MODIFIABILITY IN BEHAVIOR.

I. BEHAVIOR OF SEA ANEMONES.

BY

H. S. JENNINGS.

A thorough study of the modifiability of reactions to external stimuli in lower organisms seems at present one of the great desiderata in the study of animal behavior. Recent work has been devoted largely to the study of sharply defined forms of reaction and to the discovery of conditions under which these forms appear in the typical way. As a result there is a widespread impression that the behavior of lower organisms is composed of invariable reflexes, occurring always in the same way under the same external circumstances. This is far from the truth and leads, as it seems to the writer, to a fundamentally false conception of the nature of animal behavior. Inner states and changes are fully as important in determining behavior as are external stimuli, modifying fundamentally the reactions which the latter produce. The present studies are devoted to an analysis of some of these modifying factors; in other words to some of the inner factors in behavior.

The study of the behavior of sea anemones herewith presented was made possible by a stay at the Carnegie Research Laboratory at the Tortugas. I am under great obligations to the Carnegie Institution and to the director of the laboratory, Dr. A. G. Mayer, for opportunity to carry on the work, and for supplying every facility that could assist it. The Tortugas laboratory furnishes an ideal situation for carrying on such investigations. An indefinite number of species of sea anemones and corals can be procured at a few moments notice, and they live as well in the laboratory as in the sea, since the water becomes cooler instead of warmer when brought into the house.

I. CHANGES IN BEHAVIOR DUE TO VARYING STATES OF METABOLISM.

Nagel ('92) and Parker ('96) have shown that the food reaction of actinians toward weak stimuli becomes changed on repetition of the stimulation. A Metridium or an Adamsia at first readily takes filter paper soaked in dilute juice of crab meat. But after this has been fed several times in alternation with pieces of meat, the reaction to the filter paper becomes slower, and finally ceases, while the meat is taken as readily as before. Torrey ('04) shows that in Sagartia the state of hunger or satiety determines largely the reaction to small solid bodies. A very hungry Sagartia readily swallows inert bodies, such as filter paper and sand grains, while a fairly well fed one rejects these, though it takes meat. Has this effect of hunger and satiety any connection with the changes observed by Nagel and Parker, or are these of a different character? What relation have they to the changes due to experience in higher animals? The whole problem of the changes induced in behavior by changing metabolic states is one of the greatest importance for an understanding of the adjustment or regulation produced in behavior. I have attempted to study this matter carefully in a number of sea anemones, and to distinguish modifications due to this cause from those which result from other factors.

Stoichactis Helianthus.

This large sea anemone has often a disk 10 to 15 cm. in diameter. This is covered closely with short tentacles of uniform size, about 8 mm. in length.[1] Stoichactis is voracious; it is usually when captured ready to take large quantities of crushed crab appendages. To three specimens I fed piece by piece nearly all of three good sized ghost crabs (Ocypode). The food reaction depends on contact with the meat itself—that is, on chemical stimuli in combination with contact. Hard parts of the crab, or other indifferent objects, are usually not taken, though in rare cases even filter paper is swallowed.

Food is taken in the following way: If a piece of crab's leg, with some of the flesh exposed, is placed on the disk of a hungry

[1]For photographs of the disk of Stoichactis, see Duerden, 1902, Pl. 1.

specimen, the tentacles immediately surrounding it (including many not in contact with it) begin suddenly to wave back and forth. After an instant this usually ceases, and all is absolutely quiet for a few seconds. Then the movement begins again. All the tentacles that in their waving motion come in contact with the food, bend over against it and shrink, in such a way as to hold it down against the disk. Now that portion of the disk bearing the food begins to sink inward, by a folding of the surface. The mouth, which may be 4 or 5 cm. distant, begins to open, and the walls of the esophagus protrude from the mouth as large bladdery lobes. The region between the mouth and the food body begins to contract, the tentacles borne here collapsing and almost completely effacing themselves. By this contraction the mouth and food approach each other, the intervening region disappearing. Meanwhile other parts of the disk swell and their tentacles become plump and enlarged; this appears to be a secondary phenomenon due to the squeezing of the internal fluid from the contracted region to other parts. The esophageal lobes increase in size, becoming 2 to 4 cm. long, and half as thick; they extend toward the food, finally reaching it. By the contractions and expansions already mentioned the mouth may be moved from the center of a disk 10 cm. in diameter to within 1 cm. of the edge. By this time mouth and food may be hidden beneath the surface of the contracted disk, though in other cases they lie on the surface in plain view. Now the esophageal lobes extend over and around the food, while the tentacles progressively withdraw from it until the food body is lying on the contracted portion of the disk, completely covered by the esophageal lobes. Next that part of the disk beneath the food withdraws, involving an enlargement and further displacement of the mouth, till there is nothing beneath the food body, and it is pressed by the esophageal lobes into the internal cavity. The whole reaction is thus very complex.

Twenty or more pieces of crab, including entire large appendages, may thus be successively taken, till the body of the anemone has become a mere stretched sack full of crab appendages. But in the later reactions of a series the process of food-taking becomes much slower, the animal seeming to become gradually satiated. The food may be taken by the tentacles and held for a long time before it is finally moved to the mouth. In other cases the tentacles do not react for some minutes, the food lying on the disk undisturbed, until finally it is slowly taken. Sometimes there is an interesting combination of the positive food reaction and the negative reaction (to be described later). The food is taken by the tentacles and carried very slowly to the mouth, in the way above described, while the mouth opens and the esophageal lobes are protruded. But when the food body reaches the lobes, or sometimes before, the process stops. The food is released by the tentacles, and is finally carried away and rejected, in the way to be described. Finally, when the animal seems fully satiated, the piece of crab meat may be rejected as soon as it comes in contact with the disk. But after one or more pieces have been rejected one may sometimes see another piece accepted. The internal state is in a condition of most unstable equilibrium, and may easily incline toward the positive or the negative reaction.

Thus it is clear that in Stoichactis the reaction to a given stimulus is by no means a set, invariable property of the organism, but depends on the state of the internal processes. To the same stimulus we may get a quick positive reaction or a quick negative reaction; a slow and deferred positive reaction or a combination of the positive and negative reactions.

Peculiar effects are observed when several pieces of meat are placed at the same time on different parts of the disk. If the animal is hungry all are carried to the mouth; the entire disk folds inward and the pieces are swallowed simultaneously or successively. I have seen six pieces, placed as far apart on the large disk as possible, thus ingested. When the animal is less hungry the results are different. In some cases, when two pieces of meat are placed on the disk, one is swallowed while the other is rejected. If the rejected piece is again placed on the disk after the first piece has been disposed of, it will sometimes be swallowed.

Adding new pieces while swallowing is in progress often produces interference. Thus, in one case two pieces of meat, *a* and *b*, were placed near opposite edges of the disk. Both began to approach the mouth in the usual food reaction. Now two new pieces, *c* and *d*, were placed near the edge midway between *a* and *b*. Thereupon the reaction to *a* and *b* ceased, while *d* was transported to the edge of the disk (about 2 cm.) and dropped off. Now the food reaction was resumed, *a*, *b* and *c* traveling toward the mouth.

Piece *d* was now replaced on the disk. The reaction to the other pieces was suspended, and *d* was carried to the mouth. Here it came against the middle of the esophageal lobe that was extending toward *a*,—in such a way that *d* could not well be ingested without a rearrangement of the lobes. Thereupon *d* was again carried away from the mouth and once more dropped over the edge of the disk. The other pieces were now successively swallowed. Piece *d* was readily swallowed when given to another specimen.

The Rejecting Reaction.—After Stoichactis has become satiated, it rejects food, as we have seen. The rejecting reaction presents a number of points of much interest. By this same reaction the disk is kept clean when débris falls upon it. If a mass of waste matter of any sort (as a mass of dead plankton or a quantity of sand) is placed on the disk of Stoichactis, measures are set in operation which result, within ten or fifteen minutes, in removing this material and leaving the disk free. The behavior in bringing about this result is complex and the operation may be accomplished in more than one way.

The tentacles bearing the débris or the rejected food body collapse, becoming thin and slender, and lying flat against the disk. At the same time the disk surface in this region begins to stretch, separating the collapsed tentacles widely. As a result the waste mass is left on a smooth, exposed surface, the tentacles here having practically disappeared—though under usual conditions they form a close investment almost completely hiding the surface of the disk. Thus the waste mass is fully exposed to the action of waves or currents, and the slightest disturbance in the water washes it off. Under natural conditions this must usually result in an immediate removal of the débris. If this does not occur at once, often the region on which the débris is resting begins to swell, and becomes a strongly convex, smooth elevation, thus rendering the washing away of the mass still easier.

But the process may go much farther. If the débris is not removed in the way just described, new reactions set in. If the mass is nearer one edge of the disk this edge usually begins to sink, while at the same time the tentacles between the edge and the waste object collapse and practically efface themselves. Thus a smooth, sloping surface is produced and the waste mass slides off the disk. If this does not occur at once, after a little time the region lying behind the mass (between it and the center of the disk) begins to swell, producing a high, rounded elevation, with tentacles plump and swollen. The waste mass is now on a steep slope, and is bound soon to slide down and over the edge. Sometimes by a continuation of this process the entire disk comes to take a strongly inclined position, with the side bearing the débris below. Often one portion of the edge of the disk after another is lowered in this way, till all the waste matter has been removed. The disk then resumes its horizontal position, with nearly flat or slightly concave surface.

Sometimes the edge bearing the débris cannot be lowered, owing to the fact that it is almost against an elevation in the irregular rock to which the anemone is attached. In this case, after perhaps an attempt to bend the edge downward, the part between the edge and the waste body swells and rises, rolling the mass toward the center, while at the same time the region between it and the center sinks down. The sinking continues till it reaches the opposite edge, so that the mass is rolled across the disk to the opposite side and there dropped off the disk. The process is slow, often taking fifteen minutes to half an hour.

The rejecting reaction is characterized by great flexibility and variability. The débris or refused food sets in operation certain activities; if these do not remove the source of stimulation, other activities are induced until one is successful.

Thus in Stoichactis the same stimulus—crab's meat—may in the same individual produce sometimes the long train of activities resulting in the ingestion of food; in other cases the complicated and variable behavior resulting in rejection, in still others a combination of the two. The deciding factor is internal—the condition of the metabolic processes.

Aiptasia.

Two species of Aiptasia were studied. One was Aiptasia annulata Les.; the other a smaller and darker species, with shorter tentacles, which I have been unable to identify with certainty. I shall call it Aiptasia No. 2. Both came from the moat surrounding Fort Jefferson. Rather small specimens, with columns 4 to 10 cm. in length, were used in most of the work.

The species of Aiptasia are relatively active and quick-moving anemones. Especially is this true of Aiptasia annulata. If the tip of one of the long tentacles is touched, the whole disk and column shrinks with a sudden quick contraction, reminding one of the rapid contraction of a medusa. To the eye all parts of the body appear to contract at once. Often the disk and column have contracted strongly before the actual contraction wave has made any apparent progress from the tip of the long tentacle to the disk. Certainly in this animal the general contraction does not appear to be due to a spreading of an actual contraction wave from one part of the animal to another, through the actual pulling of one region upon the neighboring one, as it does in Hydra, and according to Torrey ('04), in Sagartia. On the contrary, there seems certainly to exist some rapid method of conduction, suggesting nervous action.

In Aiptasia annulata the use of India ink indicates the presence of cilia driving a current away from the mouth and toward the tip of the tentacles, as in Metridium.

Aiptasia annulata usually takes crab meat or filter paper soaked in the juices of such meat, but refuses neutral bodies, such as plain filter paper or sand. Aiptasia No. 2, on the other hand, is usually prepared to swallow readily balls of plain filter paper and other small neutral bodies, as well as crab meat. This furnishes opportunity for some interesting comparative experiments.

Food is taken in the following way: If a small object comes in contact with a tentacle it adheres to the surface, and the tentacle contracts strongly, the whole animal usually contracting at the same time. Then the tentacle bends over and places the food with considerable precision on the mouth. The tentacles near by likewise bend over and are applied to the food body, holding it down against the mouth. This happens even when the body is quite neutral, as plain filter paper, so that the bending of the neighboring tentacles is clearly due to some influence transmitted from the one tentacle in contact with the body. The mouth now opens, the lips protruding a little and seizing the food, while the tentacles may release it and bend away. But sometimes the tentacles follow the food into the mouth and their tips remain enclosed for some time. The actual swallowing of the food is mainly due to the activities of the lips and esophagus; it may occur without any intervention of the tentacles, when the food is placed directly on the mouth. A piece of meat or filter paper may be completely enclosed by either species within ten seconds of the time it comes in contact with a tentacle.

With these two species of Aiptasia the experiments of Nagel and Parker, mentioned on page 448, were repeated and varied, with somewhat peculiar results. Pieces of crab meat and of filter paper (plain or soaked in juice of crab meat) were given alternately to the individual under experimentation. In Metridium and Adamsia, as we have noted, the animal soon comes to reject the filter paper, while still accepting the meat.

In Aiptasia annulata a typical experiment is as follows: The animal is fed alternately filter paper soaked in crab juice and crab meat. Both are taken readily till four pieces of each have been ingested. At the fifth piece of paper—the ninth piece of the whole series—the animal balks and rejects it. But it likewise rejects the immediately following fifth piece of meat! It has evidently lost its hunger, and refuses to take anything. This is the usual result with Aiptasia annulata.

In Aiptasia No. 2 plain filter paper (not soaked in crab juice) was given alternately with pieces of crab meat. In a typical experiment six pieces of filter paper and six of meat were taken in regular alternation. But the seventh piece of paper and the immediately following seventh piece of meat were rejected.

The results above given are the usual ones. But sometimes, though rarely, results are reached which are analogous to those attained in Metridium by Parker. Thus, in one case a specimen of Aiptasia annulata accepted the first piece of plain paper, but thereafter refused paper consistently, while accepting meat offered in regular alternation with it.

For all these results the following explanation suggests itself: The animals when hungry take both meat and filter paper; when satiated they take neither. Usually the tendency to take both ceases at the same point, but sometimes the reaction to the weaker stimulus (filter paper) cease before that to the stronger stimulus—as a higher animal that is not hungry may refuse most things, while accepting peculiarly tempting morsels.

If the degree of hunger is thus the determining factor, then it should be possible to produce the rejection of the filter paper by feeding meat alone. This turns out to be the case. Indeed, usually the rejection of filter paper may be induced more readily by feeding meat alone than by feeding the two alternately, or than even by feeding filter paper alone. Thus, two specimens of Aiptasia No. 2, which we will call A and B, living side by side, were both found to take plain filter paper readily. Then A was fed alternately meat and filter paper, while B was fed successive pieces of meat. After eight pieces had thus been fed to each, A still took filter paper (though slowly), while B refused it absolutely—though B would still slowly take a piece of meat. Thus B, through satisfying its hunger with meat, had come to reject filter paper, while A still accepted it after devouring several pieces. Apparently meat is more satisfying to sea anemones than is filter paper!

In another case a specimen of the same species was fed filter paper alone. It swallowed ten pieces in succession, till the body was puffed out with them, meanwhile ejecting some of the pieces already swallowed, in the intervals between the taking of new ones.

In Aiptasia annulata similar relations were found. The animal could be caused to reject filter paper soaked in crab juice much more readily by feeding it meat alone than by feeding soaked paper alone, or by feeding the two in alternation. A large number of comparative experiments were tried, showing this result to be general. It is therefore clear that the state of hunger or satiety is the essential factor in this behavior, in Aiptasia.

The experiments showed further that it is not the mere mechanical fulness of the digestive cavity that determines acceptance or rejection, but some change in the metabolic processes themselves. Filling the digestive cavity with filter paper does not have the same effect in producing rejection as does filling it with meat. Even when the cavity is so filled that pieces of paper are repeatedly disgorged, new pieces are readily taken. In Aiptasia No. 2, a piece of paper that has been disgorged after remaining some time in the cavity, is usually swallowed again immediately, if it is returned to the disk.

As the animal becomes less hungry the details of the behavior toward food bodies change greatly. In a hungry specimen, as we have seen, the food reaction is rapid, often requiring but ten to fifteen seconds. After several pieces of meat have been ingested the reaction of all parts becomes much slower and less precise. The tentacles touched by the food may not react at all for several seconds; then they bend in a rather languid way toward the mouth, while the surrounding tentacles may quite omit their reaction. The food body is not placed so accurately upon the mouth as in the hungry individual. At a further stage toward satiation, a piece of crab meat applied to the tentacles induces either no reaction at all or a straight withdrawal—a negative reaction; they may then bend back from the disk along the column. If the meat is placed directly on the disk, in contact with the mouth, the latter may very slowly open and in a languid way partly or entirely enclose the food, even when there is no reaction of the tentacles. The mouth is thus usually readier to give the food reaction than are the tentacles.

In this condition of approaching satiation some peculiar combinations and alternations of positive and negative reactions may be observed. In a specimen of Aiptasia No. 2 after five pieces of alternate meat and paper had been taken, another piece of paper was swallowed, then after one and one-half minutes this was disgorged. The disgorged piece lay on the disk for a few seconds, then the mouth opened and began swallowing it again. But after it was about half enclosed, it was again rejected. Now it was grasped again and partly re-swallowed, then again rejected. This performance was repeated once more before this piece of paper was definitely rejected. A fresh piece of paper presented immediately after was slowly swallowed, then in two minutes disgorged. The anemone presented exactly the spectacle which we should interpret in a higher organism as a struggle between desire and repugnance for the available food.

In another case a piece of meat was presented after six pieces had been swallowed. The tentacles reacted only very slowly, but finally deposited the piece of meat on the disk, and withdrew. The mouth opened part way, then closed again without ingesting the food. Later it opened again a very little and enclosed a minute shred of the meat between its lips. The piece was thus quietly held for ten minutes, when it was seen to be sinking imperceptibly. Fifteen minutes after it was given it was completely enclosed. Many other cases were seen of partial rejection and acceptance of the same piece of meat. At times after one piece has been rejected, another is accepted.

In Adamsia and Metridium, according to Nagel ('92) and Parker ('96), after the tentacles of a certain region of the disk have through repeated trials come to reject soaked filter paper, those of another part of the same disk will still carry it to the mouth. This shows clearly that a general lack of hunger on the part of the organism as a whole cannot be the only factor involved. In Aiptasia No. 2 I tried experiments to determine whether there was the same independence in the tentacles of different regions. Crab meat was given to the tentacles of the left side; these carried it to the mouth, where it was swallowed, the tentacles of the right side playing no part in the reaction. After the tentacles of the left side had taken five pieces they reacted very slowly, a piece of meat resting against them for several seconds before it was seized. When it was finally carried to the mouth, however, it was swallowed readily. The next piece of meat, not being seized at once by the left tentacles, was transferred to those of the right side. They seized it instantly and quickly carried it to the mouth. Thus it is clear that the experience of the individual tentacles plays some part in the behavior; either from fatigue or some other cause, tentacles frequently stimulated gradually lose the tendency to respond. The fact that this result is produced by meat, the purest form of food, seems to indicate that fatigue may be the cause.

But the rest of the experiment indicates that this plays only a minor part in the change of behavior. After a short rest the giving of food to the tentacles of the left side was resumed. They continued to carry it slowly and with much delay to the mouth, where it was very slowly swallowed. After taking four more pieces, the tentacles of the left side absolutely refused to carry any more food to the mouth. The mouth had now almost ceased taking food when directly applied to it, though after some minutes the food was finally ingested. Now a piece of meat was given to the tentacles of the right side, which had only reacted once, and that more than fifteen minutes ago. Yet they behaved in exactly the same way as did the others, refusing to react at all, save by hanging back from the disk along the column.

Thus it is clear that the animal is a unit so far as hunger and satiety are concerned. If the satiety has arisen through the activity of the tentacles of one side, the tentacles of the other side are equally affected by it. It is the general progress of metabolism that is the chief factor in determining the reactions to food.

As Torrey ('04) has already noted for Sagartia, the reactions of satiated sea anemones differ in many other ways from those of hungry specimens. The well fed animal reacts much less readily and strongly to simple mechanical shock. If touched with a needle the well fed individual of Aiptasia either does not react at all, or contracts very slightly, while the hungry specimen reacts suddenly and powerfully. A slight disturbance in the water has no effect on the well fed individual, while the hungry one contracts strongly. To chemical stimuli the same relations apply. A much stronger solution of any given chemical is required in order to produce contraction in the well fed individual, as compared with the hungry one. The bearing of such facts on quantitative determinations in reaction work is evident. If we should attempt to determine the strength of a given chemical which causes contraction in Aiptasia, we should obtain totally different results, according as we used specimens that were very hungry, moderately hungry, or thoroughly satiated. No "normal" concentration for causing reaction could be determined for even a single given specimen, for the state of metabolism, and with it the tendency to react, is continually changing.

It is, of course, clear that the change due to varying metabolic states cannot be interpreted alone as a general increase or decrease of sensitiveness. Much more significant is the complete qualitative change in the nature of the reaction to a certain stimulus, due to this cause, which we have seen both in Stoichactis and in Aiptasia.

2. ACCLIMATIZATION TO STIMULI.

Sea anemones show acclimatization to stimuli in the same way as do the protozoan Stentor and many other low organisms. A light stimulus that is not injurious may cause at first a strong reaction, then on repetition produce no reaction at all, or a very slight one. This is easily shown with Aiptasia annulata in the following way: A specimen is selected with outspread disk close beneath the surface of the water. From a height of about 30 cm. a drop of water is allowed to fall on the water surface just above the disk. At once the animal contracts strongly. Waiting till it has expanded again, another drop is allowed to fall in the same way. As a rule there is no reaction to this or to succeeding drops. Sometimes there is a response to the first two or even three drops, but usually there is no reaction after the first one. A slight reaction of a different sort, that often comes on later, will be mentioned in the next section.

Experiment shows that the failure to respond is practically universal if the drops fall three minutes or less apart. With drops five minutes apart there is still marked evidence of acclimatization, though irregularities appear. With drops falling at intervals of more than five minutes I was unable to satisfy myself with certainty that acclimatization occurs.

Related to the present subject are changes in the reaction to light. Aiptasia annulata is very sensitive to light, expanding in darkness, but contracting after a few seconds when exposed to strong light. In ordinary daylight the animal remains contracted for some hours, but after such a period most specimens extend in spite of the light. In comparative darkness the animals direct the disk toward the source of light, through a contraction on the side of the column exposed to the light. After remaining undisturbed for a long time in an aquarium that is fairly well lighted, the animals give up their orientation with respect to the strongest source of light; with less light they retain it.

3. REACTIONS MODIFIED AS A RESULT OF THE PAST EXPERIENCES OF THE ORGANISM.

Under this head will be considered all positive changes in reaction, due to former stimuli or former reactions of the organism, aside from those due to changes in metabolism.

We have already described certain cases belonging here. In the reaction by which the disk is kept clean in Stoichactis we find that a mass of débris on the disk causes first one reaction, then another, till one of these or a combination of several rids the animal of the stimulating agent (see p. 451). In this case either the continuation of the same stimulus, or the fact that a certain reaction has been given, induces a new reaction, without change in the external conditions.

A similar phenomenon is often seen in the experiments with falling drops of water, described above. To the first drop the animal responds by a sudden sharp contraction, then to a considerable number of drops there is no response. Now if the drops continue, the animal usually begins to shrink slowly away from the region where the drops are falling, so that in the course of time the disk has been withdrawn some distance below the surface, though no decided reaction has occurred to any one stimulus. These facts are precisely parallel to those which I have described in a previous paper (1902, p. 50) for the infusorian Stentor.

More marked changes result when the animal is stimulated by light strokes of a rod. At the first stroke on the disk Aiptasia contracts strongly. It then extends in the same direction as before. When it is fully extended the stimulus is repeated. The animal responds in the same way as at first. This is usually continued for about ten or fifteen stimulations, the animal each time extending in the same direction as at first. But at length, when stimulated anew, the animal contracts, bends over to one side, and extends in a new direction. Under natural conditions, where stimulation at every extension would usually be due to some fixed object, this would of course put an end to the series of stimuli. If, however, the stimuli are still continued after each extension, the animal repeats for a number of times the extension in the new direction, then finally turns again and tries a new position.

This may be repeated many times. But in the course of time the reaction becomes changed in a still different manner. The anemone releases its foothold and moves to a new region. This result I have not succeeded in attaining by striking the animal with a rod each time it extends; the time required is evidently to be measured in hours. But obstructions may be so placed that every time the animal extends, the disk strikes against a solid body. In such a case it is usually found after a few hours that the animal has moved to a new region.

Thus to the same stimulus when repeated many times the anemone reacts first by contraction, then by turning repeatedly into new positions, then by moving away. The phenomena are parallel to those described by the present author ('02) for the infusorian Stentor, and by Wagner ('05) for Hydra. Beyond doubt other stimuli would here, as in Hydra and Stentor, produce the same series of reactions.

In the behavior just described there are at times certain phenomena which bear a striking resemblance to the formation of new habits. Aiptasia annulata frequently extends its body in most awkward turns, the column retaining an irregular and crooked form. This is evidently due to its method of life. The animal lives in irregular crevices and crannies beneath stones or in the hollows of the coral reefs. In order that its disk may protrude into the free water, it is often compelled to extend in the irregular way mentioned, and to retain the crooked forms thus reached. When removed from the natural habitat it still retains these irregularities of form and action. The lower part of the column may stand at right angles to the upper part, or there may be permanent S-shaped bends, or still more irregular forms. It would appear that these must have arisen as a result of the way in which it extends in its natural habitat. The peculiar methods of extension found in given individuals could then hardly be characterized otherwise than as habits, the peculiarities of form being the structural correlates of the habits.

In searching for experiments that would test the possibility of the formation of new habits in sea anemones, the following suggested itself. It should be possible to produce new habits in Aiptasia by so arranging the surroundings as to compel the animal to extend in a new way whenever it extends, and to retain the new form thus induced. If the animal when thus compelled by obstacles to extend in a new direction, still extends in the same direction after the obstacles are removed, one would be inclined to hold that a new habit had been formed.

I supposed that this result would require a long period of time. But some preliminary experiments showed it to be attained, in some cases, with such absolute ease as to raise the doubt whether we have here anything that can be called habit formation. Thus an individual attached to a plane horizontal glass surface was bent in extension far over to the left. Stimulating it repeatedly, it contracted at each stimulation, then bent, in extending, again to the left. This continued for fifteen stimulations, one succeeding another as soon as the animal had become fully extended. At the next contraction the animal turned and bent over to the right. Now when stimulated it contracted as before, then bent regularly, in extending, over to the right. It seemed to have acquired a new habit—bending to the right instead of to the left.

Attentive examination showed that when the animal contracted in response to stimulation, the concave side of the column contracted a little more than the rest, so that that side remained a little shorter. In other words, the animal did not take on an entirely symmetrical structure, but the region which was most contracted in extension remained most contracted also in the contracted animal. Now on expanding, all parts extended more or less proportionately to their extension in the contracted animal, so that the original curved form was regained. In other words, the structural conditions resulting in the curved form were not really given up even in contraction, and were only made evident when extension occurred.

If the animal was compelled by repeated strong stimulation to contract maximally in all parts, then in extension there was no greater tendency to bend in the direction previously occupied than in any other. And in about half the individuals this result followed (after once the first habitual position found in nature had been given up) even after a single stimulation, so that there was no indication of anything like the formation of a new habit.

What is the interpretation to be given to the numerous cases in which bending in a certain direction when extended *does* induce, in the way set forth above, bending in the same direction on a new extension? Is this the formation of a habit? It is certainly a condition of affairs that gives the same result as habit formation. The anemone might indeed be looked upon as a sort of structural model, illustrating the principles on which habit formation might occur. A certain action (extension in a certain direction) leaves structural peculiarities, persisting even in the intervals of action (in the contracted state), which result in a repetition of the same action. Is not this the picture that we commonly make for ourselves of the real nature of habit formation? In the sea anemone this seems to occur in a relatively gross way, but it appears difficult to point out any difference in principle between this and habit formation. If the persisting structural peculiarities were of such a nature as to be hidden from observation, there would be no ground for hesitation in calling these phenomena the formation of habits. There can hardly be doubt that the striking individual peculiarities of action and structure, described above, have arisen in precisely this way, so that it plays the part taken by habit formation in higher animals.

It would be well if the study of this matter could be extended to the same individual for a long time, beginning with a young, still regular, specimen, compelling it to live in a position where it would have to extend in a definite irregular way. In this way the development of the structural correlates of the habits (?) could doubtless be observed.

The facts may be summed up for the anemone as follows: Performance of a certain action involves the assumption of certain structural conditions. These conditions persist in a slight degree even in the intervals between the actions. At a new action they show their influence by causing it to take place in the same way as the former one. This gives the same results as what we are accustomed to call habit.

4. GENERAL AND COMPARATIVE.

The sea anemones are among the lowest of the Metazoa, and their behavior, when compared with that of most other animals, is of a very simple character. Yet it is evident that even in these low organisms the reaction to a given external stimulus depends upon many things beside the nature of the stimulus itself. Varying states of metabolism induce totally different reactions to the same stimulus, one state producing the long train of actions looking toward the ingestion of food, another inducing the equally long and variable chain of activities resulting in rejection. The same factors cause marked changes in reaction to other stimuli than possible food. Past stimuli received and past reactions performed likewise determine the reaction to a given external condition, resulting sometimes in a cessation of reaction, in other cases in a complete change in its character. Certain simple conditions produce a tendency in the organism to perform more readily an act previously performed (bending, on extension, in a certain direction).

Examination of the conditions under which the animals live shows clearly that all the usual reactions and modifications of the reactions are such as to assist in adapting the organism to its environment. In other words, they aid the physiological processes of which the organism is the seat. Aiptasia annulata, for example, lives in crevices beneath and among stones or coral rocks. It is, of course, evident that its food reactions maintain its metabolic processes, which would necessarily cease in their absence, that the rejecting reaction keeps the surface clean, so that respiration may take place uninterruptedly, and obstacles or injurious substances be avoided. The transformation of the food reaction into the rejecting reaction after the animal is satiated with food is of course as much to the interest of the sea anemone as it is to that of higher animals. If the food reaction were an invariable reflex, occurring whenever food is present, without regard to internal conditions, the results would be disastrous. The fact that the very hungry animal will take indifferent bodies that would otherwise be rejected is of course likewise adaptive; as Torrey ('04) remarks "substances with a very small food value must be of some importance to a starving polyp although they would not be desirable as food to a well nourished animal."

The tendency of Aiptasia to remain in the dark and to contract when strongly lighted keeps it in the crevices where it finds protection for its soft body. The fact that it faces and bends toward the lighted side keeps its tentacles and disk directed toward the entrance to the crevice, where food may be captured; if they were directed toward the darkest part of the crevice little or no food would be obtained. While the contraction under light is protective, it would result, if continued indefinitely by a lighted polyp, in starvation; we find that after a considerable period of light the animal extends. In correlation with its life in irregular crevices or under stones we find that Aiptasia does not take any definite position with reference to gravity, as some other anemones do. Such a reaction would render its usual habitat impossible. The tendency to react by a quick contraction when there is a slight disturbance in the water is undoubtedly protective. Yet such a disturbance when not followed by an attack from its author is not harmful and the animal under such circumstances quickly resumes its usual behavior, even though the disturbance continues. But such a disturbance maintained indefinitely would result in loss of opportunity for obtaining food, and the animal after a time shrinks gradually away from such a disturbed region. Injurious stimuli, interfering with the natural physiological processes of the polyp, cause contraction—the animal withdrawing from the field of action for a time. But this continued indefinitely would result in a loss of food and doubtless other injurious effects. We find that the animal has recourse then to extension in another direction, and finally to creeping away and establishing itself elsewhere. Located in an irregular crevice, we find that the polyp extends in various directions, until it finds a direction in which its disk and tentacles are unimpeded in their spreading to form a trap for prey. It then continues to extend in this manner, even though this may require the body to bend at right angles or to take other irregular forms. It continues to extend in this manner even when removed from its irregular crevice, and the body is found to have become structurally modified, so that a collection of Aiptasias shows many crooked and zigzag shapes, each being an adaptation to the crevice in which the animal lived. The formation of such habitual methods of extension can be imitated and modified in the laboratory.

All together, the activities and their modifications are clearly such as to directly adjust the organism to its environment, enabling the physiological processes to continue under all sorts of conditions. It has become the fashion to neglect such facts, but they fairly force themselves on the attention of the careful student of the behavior, and their existence can hardly be held to be accidental. To remove such an organism to the artificial conditions of the laboratory and then endeavor to understand its behavior is like dissecting an internal organ out of the body and trying to understand its functions when thus separated from the other structures with which it interacts. Almost everything the animal does has a direct relation to something in its usual environment, and when cut off from this environment, its activities are likely to become unintelligible. One can hardly resist the belief that the fact that these activities do assist the physiological processes of the organisms has determined their selection and retention from among other possible activities.

This adaptation and adaptive modifiability of behavior in sea anemones and their relatives has not been explicitly set forth in most works dealing with their reactions. Yet when other careful accounts of behavior in such organisms are analyzed we can discover such relations as clearly as in Aiptasia. Let us look for example at the cases of Hydra, studied by Wagner ('05), and of Cerianthus, as described in the classical papers of Loeb ('91). It will be found instructive to consider the conditions on which the retention of a certain position depends. Hydra and the sea anemones tend as a rule to retain a position at rest, with the foot attached and head free. This usual position is often said to be due to a reaction to gravity, or to contact, or to some other simple stimulus. But when we examine into the matter closely, we find that it is not an entirely simple one. Let us take first the case of Hydra. Suppose the animal is placed on a horizontal surface with head downward and foot upward. It does not retain this position, but bends the body, placing the foot against the bottom, releases its head, and straightens upward. Aiptasia shows the same reaction. In neither of these animals is the reaction due to a tendency to keep the body in a certain position with reference to gravity, for both keep the body indifferently in any position with reference to the pull of gravity, provided that the foot is attached and the disk and tentacles can be spread freely. To what then is the reaction due? Evidently there is a tendency to keep the foot in contact with a surface, for the body of the inverted Hydra is bent till the foot comes in contact. There is likewise a tendency to keep the head free, for it is released. But this is not all, for now the body is straightened, then the tentacles are spread out symmetrically in all directions. It is clear that the reaction is directed toward getting the organism into a position that may be called "normal," and this normal position has various factors—attachment of foot, freedom of head, comparative straightness of body, and tentacles outspread.

Suppose now that our Hydra has reached this position, and all the conditions remain constant; is this sufficient? We find that it is not. If the conditions remain so constant that no food is obtained, the Hydra becomes restless and changes the position of its body repeatedly, though still retaining its attachment by the foot. Later even this is given up, and the animal, of its own internal impulse, quite reverses the position attained through the "righting reaction." It now bends the body, attaches the head, and releases its foot, thus bringing it back into the inverted position.

Is this because the irritability of head and foot have become reversed, so that the head now tends to remain attached, the foot free? Apparently not, for no sooner has the animal taken the inverted position than it draws its foot forward and now performs the "righting reaction" again, so that it stands once more on its foot. These alternations of behavior are repeated, and we find that by this means the animal is moving from place to place (see Wagner, 1905, Fig. 3).

It seems clearly impossible to refer each of these acts or the whole behavior to any particular present external stimulus. An internal state—hunger—drives the Hydra to move to another region, and these different opposite acts are the means by which another region is reached. Each phase of the locomotion is evidently partly determined by the fact that a certain other phase has just been performed, partly by the general state of hunger. The same behavior is shown by Hydra under continued injurious stimuli of different sorts.

In speaking of righting reactions, it is often said that the organism is *forced* by the different irritabilities of diverse parts of the body to take a certain orientation with reference to gravity or to the surface of contact (see for example Loeb, 1900, p. 184). The facts just brought out (taken from Wagner) show that we cannot in Hydra consider this orientation forced, save in the general sense that all things which occur may be considered forced—including of course the behavior of man. Man takes sometimes a sitting position, sometimes a standing one, sometimes a reclining one, depending upon his "physiological state" and past history, and the facts are quite parallel for Hydra. So far as objective evidence shows, the behavior is not forced in Hydra in any other sense than it is in man. Both organisms take that position which seems best adapted to the requirements of their physiological processes; these requirements vary from time to time.

In the sea anemone Cerianthus the conditions for staying in a certain position are somewhat more complex than in Hydra, according to the account given by Loeb (1891). Cerianthus is usually found in an upright position, inhabiting a tube made of mucus and imbedded in the sand. If placed head downward in a test tube, it rights itself in the same way as Hydra and Aiptasia, freeing the head, bringing the foot into contact, and straightening the body. But in Cerianthus Loeb showed clearly that gravity plays a part in the behavior. If the animal is placed on its side on a wire screen of large mesh, it bends its foot down through the meshes, lifts up its head, and takes its usual position with reference to gravity. If now the screen is turned over, the animal again directs its head upward, its foot downward—as a human being under similar circumstances would do if possible. It may thus weave itself in and out through the meshes.

But to be in line with gravity, with head above and free, is not the only requirement for Cerianthus. Loeb found that it would not remain indefinitely in this position on the wire screen, as it does in the sand. After a day or so it pulls its foot out of the wire and seeks a new abode. Only when it can get the surface of the body in contact with something, as is the case when it is imbedded in the sand—in its natural habitat—is it at rest. If this condition is fulfilled, the requirement of the usual position in line with gravity may be neglected. Loeb found that when the animal is placed in a test tube, so that its body is in contact with the sides, it remains here indefinitely, *even though the tube is placed in a horizontal position* (Loeb, 1891, p. 54). The head is bent upward, but the body remains transverse to the direction of gravity.

Examples of the fact that a certain orientation with reference to gravity is not a rigid requirement even in animals that usually or at times react to this agent, are common among sea anemones and other lower organisms. Thus, Torrey ('04) shows that Sagartia, though it usually maintains an upright position, may ofttimes take a position on the surface film, with head downward. In the rejecting reaction of Stoichactis, described on p. 451, we have clearly a reaction with reference to gravity, though one which even the most sanguine could hardly denominate a fixed tropism. The situation "waste - matter - on - the - disk - not - removed - by - the - first - (usual) - reaction" is responded to by taking such a position with reference to gravity as results in removing the waste; then the reaction to gravity ceases. This is somewhat analogous to the reaction to gravity described by Bohn (1903) in the hermit crab. While investigating a shell which it may adopt as a home if fitting, this animal takes up a certain position with reference to gravity—namely, with the body on the steepest slope of the shell, and head downward; it then turns the shell over and ceases to react with reference to gravity. Of a different but equally significant character are the variations shown in the reactions to gravity by the low acelous flatworm Convoluta, as described by Bohn ('03b) and Gamble and Keeble ('03). Under conditions that are favorable Convoluta remains on the surface of the sand. But when the sun becomes hot, or when the tide rises, so that the animal is likely to be washed away, it becomes "positively geotropic," going downward in the sand, where it is protected. When the tide falls again Convoluta becomes "negatively geotropic," thus reaching the surface of the sand, where it obtains food and carries on its usual activities. These alternations of reaction become a fixed habit with Convoluta, so that when removed to an aquarium it still goes downward at high tide, upward at low tide, though the conditions surrounding it remain constant; it may thus be used for a time as an in-door tide indicator. Gradually, however, when removed for a long time from the influence of the tides, this alternation of reactions to gravity ceases, showing it to be a true habit, resulting from individual experience. Many other instances of reactions to gravity, of the most diverse sorts and variable character, could be given. Gravity affects organisms in many diverse ways—determining the distribution of internal substances of differing specific gravity, causing differences in the ease of movements in diverse directions, inducing strains or pressure in unaccustomed parts of the body when an unusual position is taken—indeed, influencing the life processes in almost every detail. Any of the points at which it comes in contact with the life processes may serve as the basis for a reaction, so that we find behavior induced by relations to gravity in different organisms to be of the most diverse character. We have been assured by various writers that the reaction to gravity must be explained in the same way in all cases, but this is evidently said rather in the capacity of a seer or prophet, than in the capacity of a man of science whose conclusions are inductions from observation and experiment.

Returning to Cerianthus, we find, according to Loeb, that even the usual position in line with gravity and with sides in contact, does not satisfy the animal indefinitely, if left quite undisturbed. If it secures no food it again leaves its place and seeks another region.

Thus in order that Cerianthus may remain quiet in a given position, a considerable number of conditions should be fulfilled, constituting the usual, and perhaps what we may call the "normal" state of affairs for this animal. These conditions are the following: (1) The foot should be in contact; (2) the head should be free; (3) the body should be straight; (4) the axis of the body should be in line with gravity, with the head above; (5) the general body surface should be in contact; (6) food should be received at intervals. If these conditions are largely unfulfilled, the animal becomes restless, moves about, and finds a new position. But no one of these conditions is an absolute requirement at all times, unless it be that of having the head free. In the wire screen the animal remains for a day or two in the required position with reference to gravity, even though foot and body surface are not in contact. In the horizontal tube it remains with foot and surface in contact, though the body is not straight nor in line with gravity. If all conditions are fulfilled save that of food, the animal remains for a time, then moves away.

Clearly, the holding of any given position depends, not on the relation of the body to any one or two sources of stimulation, but on the proper maintenance of the natural physiological processes of the organism. The actinian does not always maintain a certain position with relation to gravity, nor does it always keep its body straight, nor its foot in contact, nor its body surface in contact. It does not at all times receive food. It may remain quiet for considerable periods with one or more conditions lacking. The organism tends on the whole to take such a position as is most favorable to the unimpeded course of its natural physiological processes. Certain usually required conditions may be dispensed with provided other favorable ones are present. The behavior, like that of higher animals, represents a compromise of the various needs imposed upon the animal by its physiological processes.

Examination of the literature shows that throughout the Cœlenterates there is a similar dependence of behavior on the progress of the internal physiological processes, particularly those of metabolism. The state of metabolism decides whether Hydra shall creep upward to the surface or shall sink to the bottom (Wilson '91), how it shall react to chemical and to solid objects (Wagner '05), whether it shall remain quiet in a certain position, or shall reverse this position and undertake a laborious tour of exploration. In the sea anemones it determines, as we have seen, even the details of long trains of reaction. The state of the metabolic processes appears to be the most important determining factor in the behavior of Cœlenterates.

The same dependence of behavior on the internal physiological processes is found in other groups, even in those much lower than the Cœlenterates—the Protozoa, and particularly the Bacteria. This is brought out especially in some of the work of Engelmann. A number of examples of this relation will be given in the paper which follows the present one, so that they may be omitted here. The fact that in higher animals behavior depends largely on hunger and satiety is, of course, so well known that it need not detain us.

The relation of behavior to the internal physiological processes, of which we have given some examples in the foregoing pages, is manifestly of the greatest significance for the understanding of behavior. The facts adduced show directly that in many cases the determining factor in reactions to stimuli is not the anatomical configuration of the body, taken in connection with simple laws of conduction, but is the relation of the action of the external agent to the internal processes. The problem presented by the fact that the same stimulus, in the same intensity, applied to the same part of the body, produces qualitatively different and even opposite results, depending on the inner metabolic states, seems not to have received the attention it deserves. It evidently places marked difficulties in the way of a simple mechanical conception of the reflex process, based merely on the anatomical structure of the organism. The internal physiological state determines in some way which of various courses within the body the transmitted stimulus shall follow and what organs it shall arouse to activity. The organism cannot be looked upon as a static structure, on which external agents must act in a simple invariable way. *The organism is a process*, and some of the chief determining factors in behavior are given by the relation of the internal to the external processes. As the internal processes change, the reaction to external agents changes correspondingly. We find that reactions which assist the existing internal processes are continued or repeated, while those which oppose them are changed. This gives one of the chief bases for the regulatory character of behavior, as I shall attempt to set forth in farther detail in the paper which follows the present one. The metabolic processes, while the most striking of those taking place in the lower organisms, are of course not the only ones occurring in animals. An immense number of other processes are in progress, and the relation of external agents to these processes ,may and does equally determine behavior. This gives the phenomena of behavior their complexity, preventing them from being in relations of *simple* dependence on external agents, as they are often represented of late. Such a view quite underestimates the difficulty of the problem of behavior. The dependence on external agents exists, but is complex, and can usually not be predicted without a knowledge of the present internal state of the organism—this depending on its past history and the course of its various internal processes.

It would of course be more convenient if the problems of behavior were as simple as they are often proclaimed to be. Work revealing their complexity is naturally not received with the acclaim that greets the announcement that all these things are simple and easy. But if our object is really to obtain control of the vital processes, then we must face them in all their complexity. To control animal behavior it is necessary to study animal nature, in much the same way that it is necessary to study human nature in order to control human behavior. It is necessary to know the past history of the organisms, and what is going on within them, in order to predict what they will do. He who expects even the lower animals to behave always in certain simple invariable ways when acted upon by the various forces of nature has many disappointments in store, when he comes to make a thorough study of the matter. The internal modifying conditions must be made the object of deliberate and extended investigation in lower animals as well as in higher ones, before the study of behavior can be placed on a really scientific basis.

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