THE REACTIONS OF CERTAIN MYSIDS TO STIMULATION BY LIGHT AND GRAVITY

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Introduction

Delage (1887) was the first to show that the statocysts of mysids have a balancing function. Since then various authors have made further contributions to the problems of orientation and movement in this group, notably Bethe (1895), Bauer (1908), Menke (1911), von Buddenbrock (1914) and Fraenkel (1931). We still, however, lack any comprehensive account of the behaviour of mysids under laboratory conditions; in particular, attention does not seem to have been paid to the difference in behaviour when "light-adapted" and when "dark-adapted", and also, the tactile sense of these creatures appears to have been disregarded.

The present paper is an attempt to fill some of these gaps and to suggest certain correlations between the behaviour of mysids as seen in the laboratory and in the sea. The following account deals mainly with observations on *Hemimysis lamornae*, but other species, for example *Mysidopsis gibbosa* and *Paramysis arenosa*, have been observed. There do not appear to be any significant differences in behaviour between these species.

The observations recorded here were begun at the Marine Station, Millport, and continued in the zoological laboratories of the University of Glasgow and later at University College, Cardiff. I wish to thank Mr F. S. Russell, F.R.S., for his interest and advice during the course of the work, and Prof. W. M. Tattersall for the identification of certain mysids.

The Reactions of Mysids to Light

Light Adaptation

Franz (1911) and Fraenkel (1931) have described how *Hemimysis lamornae* behaves when light-adapted. The individuals are seen to swim to and fro in the direction of the incident light. One of the chief peculiarities of this reaction is the regularity of the change from positive to negative phototaxis. Each excursion persists for an approximately equal amount of time so that the animal is seen to be swimming backwards and forwards through the same area of water. The reversal of the taxis involves reorientation of the animal so that it is always swimming head foremost. In some degree this appears to parallel the spontaneous change of sign of phototaxis found by Clarke (1932) in

Daphnia, although here one direction of movement was primary, and the movements in the secondary direction were not so long in extent and were of shorter duration. Moreover, in *Daphnia* reorientation is not involved, for Clarke (1932) found that the direction of the excursion was controlled by the postural angle of the antennae, the same orientation of the body to the light source being maintained throughout.

Fraenkel (1931) shows that this movement of mysids is telotactic in nature and not topotactic; for, if two light sources are supplied so that the incident rays cross at right angles they react to one and neglect the other.

From my own observations I conclude that this reaction, as described above, takes place only when light is falling horizontally; for when the lighting is from above the mysids tend to remain on the bottom or very close to it and similar horizontal excursions appear to be made in any direction.

It should also be mentioned here that the phototactic reactions described above are only shown by those mysids which are swimming freely in the water. The conditions under which they swim a few inches from the bottom have been discussed by Cannon & Manton (1927) who point out that in *Hemimysis lamornae* it is a habit, under certain conditions (principally lack of food material suspended in the water), for the animals to descend and stir up the bottom deposit. In this attitude the head is directed vertically downwards and I have not been able to detect any response to light.

The Response to Light of Dark-Adapted Individuals

The subject of this section does not appear to have been dealt with by previous workers, except somewhat briefly by Menke (1911).

Mysids may be dark-adapted in an ordinary photographic dark room and their movements may then be watched by means of a dull red light to which they do not react. This method has been used by other observers (see von Buddenbrock, 1914).

Mysids of all the species investigated showed a much greater tendency to leave the bottom in darkness than in light. A few minutes after the room light was extinguished they were found to be swimming freely in their tank. Under these conditions they may rise to the surface of water contained in tubes of a metre or more in height. This reaction is best classified as a negative geotaxis.

If, when mysids which are dark-adapted are swimming freely in their tank, a light is switched on, they immediately swim to the bottom of the tank with great rapidity and even appear to be trying to swim through it. It is important to note that this downward movement is made quite irrespective of the direction of the stimulating light source; the light stimulus is equally effective from above, from below or horizontally. The movement is always downwards even if this involves approaching the light source. It seems quite impossible to classify this response as any type of phototaxis and, therefore, it may be regarded as light inducing a positive geotaxis.

This effect of light on dark-adapted mysids is in marked contrast to the response to the same stimulus which is exhibited by planktonic forms or by bottom-living creatures, such as cumaceans, which lack definite receptor organs of gravitational stimuli. For in these latter animals the response can be classified in terms of phototaxis alone.

In the mysids we have gravitational and light stimuli acting together, and the response, which is a resultant of these two may be classified as a special instance of telotaxis.

Fraenkel (1931) defines telotaxis (p. 82) as the "assumption of a position so that a certain region of the receptor apparatus is acted upon by the stimulus". Here, where there is a combination of gravitational and light stimuli, it is possible to regard the light as stimulating the animal to assume such a position that a definite region of the gravitational receptor apparatus is acted upon by the stimulus of gravity. Alternatively, it is possible to argue that this response should be regarded as an example of mnemotaxis. Whichever is the correct view in terms of taxes, it seems clear that we are concerned with a combination of stimuli. To demonstrate this, the statocysts, which are the receptors of gravitational stimuli, can be removed.

Observations on Mysids with the Statocysts removed

The Removal of the Statocysts

In small mysids such as *Hemimysis lamornae*, it is only practicable to remove the uropods entire. In larger species it is easier to remove the ramus of the uropod containing the statocyst without damaging the other ramus. However, the results did not differ whichever method was adopted, but the latter operation probably affects the physiological condition of the specimen less.

It cannot be pretended that the operation is anything but severe; in my experience it was unusual for a specimen which had been so treated to live for more than a few (three or four) days. Delage (1887) apparently did not meet with this difficulty. Bethe (1895) recorded that in a mysid from which he removed the uropods a change in the posture of the abdomen was noted; he does not say to what species it belonged. A similar change of posture was especially looked for in *H. lamornae* but no such change was noted.

Behaviour of Mysids without Statocysts

Since Delage (1887) first removed the statocysts of mysids to prove their orientating function, similar experiments have been carried out by various of the authors already mentioned, particularly by von Buddenbrock (1914) who made an exhaustive study of their orientation.

Von Buddenbrock came to the conclusion that if the statocysts of mysids are removed normal orientation is maintained, in the light, by the eyes working through the "dorsal light reflex"; and in the dark, by a "general position reflex". The exact working of this general position reflex is not fully understood, but in the absence of light and with the normal gravitational receptors removed, it suffices to keep the creature correctly orientated even if the body has been unbalanced by the unilateral removal of one of the antennae.

A point of interest, to which little attention seems to have been paid, is that, when the statocysts of a mysid have been removed and it then reorientates itself to light by the dorsal light reflex it will usually become negatively phototactic and move away from the light (a few instances of positive phototaxis under these conditions have been met with). It will be realized that to orientate with the dorsal surface to the light and then move away from the light source interferes seriously with normal movement; for it means that the creature is moving with the ventral surface, and not the head, foremost. When positively phototactic the mysid similarly orientates itself with the dorsal surface towards the light source and then moves towards it dorsal side first.

This orientation and movement can be produced in any plane. By lighting from below the animals can be induced to turn on their backs and swim upwards ventral side foremost.

A variation of this behaviour has been met with in some specimens of *H. lamornae*. Here after the animal has reorientated itself with its back towards the source of light it makes the excusion by swimming head foremost as is normal, and then at the end of the excursion coming to rest with the dorsal surface again directed towards the source of light.

The phototactic nature of the movements of the individuals which behaved in this way was very striking.

The behaviour of dark-adapted mysids whose statocysts had been removed, seemed to differ somewhat from that of the normal individuals in that they did not appear so active in the absence of light; a slight negative geotaxis appeared to exist although Menke (1911) did not apparently find this to be so.

It should be noted here that there are certain practical difficulties which were met with in making the observations. It was found that *H. lamornae* from Plymouth sent to Cardiff did not appear to respond as readily as this species and others did when sent to Glasgow from Millport. It is believed that this may be due to a different physiological condition correlated with the fact that this species lives in the tanks at Plymouth, but that when supplied from Millport it was taken with other mysids from the sea. Another difficulty is the very strong tactile sense possessed by these animals, contact with the sides and bottom of the tanks interfering seriously with the responses that were being studied; this point will be dealt with more fully below.

To conclude this section it is necessary to point out that the behaviour of mysids whose statocysts have been removed becomes more easily explained in terms of phototaxis than in the normal animals; and approximates, under experimental conditions, both to that of planktonic creatures, such as decapod larvae, and to that of such bottom-living animals as cumaceans, where orientation and movement are both controlled by the direction of light.

The Importance of the Tactile Sense

The responses of mysids are observed when they are swimming freely in the water, but a number of collisions with the sides and bottom of the vessel containing them are inevitable. With normal specimens this is not important as they quickly leave the sides and care is taken not to stimulate them when they are in contact with a solid object. When the statocysts have been removed the tactile sense becomes very important; specimens often remaining in contact with the sides or bottom of the vessel for long periods and sometimes it is necessary to remove one forcibly from the side into midwater in order to apply a stimulus. It may be mentioned here that those without statocysts appear to lose the ability to use the ordinary escape reflex of mysids in which the abdomen is sharply flexed under the head and thorax, causing the animal to jump in the water. It is not that the loss of the uropods makes the sudden flexure valueless, it is apparently not attempted at all. Also the conclusion has been reached that these specimens without statocysts do not stand on their heads trying to swim through the bottom of the vessel as has been described above; or at least it is not such a conspicuous part of their activities as it is in normal creatures.

In order to demonstrate the importance of the statocysts and to overcome the difficulty introduced by the tactile sense the following experiment, in which the animal is allowed to remain in contact with a surface throughout, has been devised.

The mysid is drawn up into a glass tube in which it can move freely but is always in contact with some part of the glass. For *H. lamornae* tubing $\frac{1}{5}$ in. (or 5 mm.) in diameter is sufficient. When the tube is entirely filled with water it is held horizontally, the water being prevented from running out by means of corks or the presence of the experimenter's fingers. The light should be dim, or better, red. The tube is now revolved around its long axis; if the mysid is a normal one it will preserve its original orientation with respect to gravity by creeping round the tube as it is turned. If, however, the animal has had its statocysts removed it remains clinging to the wall of the tube and makes little or no effort to retain a definite orientation with respect to gravity and thus revolves with the tube.

Discussion

The two most important points which arise from the foregoing observations and experiments are (1) that the normal orientation and tactile responses of mysids are the result of stimulation by both light and gravity, and (2) that if the gravitational receptors are removed the behaviour becomes more like that of a planktonic crustacean, or a cumacean; and further that, as may be expected in a bottom-dweller, the tactile sense is important.

Since Tattersall (1936) has summarized the available information concerning the vertical movements of mysids in the sea, it is interesting to compare these field results with the observations made in the laboratory.

It seems that certain species are to be met with in the plankton both by day and by night and that an upward movement takes place during darkness. The behaviour of this group of species is paralleled by many planktonic crustacea other than mysids such, for instance, as decapod larvae. In addition there is another group of species which live on the bottom during the day and at night tend to rise into the plankton; in the majority of species they do not rise above twenty metres from the bottom, although one, *Anchialina agilis*, was found by Russell to rise right to the surface about midnight. The behaviour of this latter group, especially that of *A. agilis* is paralleled to a certain extent by some other bottom-living crustaceans, namely cumaceans.

This behaviour, which has been found to take place in the sea, can be correlated with the laboratory observations if it is assumed that the rising at night is due to a negative geotaxis which is reversed and becomes positive in the presence of light. Whether this is the correct interpretation or not it does draw attention to the importance of geotaxis as a possible factor in vertical migration.

The explanation of the diurnal vertical migration of the plankton along the lines of "taxes" is a difficult subject which is as confused to-day as ever, so it is not intended to discuss the matter at all fully here, but merely to point out where the evidence derived from mysids may be of value.

Russell (1927) writing of the difficulty of differentiating between geotaxis and phototaxis, as, of course, in the sea they would both be acting in a vertical direction, remarks "a downward movement may as well be interpreted as a negative phototropism as positive geotropism". In mysids, as a result of the experimental work, it does seem possible to differentiate between phototaxis and geotaxis. Here the influence of light would appear to act through geotaxis. Clarke (1936), as a result of his work on *Daphnia* and further work in the sea, is inclined to seek a similar explanation of migration through a combination of geotactic and phototactic stimuli.

Some authors are inclined lightly to dismiss the influence of gravity, for in the laboratory the control of the direction of movement is found in the great majority of planktonic animals to be under the influence of light. Spooner (1933) has drawn attention to the orientating function of light. This directional effect of light is, however, really the dorsal light reflex, or its equivalent (e.g. an "anterior light reflex" in some animals where the head is directed towards the light), but because this is the strongest reflex present and overpowers others that may exist, it does not show that a gravitational stimulus acting through a general position reflex is not present. In fact it would be only through some such mechanism that orientation would be preserved through the hours of darkness. That gravity is reacted to by *Daphnia* was shown by Clarke (1930) and the present writer has shown elsewhere how the zoea larvae of Brachyura retain an unstable orientation in the absence of light (Foxon, 1934), and it seems likely that the behaviour of *Apus* quoted by Lochhead (1936) may belong to the same category.

It is known that the conditions of laboratory investigation differ markedly from those found in the sea, particularly as regards the composition and intensity of light. Russell (1927) has pointed out that the contradiction, that whereas in the sea most planktonic creatures make a downward movement in the day but in the laboratory move towards light, can be resolved when the intensity of light is taken into account. From this then it can be assumed that a downward movement would be caused by a negative phototaxis and would continue until a certain lower intensity of light was reached; the upward movement would not, however, take place when the light stimulus was entirely removed unless orientation was maintained and upward swimming took place. Therefore a negative geotaxis must be postulated for upward movement in the dark. As the evidence that normal orientation is maintained in the dark is growing, this assumption does not appear to be unwarranted.

As regards mysids it seems reasonable to assume from the evidence brought forward here that the downward movement is a reversal, in light, of a negative geotaxis which persists in darkness. That is, that it is a combined phototactic and geotactic response. That this is the mechanism involved in other groups of animals cannot be assumed without the greatest caution.

It has been noted above that the behaviour of mysids in the sea is closely paralleled by that of planktonic forms of decapod larvae and bottom-living cumaceans according as to whether the particular mysid is planktonic or benthic. In the laboratory, however, the behaviour of cumaceans (see Foxon, 1936) and decapod larvae on the one hand is quite different from that of normal mysids on the other, for both the former groups display strong phototactic reactions which completely obscure any signs of geotaxis. Thus the behaviour of cumaceans and decapod larvae is more like that of mysids whose statocysts have been removed. It appears most probable that, although in the sea the vertical movements of cumaceans on the one hand and mysids on the other hand are roughly parallel, the actual mechanisms producing these results may vary in the two groups. To quote Russell (1927) once more, he says (p. 253), "The writer is not going to generalize on the actual method by which the animals keep around the optimum. It may be phototropism, geotropism or acceleration and inhibition of motion. It may be a combination of all. From the evidence of laboratory experiments it may differ for different animals...." From the evidence at present brought forward it seems probable that more often than has been generally thought, these vertical movements are a result of a combination of light and gravitational stimuli (inhibition of motion is not a likely factor for reasons brought forward elsewhere; see Foxon, 1934). In addition it appears that these stimuli may not always work in the same way. In the majority of animals, as for instance in decapod larvae, light seems to have a simple phototactic effect, and in others (mysids), to work mainly through geotaxis.

Summary

Light-adapted mysids as exemplified by *Hemimysis lamornae* display photo-telotaxis which regularly alternates in sign from positive to negative and *vice versa*. This reaction may be disturbed by other activities such as feeding; it only takes place in horizontal illumination.

Dark-adapted mysids display negative geotaxis. When a light stimulus is given this geotaxis is reversed in sign irrespective of the direction of the incident light.

When the statocysts of the mysids are removed their responses are much more like those of planktonic creatures. In the light normal orientation is maintained by the "dorsal light reflex", and in darkness by the "general position reflex". In the darkness a feeble negative geotaxis is sometimes seen. In light, phototaxis is seen in both light-adapted and dark-adapted conditions; in the majority of cases it is negative but on occasion has been seen to be positive.

The sense of touch is very important and introduces certain observational difficulties. An experiment to show the relation of the statocysts to gravitational stimuli and overcoming this difficulty has been devised.

The vertical movements of mysids in the sea have been compared with the laboratory observations and it is shown that this behaviour can be interpreted as caused by negative geotaxis which is reversed in the presence of light.

It is suggested that certain planktonic forms retain their orientation in darkness by means of the "general position reflex" and that their upward movements exhibited in the dark are due to a negative geotaxis.

Although the reactions of normal mysids in the laboratory are markedly different from those of such animals as cumaceans and decapod larvae, in the sea a general similarity between their behaviour exists. It is suggested that this similarity of behaviour in the sea is brought about by stimuli acting in somewhat different ways, and that this difference of method accounts for the differences found in the behaviour in the laboratory. Thus whereas in mysids light is regarded as altering the sign of a pre-existing negative geotaxis, in the other groups it seems that a simple phototaxis (negative) acting in opposition to a weaker negative geotaxis causes a downward movement in light which is reversed in darkness.

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