SOME POINTS REGARDING THE BEHAVIOR OF METRIDIUM.

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It has recently been shown that the reactions of many sea anemones are modifiable, in dependence on a variety of internal conditions (Jennings, 1905). The purpose of the work here presented was to determine how far similar relations hold for *Metridium marginatum*. Since *Metridium* is the commonest of our sea anemones, and the one most used in investigation and instruction, it is important that its behavior should be well known. The work was suggested by Dr. H. S. Jennings, and carried out under his direction at the Marine Biological Laboratory at Woods Hole.

I. Changes in the Reactions to Certain Sorts of Food Bodies.

The point to which experimentation was first directed was the interpretation of the results of certain experiments of Nagel (1892) and Parker (1896). In Parker's experiments alternate pieces of meat and filter paper (soaked in meat juice) were given to the tentacles of one side of the disk of *Metridium*. It was found that while the meat was swallowed each time with equal readiness, the time taken in swallowing the paper increased, and after three or four trials the animal no longer ingested the paper, though the latter contained each time the same amount of meat juice as at first. After reaching this result with the right side of the disk, the same series of experiments was performed on the opposite side of the disk of the same specimen. It was found that the left side had not become modified by the experience of the right side. It at first took the paper, then by the same gradual change seen previously on the right side, it came to refuse the paper. A series of records of the times required for swallowing the meat and paper in such an experiment by Parker are given in the following table:

	Right Side.	Left Side.		Right Side.	Left Side.
1. Meat	85 sec.	45 sec.	9. Meat	70 "	35 sec.
2. Paper	80 "	90 "	10. Paper	—	85 "
3. Meat	50 "	45 "	11. Meat	40 "	30 "
4. Paper	90 "	—	12. Paper		95 "
5. Meat	40 "	45 "	13. Meat		35 "
6. Paper	105 "	55 "	14. Paper		—
7. Meat	50 "	35 "	15. Meat		35 "
8. Paper	—	105 "	16. Paper		—

What is the cause of the change of behavior in these experiments? Several possibilities suggest themselves:

1. Jennings (1905) found that in *Aiptasia* similar effects were produced, and in this case the result was evidently due mainly to changes in the state of hunger. The very hungry *Aiptasia* took meat and paper readily, but after feeding a short time it refused paper, and later it came to refuse meat also. The animal could be caused to refuse paper more readily by feeding it meat alone than by feeding paper alone or by feeding the two in alternation. It was evident that the changed reaction toward paper was due to loss of hunger. We must inquire whether this factor plays a part in *Metridium*.

2. Nagel (1892) referred the changes in reaction toward paper to a process corresponding to what we call *judgment* in higher animals; he held that the animal discovers by experience that the paper is unfit for food, and thereafter refuses to take it. Such a process in so low an animal would of course be of great interest, and the evidence for it needs to be examined carefully. Nagel held that it was owing to the lack of close nervous interrelation of parts in these animals that the experience of one side is not transmitted to the opposite side.

3. Parker sums up the phenomena shown in these experiments as follows: "The successive application of a very weak stimulus is accompanied, not by the summation of the effects of stimulation, but by a gradual decline in these effects, till finally the response fails entirely" (Parker, 1896, p. 116).

In my experiments I attempted to test these different possibilities, and to work out in a systematic way the various factors which modify reactions in *Metridium*.

The taking of food has been well described by Parker (1896). It is important to note that ciliary action plays a large part in the taking of food by *Metridium*. Muscular movements of the tentacles, disk, and œsophagus also plays a part, but a less important one than in the anemones studied by Jennings (1905). The tentacles bearing bits of food are bent toward the mouth, and the cilia of the tentacular surface carry the food toward the mouth opening. The cilia of the œsophagus are usually beating outward, but when food enters the mouth the stroke of the cilia of the part in contact with the food becomes reversed, so that the food body is conveyed inward (see Parker, 1896, 1905). I have found that the reversal of the œsophageal cilia is frequently caused in *Metridium* by indifferent solids, such as filter paper, so that such bodies are ingested.[1] There is much variation in regard to this matter, some individuals take filter paper readily, others slowly and only at times, others not at all. As we shall see later, this depends largely on the degree of hunger.

We will now take up experimentally the various possibilities of modification above distinguished. In studying these matters, it is most important that specimens which are fresh and in good condition should be used, otherwise clear results will not be obtained.

1. *Hunger*.—Conditions of hunger and satiety affect the food reactions of *Metridium* in a most decided way. When the animal is very hungry (and in good condition otherwise), the column is extended, becoming long and slender, while the disk is widely spread, and the tentacles extend a considerable distance beyond its edge. If the animal remains contracted, it can often be induced to extend by placing a piece of clam meat or some meat juice on the infolded disk. Two or three applications of food will often cause the most obstinately contracted specimens to expand beautifully. If now a piece of mussel of considerable size (having an area equal to the cross section of the column, with a thickness of three or four millimeters) is brought near the edge of the disk, so as to come in contact with the tips of two or three tentacles, a decided reaction is produced. The tentacle tips adhere to the meat, and the tentacles and adjacent parts of the disk contract quickly, so that the piece of meat is drawn inward. It

[1] This was possibly due, as Parker (1905, 1905*a*) has set forth, to the paper's having been touched by the fingers; this matter was not tested.

thus comes in contact with many other tentacles, these bend down upon it. Then all bend over toward the mouth, while at the same time this portion of the disk contracts. Thus the food is brought nearer the center of the disk. The mouth meanwhile opens, and the food is passed into it, partly by the ciliary action of the tentacles, partly by muscular contractions of tentacles, disk and mouth. The latter factors play a more important part in the reaction of a hungry specimen to a large piece of food than does ciliary action.

After ten or a dozen good-sized pieces of meat have been swallowed, the reaction becomes much slower. If the meat is brought in contact only with the outer tentacles, these no longer react, and such food is not taken. If placed on the inner tentacles, the meat is slowly transferred to the mouth, where it is swallowed. The animal is frequently in this condition when brought into the laboratory; food placed on the outer tentacles is refused, while that on the inner tentacles is taken.

The reaction of the tentacles becomes slower as more food is taken, so that the process of ingestion takes a much longer time than at first. Finally, all the tentacles cease reacting to food, and it is not carried to the mouth. But if the meat is placed by the experimenter directly on the mouth, it is ingested. This appears to take place almost alone through the action of the cilia; the reversal of the cilia seems to be more nearly independent of the physiological states of the animal than are the contractions of the muscles. The mouth never reaches a condition where it rejects pieces of mussel placed directly upon it. So much food may be taken that the body becomes puffed out to form a swollen sack, yet new pieces are forced inward. Large pieces of meat may however be refused even when placed directly on the mouth, the lack of assistance from muscular contractions appearing to make it impossible for the cilia to draw them inward. The feeding may be carried so far as to cause internal disturbance, resulting in the disgorgement of the food. But immediately after such disgorgement the mouth will take new food. Sometimes when the animal is nearly filled, a large piece of meat placed on the mouth is partly swallowed, then partly disgorged by a convulsive movement, then the swallowing is resumed. This may happen repeatedly.

The loss of reaction on the part of the tentacles after much food has been taken is not due to fatigue resulting from their activity in taking food. This is demonstrated by the following facts: (1) The animal may be fed from one side of the disk till it is satiated. Now meat given to the opposite side of the disk is not taken, though the tentacles of this side have not been active, and so cannot have become fatigued. (2) Seven hours after the animal has been fed all it will take, the tentacles still refuse to take food, though they have had this period for recuperation. Actual fatigue, as we shall see later, lasts but a few minutes.

The effects of hunger and satiety are further seen in the reactions of *Metridium* to indifferent bodies, such as bits of filter paper. These are commonly taken readily by hungry specimens of *Metridium*. The tentacles react to them, just as to meat, so that they are carried to the mouth. Here they cause the reversal of the ciliary movement in the same way as does meat, so that they are carried inward. But after the animal has been fed a considerable quantity of meat, it will no longer take filter paper. First the outer tentacles refuse it, later the inner tentacles, and finally the mouth. A piece of filter paper placed squarely on the mouth no longer causes the reversal of the stroke of the cilia of the œsophagus, so that it is not carried inward.

The fact that the reversal of the cilia under such stimuli depends on the physiological state of the animal is one of much interest. It shows that the cilia are not entirely independent of such states, as some other facts would seem to indicate.

Seven hours after the animals had been fed an abundant meal of mussel meat, they still refused to take filter paper, though before the meal paper was taken readily.

Thus it is clear that the state of the processes of metabolism is in *Metridium*, as in other sea anemones, a most important factor in determining behavior under mechanical and chemical stimuli. But it is equally clear that this will not explain the results of Parker's experiments, described in the first paragraphs of this paper. Parker found that after one side of the disk has refused to take paper, the other side still accepts it. In repeating

Parker's experiments, I fed in one case six successive regions of the disk, each till it had rejected food, the next would then take it as readily as at first. This refusal then cannot be due to a general lack of hunger, and we must examine the other explanations that have been given.

2. "*Judgment.*" — If the animal comes to reject paper through experience of the fact that the paper is not good for food, there must be some way in which this experience is obtained. It might be supposed that this comes through swallowing the food; being indigestible, its effect after swallowing might cause the animal thereafter to reject it. This was tested by preventing the swallowing of the paper. The animal was fed meat and paper in alternation, as in Parker's experiments. But after the paper had been carried to the mouth and was passing down in the œsophagus, it was removed with a fine pair of tweezers. This is easily done without disturbing the animal. Thus the bits of paper never reach the digestive cavity. Yet the animal comes to reject them as quickly as before. After a few alternations of meat and paper, only the meat being completely swallowed, the animal ceased to take the paper, while it still accepted the meat. Hence the effect of the paper after it reaches the digestive cavity is not the cause of its rejection.

Furthermore, nothing like a contrast or comparison between the meat and the filter paper is necessary in order to induce the rejection of the paper. If successive pieces of paper were fed alone to the anemones, they soon came to reject these as before. In such cases it is noticeable that the animal takes a larger number of pieces of paper than when the paper is fed in alternation with meat. The number of pieces required is about the same as the number of pieces of meat and paper together that result in rejection of the paper when the two are given in alternation. This fact throws some light on the cause of the rejection, as we shall see later.

3. *Repetition of Weak Stimuli, till Effect Fails.* — Is the loss of the positive reaction to the paper due to the general fact that weak stimuli, when repeated, gradually lose their effect? This was tested by excluding this factor from the experiments, in the following way. A given specimen was first tested and found to

accept filter paper (in some cases plain, in others soaked in meat juice). After this first test, the same region of the disk was fed successive pieces of meat, which were all readily taken. After eight to twelve pieces of meat had been accepted, a piece of filter paper like that originally accepted was given to the same region of the disk. *It was not accepted.* This experiment was repeated with many specimens, always with the same result. This result was likewise reached if the animal was not allowed to complete the swallowing of the meat, the latter being removed after it had passed into the œsophagus. This, of course, shows conclusively that loss of hunger is not the cause of the change of reaction toward the paper.

The placing of meat juice on a certain region of the disk causes the food reaction, as Parker has shown. If this experiment is tried successively a dozen times in the same region of the disk, the animal comes to reject filter paper in this region, as in the experiments described in the foregoing paragraph.

Thus it is not necessary that weak stimuli should be repeated in order that the animal shall reach a state in which it fails to react to them. Repetition of strong stimuli (meat) causes failure to react to weak stimuli just as readily as does repetition of the latter. Repetition of strong stimuli alone, of weak stimuli alone, and of the two in alternation, all have the same effect ; the animal ceases to react to weak stimuli.

In all cases in which meat is fed to a given region, moreover, the reaction to strong stimuli ceases some time later than that to weak stimuli. After giving a certain region sixteen to twenty pieces of meat, meat is no longer accepted here, though other regions of the disk take it readily.

4. *Fatigue.* — The facts brought out in the foregoing paragraphs seem to make possible a clear interpretation of the rejection of the paper. It is evidently a case of plain fatigue. After stimulating a certain region of the disk a number of times, it ceases to react — first to weak stimuli, then to strong stimuli — though other parts react as before. The same results are produced whether the successive stimuli are all strong or all weak, or partly strong and partly weak. It appears evident therefore that it is the reaction of the animal, not the precise character of

the stimulus, that causes the fatigue. This is perhaps what should be expected when the nature of the food reactions is taken into consideration. In taking food the region in contact with the food produces a very large quantity of mucus, enveloping the food body. It is not surprising that successive immediate repetitions of this excessive production of mucus gradually exhausts the region. As is usual in fatigue, strong stimuli may produce reaction for some time after weak ones have failed.

The fatigue thus caused usually lasts only two to five minutes. After this period has elapsed the fatigued region is frequently as ready to take food as before — provided the animal is still hungry.

Nagel and Parker have held that the result of their experiments "illustrates the extreme looseness, or even independence, of the nervous activities of the two sides of the animal" (Parker, 1896, p. 116) — since the effects of the experience of one side are not transmitted to the other side. With the recognition that these results are a simple matter of fatigue, they perhaps cease to have any bearing on the question of the closeness or looseness of nervous interconnection. In the highest organisms, as man, fatigue induced by repeated contractions of a finger of the left hand, in erogographic experiments, is not transmitted appreciably to the right hand. But the experience gained by touching a hot iron with the left hand would nevertheless later prevent the right hand from touching it.

II. Other Modifications in Behavior.

A very peculiar modification of behavior is seen in the following: A specimen refuses to take filter paper, though it still takes meat. After it has thus refused paper, two or three pieces of meat are given in succession, and taken readily. Now the bit of paper is again placed on the disk, and it too is swallowed. Clearly, the uninterrupted taking of a number of pieces of meat changes the physiological condition of the animal in some way, preparing it for the taking of any object with which it comes in contact. (After a larger number of pieces of meat, the paper is refused, as we have before seen.)

Acclimatization to weak stimuli is readily demonstrated in fresh, active specimens of *Metridium*. If a light stream of water is directed with a pipette against the expanded disk, the animal contracts strongly. Waiting till it has again expanded, the stream of water is directed upon it as before. This time it does not react. In specimens that are not in good condition, this change of behavior cannot be seen. The animal does not contract at all save under strong stimuli, and if such are repeated, it contracts as at first.

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