PHOTOTAXIS IN FIDDLER CRABS AND ITS RELATION TO THEORIES OF ORIENTATION.

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In the phototactic movements of animals which orient themselves definitely to the light it is almost always the longitudinal axis of the body which is kept parallel to the rays. It is therefore not without interest in relation to the much discussed "theory of tropisms" to find an animal which orients itself sidewise instead of in the usual manner. Such an animal is the common fiddler crab of the Atlantic coast, *Uca pugnax* (Smith), which shows a very decided positive phototaxis, especially in strong light. Like many other crabs the members of this species run sidewise, and in fact they are so constructed that they would find great difficulty in any other form of locomotion. When recently brought into the laboratory they seem remarkably attracted by a bright light. They gather on the side of their enclosure nearest the light and often struggle for a long time to get nearer the source of attraction. By changing the position of the light the crabs may be made to follow it about in any desired direction, changing their course promptly whenever the light is moved. There is lateral instead of longitudinal orientation to the direction of the rays.

When the crabs reach the side of the dish they usually do not maintain their lateral orientation. They frequently face the light, holding their eyes erect and moving from side to side in the endeavor to get as near the light as they can. Very often they settle down facing the light, remaining there for a long time as if spell-bound. There seems to be no tendency to get into a position of lateral orientation once the animal attains to a position of proximity to the light. This orientation is necessary if a certain object is to be followed, but, so far as I can determine by watching its behavior, the crab does not tend to assume it except during loco-

motion. When it has gone as far toward the light as it can it settles down preferably in a position of longitudinal orientation.

When a crab that is facing the light is subjected to very strong illumination it will often raise its body so as to stand supported on the tips of its claws. If the light is withdrawn a short distance the body comes to rest again upon the bottom of the dish. The crab may be made to repeat this act many times by causing the light to approach and recede. The behavior of the animal is apparently the involuntary result of the increase in the tension of the leg muscles brought about by strong illumination.

Similar increase in muscular tone by light is shown in the behavior of the eye-stalks. When a fiddler is seized the eye-stalks are drawn back into the orbits and tightly held there. If, however, the crab is brought very close to a strong light the eye-stalks are erected. If the animal is removed a little further from the light the eye-stalks are pulled back into their orbits again. When brought into strong light the crab is apparently no longer able to hold the eye-stalks down and they come up in spite of the instinct to hold them in a protected situation. If the cornea of one eye is blackened over usually only the unblackened eye rises upon exposure to strong illumination, but the blackened one sometimes does so to a greater or less extent, owing perhaps to the fact that the two eyes usually make associated movements.

The experiment of crossing the eye-stalks was tried in order to see what effect would be produced on the animal's reactions to light. The eye-stalks of the fiddler crab are long and they may readily be crossed like the parts of a letter X and tied in the middle. Crabs treated in this way show great confusion in their reactions to visual stimuli. When approached they give signs of alarm and frequently run directly towards the source of danger. When a light is moved suddenly they often run towards it instead of away as they usually do from all moving objects. Normal phototaxis, however, is mainly destroyed. The crabs neither go directly toward or away from the light with any regularity; in fact, they seem to pay little attention to the light, owing perhaps to the discomfort of their unusual predicament. There is no definite reversal of phototaxis, which I thought might occur under the circumstances, although there is often a reversal in the responses to moving objects. The crabs' actions, however, are hesitating and uncertain; often they move a distance one way and then in another as if the result

of their movements were something unexpected. In a crab with crossed eyes the behavior of objects in its visual field consequent on its movements is different from what it is accustomed to. Under normal conditions fiddler crabs probably possess binocular vision so far as may be judged by the behavior of the eye-stalks and the arrangements of the facets of the eyes, but when the eyes are crossed the animals have two visual fields which give quite different impressions, thus adding further to their confusion. The visual world of such crabs doubtless seems a hopelessly mixed up affair, and it is not surprising that the animals often sulk as if discouraged with their efforts. Crabs kept for several days in order to ascertain if they would improve in the appropriateness of their responses gave only negative results.

The phototactic reactions of fiddler crabs are very easily checked or overcome by fear. When a light is brought near the animals they often scurry away in great haste, and at first one might be led to interpret this behavior as a manifestation of negative phototaxis, but it is a very different phenomenon. Even when showing a strong positive reaction the fiddlers often flee in apparent alarm upon a slight movement of the light. If the movement is a sudden one they are more apt to beat a retreat, while they follow slower movements without fear. When exposed to strong illumination for some time they become more insensible of their surroundings and are dominated almost entirely by the stimulus from the light without regard to movements made near them which at first would send them scurrying off in great haste. They get, as it were, "warmed up" to the work, becoming not only less responsive to other stimuli, but more vigorous in their phototactic activity. I have described similar phenomena in the water-scorpion, *Ranatra*, and other observations have shown that it is a not uncommon trait in tropic responses.

I do not wish to add further to the confusion that exists in the use of the term tropism, but I believe that the retreat of the fiddlers from a moving light cannot properly be described as a tropic reaction. It may be related to tropic reactions as vision is according to RADL, but it is not so much a response to the light *per se* as to a sudden movement or appearance of the light. If we described as negative phototaxis all movements however caused which were directed away from the light we should have to include the flight of the fiddlers under this designation, and say that a sudden move-

ment of the light caused a reversal in the sense of the response. But will anyone maintain that when a wild animal runs away in alarm from a sudden blaze it manifests a negative phototaxis? It is with such an action as, this, rather than with the reactions commonly included under the head of negative phototaxis that the retreat of the fiddlers is more closely related. The flight of the crabs from light has all the characteristics of their flight from moving objects in general. Whenever one enters a room where the crabs are kept or makes a small movement in their vicinity they promptly scuttle away; and they often detect one's presence on a beach for a distance of several rods and make for their holes. These reactions we commonly attribute to fear, whatever physiological explanation we may offer for them, and anyone who has observed the fiddlers scurrying away from a moving light can hardly fail to ascribe their behavior to the same cause.

The point of principal interest in the phototaxis of the fiddler crabs is the relation of their lateral orientation to the theories of tropisms. Can we regard orientation as a direct response in which the animal is involuntarily forced into line, or is it rather to be considered as coming under the pleasure-pain type of behavior, and as therefore related to the voluntary seeking of a certain end which is exhibited in the behavior of higher forms? In order to explain the orientation of a highly organized form like an insect or crustacean in which, in most cases, response to light takes place through the eyes, we may assume that light falling more strongly on one eye sets up impulses which are transmitted more or less directly to the leg musculature. We may assume that the extensors of the opposite side are stimulated, or the flexors on the same side, or both, and that in consequence of this distribution of impulses the animal moves until its body is in line with the rays. In such a case the movements involved in orientation are the same as those employed in ordinary locomotion only the activity of the legs on one or the other side is accentuated according to the position of the body in relation to the direction of the rays.

In the fiddler crab, however, the case is different, and we cannot explain the phenomenon in this way. The legs of the fiddler move in a plane approximately at right angles to the sagittal plane of the body, but they are capable of a certain amount of forward and backward motion which may be employed to change the direction of locomotion. The movements involved in orienta-

tion are different from those employed in ordinary running. They are special movements employed to check deviations from a certain course, a circumstance which would greatly complicate any attempt to explain orientation as a comparatively direct response. The results of observations on fiddler crabs tend to confirm the conclusion reached in studies made on the phototaxis of *Ranatra*,¹ namely, that light is followed much as an animal pursues any other object of interest such as prey or its mate, and until we can give a physiological explanation of these phenomena we are not, I believe, in a position to give a satisfactory explanation of orientation to the direction of the rays of light.

¹ The reactions of *Ranatra* to light. *Jour. Comp. Neur. and Psych.*, vol. 15, 1905.