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A CONTRIBUTION TO THE PHYSIOLOGY OF THE NERVOUS SYSTEM OF THE MEDUSA GONIONEMUS MURBACHII. PART I.—THE SENSORY REACTIONS OF GONIONEMUS.

BY ROBERT M. YERKES.

CONTENTS.

I. Characteristics, Distribution, and Habits of Gonionemus.

GONIONEMUS MURBACHII, one of the Trachomedusæ, has four radial canals from which the gonads are suspended in irregular folds. The tentacles vary in number from thirty to eighty. They are usually not more than four centimetres in length, and each has near its distal end a viscid or suctorial body by means of which the animal is able to attach itself to objects. The portion of the tentacle distal to this body frequently makes a sharp angle with the other part and is much lighter in color. On the margin of the swimming bell, at the base of each tentacle, there is a body which appears greenish yellow when seen from the aboral side and brownish from the oral, whose function is supposed to be sensory. And between each pair of tentacles, rather irregularly situated with reference to them, is a small oval sac, the lithocyst,[1] which contains a spherical body, the lithite. The lithocyst is thought to have to do with the orientation of the organism.

The manubrium is quadrate in cross section, with a short stalk. The lips, normally four, are very irregularly folded. When the animal is at rest the bell is almost hemispherical and has a marginal diameter of from one to two centimetres.[2]

According to Murbach, the species of medusa on which the studies of this paper were made was first noticed on the North Atlantic Coast at Wood's Hole in 1894, and it was described by him from this locality in 1895 (Murbach, :95). It was thought by him to be identical with G. vertens, described by A. Agassiz from the Gulf of Georgia, Washington, in 1862 (Agassiz, :62, p. 128). But recently differences in these two forms have been noted, which cause Mayer (:01, p. 5) to regard them as distinct species. He therefore proposes to give to the Wood's Hole species, which until a few months ago was known as G. vertens, the name G. murbachii, after Murbach, the describer.

Gonionemus murbachii has been found at various points on the Atlantic Coast, but it is by no means common. At Wood's Hole it occurs from June to October in a small pond connected with the harbor, the Eel Pond. Rarely it has been found elsewhere in the vicinity.

Apparently the most favorable habitats for these medusæ are quiet protected harbors or ponds which are affected by the tides, but whose currents are not sufficiently strong to tear the animals from their attachments and carry them seaward. Such places usually abound in vegetation, to which the animals are found attached, and have a rich food supply. In the Eel Pond there is a great deal of eel grass, and it is clinging to the leaves or roots of this grass that Gonionemus is most commonly found. Any disturbance in the water, such as stirring the grass with an oar or dip net, causes the animals to free themselves from the object to which they are attached, — either by the viscid bodies of the tentacles or by the lips of the manubrium, — and to swim to the surface. A convenient mode of capturing them is to disturb the water and then dip them up as they appear at the surface. Upon reaching the surface they at once turn over, the mouth of the

[1] This organ is often called the otocyst, but since this term is associated with the sense of hearing, for the existence of which there is no evidence in Gonionemus, it seems desirable to use lithocyst.

[2] For fuller description and drawings of Gonionemus, see Hargitt, :01, p. 294, and :01[a], p. 593.

bell thus becoming uppermost, and begin to sink by force of gravity. Under ordinary circumstances the medusæ are not seen at the surface of the water. It would appear, therefore, that they do not migrate upward in any definite way for the purpose of feeding or in response to light. Surface towing at night proves that there are few, if any, more at the surface then than in the daytime.

The food of Gonionemus consists of small fishes, crustaceans, larvæ of various kinds, and such dead organic material as comes within its reach. Often a Gonionemus is found attached by a few tentacles to a weed, with the exumbrellar surface of the bell against the weed and the manubrium swinging free in the water. It is evident that the animal can in this position seize food, if any chances to pass within reach. It seems probable that the restricted distribution of Gonionemus is due to the distribution of the food supply, for within the Eel Pond those regions in which the animals are abundant are frequently found to contain masses of decomposing organic matter. It should be remarked, too, that the Eel Pond receives a great deal of refuse during the spring and summer, and for this reason is probably a favorable habitat for Gonionemus.

II. Problems of Neural Physiology.

The physiological problems whose solution was sought in the following experiments naturally fall into two groups: (1) Those concerning the functions of the sense organs, and (2) those which have to do with the rôle of the so-called central nervous system.[1]

Chief among the problems of the first group are the following:

1. Has Gonionemus a sense of taste (*i. e.*, a chemical sense) distinguishable from the tactual sense?

2. If there is such a sense, where is it located?

3. Are all parts of the body equally sensitive to all forms of stimuli, and if not, what is the localization?

4. Do different qualities of stimuli call forth different kinds of reactions, or is intensity of stimulus alone significant?

5. Do any stimuli have a directive influence upon the movements of the medusa?

Of the second group may be mentioned:

1. Do the special reactions of parts of the medusa, such as the tentacles or manubrium, depend upon the central nervous system?

[1] This paper deals with the first group of problems only.

2. Is there any evidence of nerve centres?

3. What is spontaneity, and what is its relation to the nervous system?

4. Is coördination dependent upon the central nervous system?

5. Are there any evidences of the functional importance of the central nervous system?

III. Reactions to Stimuli.

A. To chemical stimuli. 1. *Foods.* — Since in nature the feeding reactions of Gonionemus are inseparably connected with reactions to mechanical stimuli, it is not possible to decide without careful study whether any particular reaction is a response to taste or to touch. Food is obtained by contact; the animals swim about and as soon as the tentacles touch an object of nutritive value they adhere to it and close around it. If the object be a living organism, the nematocysts are discharged for the paralyzing of the prey. The lips of the manubrium, probably by means of a secretion, hold food which comes in contact with them, thus enabling the manubrium to surround it. Hungry Gonionemi swim about almost constantly with their tentacles extended. Well fed individuals are more frequently found at rest with contracted tentacles. Obviously both locomotion and the extension of the tentacles increase the animal's chances of obtaining food.

An experimental study of the reactions of Gonionemus to chemical stimuli was begun by observation of the manner in which normal animals react to fish-meat. A small piece of fresh fish placed upon the tentacles causes a reaction which usually presents five fairly well marked phases: (1) Those tentacles that have been touched by the meat contract, twisting about one another in such fashion as to hold the food and carry it along with them; (2) the group of contracting tentacles bends in toward the mouth; (3) that portion of the margin of the bell bearing the contracting tentacles contracts, thus drawing the tentacles nearer to the manubrium; (4) the manubrium bends over toward the side from which the food is being brought, until finally the lips touch the food; and (5) the meat, adhering to the lips, is slowly surrounded by the manubrium.

If the piece of meat be placed near, instead of in contact with, the animal, there is at first no reaction; but after a few seconds the tentacles nearest the food begin to move about, and unless they happen to reach the meat there soon follows a general contraction, or series of contractions, of the bell, which may take the animal either toward or away from the source of the stimulus. To all appearances the tentacle movements and the swimming are not definitely directed "food-seeking" movements, but simply motor reactions to a stimulus, — reactions, moreover, which cannot be distinguished from those in response to touch, light, electricity, and other stimuli. By the chemical stimulus of meat the medusa is aroused to activity, and usually in swimming about sooner or later comes in contact with the food. The stronger the stimulus, within limits, the quicker, more violent, and persistent the reaction. In these reactions to food at a distance, which evidently cannot be interpreted as "food-seeking" in the psychological sense, there is excellent evidence of a sense of taste.

In order to determine whether the food-taking reaction described is a response to all kinds of stimuli, or a specific reaction to nutritive substances, experiments were made with solutions of meats, acids, alkalies, and salts. In these experiments a Gonionemus was put into a two-inch Stender dish containing sea-water, and the stimulating substance applied to it with a capillary pipette. After each test the dish was washed out and refilled. Solutions of fish-meat were made by macerating fishes, allowing the mass to stand for an hour and then twice filtering.

To a strong solution of fish-meat applied to the tentacles the "food-taking" reaction is uniformly given. In order to be certain that the response was not due to mechanical stimulation, these experiments were checked by testing the animal's reaction to a current of sea-water from the pipette. To this stimulus, even though it were sufficiently strong to move the tentacles mechanically, there was seldom any more than a slight contraction of the tentacles in the region of the disturbance.

If a fish-meat solution to which the "feeding reaction" is regularly given be diluted, it will finally cease to call forth the complete five-phase reaction, and instead only the first, or first and second phases will appear. It is thus possible by using different strengths of the solution to get partial reactions.

Comparison of the reactions to food and to a current of water shows that quality of stimulus is of importance, and experiments with different solutions of fish-meat prove that intensity is also significant.

A drop of a solution of acetic acid ($\frac{n}{25}$ was used) applied to the tentacles invariably causes their sudden contraction, and in most cases a subsequent contraction of the bell, which is frequently continued into a long swimming bout. The stronger the stimulus the quicker and more prolonged the reaction. Very weak acid causes only a slight local contraction of the tentacles. Other acids, alkalies, and salts produce similar reactions. These observations prove that foods cause a special "feeding reaction," which is not given normally in response to other stimuli.

Before finally deciding, however, that the "feeding reaction" is given only in response to nutritive substances, it is necessary to inquire whether some strength of almost any stimulus may not produce this result; in other words, whether the intensity of the stimulus, rather than the quality, is not the determinant of the reaction. With this point in mind, the reactions of Gonionemus to a series of strengths of HCl, KOH, NaCl, and several other chemicals were noted. In no instance were "feeding reactions," as in the case of foods, regularly given. Now and then a partial food-taking reaction appeared, but to no intensity of the chemicals tested was this given frequently enough to make it significant.

In the description of the "feeding reaction" mention was made of the peculiar twisting of the tentacles. This "corkscrew" movement is given in response to most foods, and especially to gelatine and meats. It is evidently serviceable for the holding of the food while it is being carried to the lips. That this twisting is a highly specialized reaction is proved by the fact that it is given only in response to foods and to "motile touch." To all other forms of chemical and mechanical stimulation, to light, and to electricity, the usual reaction is a straight contraction.

It seems well to consider here the effect of "motile touch" stimuli, applied to the tentacles, even though it does not naturally come in a section devoted to chemical stimuli. If the tentacles of an animal which is somewhat hungry be stimulated by quickly drawing a glass rod along them, they will suddenly twist about one another, just as when gelatine or meat is used. The twisting is usually followed by phases two and three of the "feeding reaction" (p. 437). Since this reaction is caused in so definite a manner by no other mechanical stimulus, there must be something in the character of the touch which determines the reaction. It seemed possible that the greater intensity of the "motile touch," as compared with an ordinary contact or pressure stimulus, might be the important factor; but comparison of the reactions to different kinds and intensities of stimuli proves that this is not true. Undoubtedly the stimulus given by a moving object is of vast significance in the life of Gonionemus, while simple contact, unless it be with food, is of less importance. For presumably the medusa lives in great part upon small, free-swimming animals which come in contact with the tentacles and whose capture is facilitated by a quick, twisting response of these organs. It would seem, therefore, as if this phase of the "feeding reaction" occurred in response to a particularly significant kind of tactual stimulus because of its importance to the animal. The reaction-time to "motile touch" is short as compared with that to food or to any other tactile stimulus, it being about 0.30–0.35 of a second as compared with 0.40–0.50. In the capture of rapidly moving animals speed of reaction is all-important; hence, the development of this unusually quick, special reaction to a particular kind of mechanical stimulation. Ordinarily the chemical sense determines that the tentacles shall twist in their response to foods, and this because the nutritive substance can thus be brought to the mouth. But if, in case of the "motile touch" given to Gonionemus by a passing animal, the twisting reaction of the tentacles were given only as a result of the chemical stimulus of food, the probability is that the prey would have escaped before the reaction could occur. A "motile touch" stimulus initiates the "feeding reaction" by calling forth the first phase; but unless it is supplemented by a taste stimulus later, the "feeding reaction" is not continued.

In the typical "feeding reaction" the manubrium bends toward the food. If during such a movement the piece of food be moved to the opposite side of the bell, the manubrium, too, in a few seconds will bend in the opposite direction, that is, again toward the food. The motor reactions of this organ are therefore definitely determined and directed by the source of the stimulus. Strong stimulation of any part of the bell usually causes the manubrium to point to the region of disturbance. This is a reaction which is probably to be explained on the basis of its value as a part of the "food-taking" activity; for again, as in the case of "motile touch," the stimulus usually indicates the presence of food, and the most serviceable reaction for the organism would seem to be a movement of the manubrium toward the stimulated area.

According to their effects upon Gonionemus, chemicals may be classified in three categories: (1) those that cause the special "feeding reaction," which in its perfect form consists of five phases, any one or more of which may appear without the others; (2) those which call forth "locomotor reactions." The locomotor reaction may be preceded by contraction of the tentacles and by movements of the manubrium; but to all strong stimuli it is a quick, sharp contraction of the bell, which causes locomotion of the animal by forcing water out of the cavity of the bell. Weak stimuli often cause movements of the tentacles, which may or may not be followed by bell contrac-

TABLE I.

Reactions of Gonionemus to chemical stimuli.

Indifferent.	Feeding reaction.	Motor reaction.
Sugar [1]	Fish meat	Decomposing meats
Starch [1]	Crab meat	NaCl ($10n$ solution)
NaCl	Shrimp meat	KCl ($\frac{n}{4}$ solution)
CaCl	Clam	KOH
Filter paper	Beef	
Wood	Bread	HCl
Sand	Gelatine	HNO_3
		H_2SO_4
		Tannin
		Acetic acid
		Alcohol
		Chloroform

[1] Either starch or sugar may occasionally give partial feeding reactions.

tions. And, finally, (3) there are substances to the chemical influence of which the animals are apparently indifferent. Such substances may influence the organism, but they cause no visible reactions. According to their effects upon Gonionemus a number of substances that have been tested are classified in the accompanying table. It is of course uncertain whether wood, sand, and filter paper furnish chemical stimulation. But, however that may be, the table shows discrimination between foods and non-foods, and proves the presence of a sense of taste in addition to the tactile sense.

2. *To acids and alkalies.* — From reliable solutions of the chemicals used the desired strengths were made by adding distilled water. To solutions of hydrochloric, nitric, sulphuric, or acetic acids of $\frac{n}{100}$ or stronger, locomotor reactions were always given. Rarely partial feeding reactions resulted from acid stimuli, but in no case was a complete reaction noticed.

TABLE II.

Reactions of Gonionemus to different strengths of HCl and KOH.

Strength of solutions.	HCl. Response.	KOH. Response.
1 n	Quick motor reaction.	Quick motor reaction.
2 $\frac{n}{25}$	Less violent motor reaction.	Less violent motor reaction.
3 $\frac{n}{50}$	Local reaction of tentacles, followed by motor reaction.	Slower motor reaction.
4 $\frac{n}{100}$	Delayed motor reaction.	Slower motor reaction.
5 $\frac{n}{150}$	Delayed motor reaction.	Contraction of tentacles, followed by motor reaction.
6 $\frac{n}{200}$	Contraction of tentacles, followed by motor reaction after a few seconds.	Contraction of tentacles, followed by motor reaction.
7 $\frac{n}{300}$	Contraction of tentacles, and delayed motor reaction.	Occasionally partial "feeding reaction," but usually motor reaction after delay.
8 $\frac{n}{400}$	Slight tentacle reaction. Motor reaction very slow.	Tips of tentacles alone react. Motor reaction to large quantity of reagent.
9 $\frac{n}{600}$	Tips of tentacles alone react. Motor reaction to large quantity of reagent in bell.	No reaction which could be certainly traced to the alkali.
10 $\frac{n}{1200}$	Indefinite reaction of tips of tentacles.	No reaction.

With a view to testing the limits of effectiveness of acids and alkalies, observations were made with a series of solutions of HCl and KOH. These solutions were made up with distilled water, but as this is itself a stimulus, the results of tests with these solutions were compared with those gotten with solutions made up with sea-water. In the experiments the solution was applied with a capillary pipette first to the tentacles and then, if there was no response, to the margin and bell. The results of these experiments are given in Table II.

Concerning the limits of sensitiveness Kahlenberg (:98, p. 17) states that $\frac{n}{800}$ HCl is slightly astringent to the human taste, and

Richards ('98, p. 122) claims that for sulphuric, nitric, and hydrobromic acids the limit of taste for man is about $\frac{n}{1000}$. The experiments with Gonionemus show reactions to $\frac{n}{1200}$ HCl. Kahlenberg is authority for the statement that man is unable to distinguish from distilled water $\frac{n}{800}$ KOH, while $\frac{n}{400}$ can be faintly tasted. Gonionemus is extremely sensitive to KOH, but the limit is a less dilute solution than that for acids.

In general it may be said that placing Gonionemus in solutions of acids from n to $\frac{n}{150}$ at first causes a marked acceleration of the rhythmic contractions of the bell. There is almost continuous swimming accompanied by movements of the tentacles and manubrium. If the animals are left in the solution for a few seconds, coördination is lost, and this is soon followed by paralysis of the entire organism.

3. *Localization of the chemical sense.*— Among animals related to Gonionemus the sense of taste and its localization have been studied by Pollock and Romanes, Nagel, Loeb, and Parker. Pollock and Romanes ('82, p. 474) studied the reactions of the sea anemone to chemical stimuli. They believed the reactions to be due to smell, but later investigations have proved this conclusion erroneous. Until 1891 it was generally believed that the tentacles contained the taste organs; Loeb ('91, pp. 69–70) then discovered that sea anemones without tentacles will accept food and reject other substances. From this he concluded that the tentacles are not the only bearers of taste organs. A year later Nagel ('92, p. 334) studied taste and its distribution in several actinians and found them all provided with a delicate and definitely localized chemical sense. According to him the tentacles are very sensitive to all stimuli, the edge of the mouth is insensitive and the localization is the same for taste, touch, and temperature. To settle a point of disagreement between Nagel and Loeb concerning the distribution of the organs of taste, Parker ('96, p. 107) made a careful study of Metridium. The results of his work agreed with Loeb's, in that a certain zone of the mouth region, in addition to the tentacles, is chemically sensitive. Parker was able to distinguish taste and touch in Metridium and to note specific reactions to foods.

An investigation of the localization of the chemical-sense organs of Gonionemus by means of stimuli given with a capillary pipette [1] en-

[1] Although chemicals thus applied diffuse rapidly, it is possible with care and numerous repetitions to get fairly accurate results. I used colored solutions in most cases, so that the diffusion could be watched.

ables me to arrange the important regions of the body in order of increasing sensitiveness, thus: (1) Exumbrella (insensitive); (2) Velum (insensitive); (3) Subumbrella; (4) Margin; (5) Manubrium; (6) Lips; (7) Tentacles (increasingly sensitive toward the suctorial body); (8) Tips of tentacles.

Of all regions the tips of the tentacles are by far the most sensitive. Their reaction-time is shorter than that of any other region, 0.40–1.00 second. The subumbrellar surface of Carmarina hastata is said by Nagel ('94, p. 517) to be absolutely insensitive to chemical stimuli and very sensitive to mechanical stimuli. This is not true of Gonionemus, for even after the margin of the bell and the whole of the manubrium have been cut away, so that a stimulus can affect only the subumbrella, contractions (beats of the bell) occur in response to stimuli. The velum and exumbrella of Gonionemus are quite insensitive to all chemicals. Even destructive acids may be poured upon them without causing any reaction.

B. To mechanical stimuli. — As it has been found convenient in describing the reactions to chemical stimuli to make frequent comparisons with the reactions to mechanical stimuli, it will not be necessary in this section to do more than describe the methods of experimentation and summarize the results.

A fine glass rod was employed to give *tactile* stimuli. With this, fairly accurate localization was possible. The tentacles, if touched lightly, contract independently, whereas the *tactile* stimulation of any other portion of the organism usually causes a "locomotor reaction." It is noticeable that the tentacles react much more quickly than the bell. This is probably because they contain within themselves the necessary mechanism of response, whereas the bell contracts only after the transmission of impulses to and from the nerve ring. Since transmission is comparatively slow in medusæ,— it being for Aurelia, according to Romanes ('85, p. 88), only 18 inches per second, it is probable that the slowness of response on the part of the bell is in part attributable to this cause. Weak tactile stimuli on the bell frequently cause no reaction, or they may be reacted to after two or three seconds' delay.

The localization of the sense of touch is similar to that for chemical stimuli, the only difference being that to chemicals the manubrium is more sensitive than the margin of the bell, whereas the reverse is true for mechanical stimuli. If anything, the subumbrellar surface is more sensitive to chemicals than to touch. In order of increasing sensitiveness to touch, the parts, then, would be: (1) Exumbrella (insensitive); (2) Velum (insensitive); (3) Subumbrella; (4) Manubrium; (5) Margin of bell; (6) Tentacles (base); (7) Tentacles (tip).

Currents of water if locally applied cause some form of the "motor reaction," never the "feeding reaction." If the animals are forced to swim in a current, their tendency is to move against it—*i. e.*, a positively rheotactic reaction. The probable cause of this will be mentioned in the section on the directive influence of stimuli. Any disturbance in the water causes the animals to move about. This is a motor reaction whose significance would appear to rest on the fact that such disturbances usually indicate the presence of food, which random swimming movements may enable the medusa to capture.

Jarring, pinching, and all other forms of mechanical stimulation tried, invariably induce motor reactions. In the life of Gonionemus mechanical stimuli are of almost, if not quite, as much importance as chemical. The tactile sense enables it to obtain food just as often, it would seem, as the chemical. For higher animals mechanical stimuli serve as warnings of danger and frequently precede sudden motor reactions whose end is escape from the stimulus, but in the medusa the "feeding reaction" is fundamental, the escape from danger a secondary and relatively unimportant matter.

C. **To photic stimuli.** — The reactions of Gonionemus to light consist of (1) tentacle contractions, (2) movements of the lips and manubrium, and (3) contractions of the bell (swimming). The reaction-time to light is much longer than that to any other stimulus studied.

According to Berger (:00, p. 6), Gonionemus is active in "ordinary evening light," but strong light (electric) causes the inhibition of movement.

Romanes ('85, p. 39) has observed that Sarsia, one of the naked-eyed medusæ, is extremely sensitive to light. A flash of light usually causes one or two contractions of its bell. This is sometimes the case in Gonionemus, but it is not a predictable reaction, except to very strong light. Romanes proved the dependence of this reaction upon the presence of light, instead of the change from light to darkness or the reverse. The change from light to darkness, he claims (p. 40), is inhibitory of action. His statement is not very apt, however, for what we have in that case is merely the absence of any motion-producing stimulus. His further observation that Sarsia is more active in light than in darkness holds also of Gonionemus. Furthermore, Gonionemus always settles down in a shaded region, — in other words, it is negatively photokinetic or photopathic.

When a number of the medusæ are placed in a glass vessel before a window they usually collect in the darkest region of the vessel. A simple test of this was made by putting a number of the animals in a dish having a bottom 16 × 10 inches and a depth of 3½ inches, one-half of which was covered with a black cloth. By way of illustration, the results of one test were as follows: eight animals were put into the dish in the afternoon at four o'clock; within fifteen minutes all were in the light half of the vessel, and there they remained with some changes of position until nine o'clock in the evening. At seven o'clock the next morning only one was in the light region, and of the others several were attached to the sides and bottom of the dark region of the dish. Similar results were gotten with several lots.

Again, when Gonionemi in a glass collecting pail are disturbed by agitation of the water, they swim about rapidly and in a few minutes most of them are found on the more intensely illuminated side of the vessel. If, now, they are allowed to remain undisturbed for an hour, they will be found either equally distributed throughout the vessel or collected in the darker region.

There are here two questions to be answered. First, why do the animals at first come to the light? Secondly, why is it that they are later found in the shaded regions? The following statement of the relation of the motor reaction of Gonionemus to stimulation by light accounts for the facts. In ordinary daylight they are, *when swimming*, positively phototactic; in very weak light, on the contrary, they are not directed by the stimulus to any considerable degree, and therefore appear to be indifferent. They come to rest in an intensity of light which is below that necessary to direct their movements to any important extent and are therefore negatively photopathic. These statements may at first seem contradictory, but I believe they are not. It is known that some animals swim toward a source of light (*i. e.*, continue a positively phototactic reaction) until they are in an intensity of illumination far above that of their normal habitat, but, as soon as the effectiveness of the unusual stimulus wears off, or any combination of conditions destroys the directive influence of the light, they wander back to that intensity to which they are accustomed. It might be said, therefore, that they are positively phototactic to intensities of light to which normally they are negatively photopathic. Such I believe to be the case for Gonionemus. Intense light directs its movements and forces it to go toward the source of the stimulus; but it comes to rest in relatively dark regions only.

D. The directive influence of stimuli. — Are the movements of Gonionemus definitely directed by stimuli? The observations which have been described enable us to classify the reactions of Gonionemus as follows.

A. Motor Reactions (Swimming).

1. General reactions (" Locomotor reactions"), which are due to the stimulation of the organism as a whole.
2. Special reactions, which are due to the stimulation of certain parts of the organism.
    a. Tentacle movements.
    b. Manubrium movements.
    c. Bell contractions, which result from a local stimulus of the margin or bell. These are directed.

B. Feeding Reactions.

1. Tentacle reaction (twisting).
2. Manubrium and lip movements.
3. Margin and bell contractions.

Under *A* 1 come all movements that are not determined by local stimulation. They are such reactions as are caused by changes in osmotic pressure, or the chemical constitution of the medium in which the medusa exists. Under *A* 2 are classed all reactions to stimuli which affect only certain organs, or which stimulate symmetrical points of the organism unequally. All such stimuli have a directive value. For if one region only of the margin is stimulated, there occurs a quicker and more forceful contraction in that region than elsewhere; hence the body is given an impetus in a certain direction. If, for example, a strong chemical be applied to a portion of the margin, there follows a sudden contraction of the bell which carries the animal away from the stimulating substance. Observation shows that in case of harmful stimuli the movement is usually away from the side stimulated; the reverse is true for foods. Chemical stimuli evidently determine the direction of the movements of Gonionemus. From this it is probable that the chemical sense is of value in obtaining food at a distance from the organism. Mechanical stimulation is likewise directive in a similar way, as is clearly shown by the reactions to a touch on one side of the bell.

Light also, it would appear, directs the animal's movements by unequal stimulation of symmetrical points. It is impossible, because of the form of the medusa and its mode of locomotion, that the direction of its movements be as accurately determined by light stimulation as are those of certain Entomostraca, of the larvæ of some worms, and of other animals whose structure permits of more accurate orientation in reference to the source of light.

We are now in a position to say that Gonionemus neither seeks nor avoids things in the human sense of these terms. Its reactions are definitely determined by the quality, intensity, and location of the stimulus and not by the end to be attained. In general the quality of stimulus determines the kind of reaction to be given (whether motor or feeding, etc.); the intensity determines the quickness, duration, and extent of the reaction; the location of the stimulus determines the part or parts to react, and the direction of the movement. Food is found by movements which, although apparently fortuitous, because they are very imperfectly directed and determined by the unequal stimulation of symmetrical points in the body, are not wholly so.

IV. Summary.

1. Gonionemus has a delicate chemical sense.

2. All portions of the body, except the exumbrella and the velum, are sensitive to both chemical and mechanical stimuli.

3. The tentacles are the most sensitive portions of the organism to chemical, mechanical, and photic stimuli.

4. Gonionemus gives two important kinds of reaction to chemicals: (1) the "feeding reaction," to all nutritive substances; and (2) the "locomotor reaction," to substances which are harmful.

5. The kind of reaction given by the organism, or by any part of it, to a stimulus depends upon the quality of the stimulus.

6. Intensity of stimulation determines the quickness, duration, and extent of a reaction.

7. When chemical, mechanical, or photic stimuli affect symmetrical points of the body unequally, they have a directive influence upon the movements of the organism.

8. Gonionemus is positively photo*tactic* in daylight.

9. It is negatively photo*pathic* to daylight and to greater intensities of light.

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