective or physiological ends.