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LITERATURE FOR 1913 ON THE BEHAVIOR OF THE LOWER INVERTEBRATES

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In continuing his studies on the rheotaxis of isopods Allee (1, 2) has found that when the positive rheotaxis of *Asellus* is strong there is a high degree of efficiency in the reactions to the current. Low efficiency is correlated with indefinite or negative responses. When molting occurs sensitiveness to currents is greatly reduced. Low oxygen content and KCN cause a reduction or reversal of the usual reactions. There is little relation between the vigor of the reaction to mechanical shocks and the sign of the rheotactic response. KCN, and lack of oxygen produce at first an increase of sensitiveness to shocks followed by a period of dulled sensitivity. Often sensitiveness is increased during the molting period. No daily rhythms of behavior were observed.

In a series of experiments on the taste and smell of the crustacean *Palaemon*, Balss (3) concludes that the olfactory sense is located partly in the antennae and partly in other parts of the body. Taste is located not in the antennae, but in the mouth parts and tips of the thoracic legs.

The extensive studies of Bancroft (4) on the much discussed subject of the phototaxis of *Euglena* have shed much light on several of the vexed questions involved. Orientation which has been considered a function of differential sensibility is found to stand in no necessary relation to the latter. Positive reactions

"may be accompanied by motor reactions to either sudden shading or sudden illumination," and "the ability to react to sudden changes in illumination by means of motor reactions is possessed by Euglenae which are not heliotropic. Conversely, there are heliotropic Euglenae that cannot be made to respond to changes in illumination." The orientation to light and the ability to react to sudden changes of light intensity being to a large extent independent variables, it is concluded that the two types of reaction depend upon different mechanisms. Orientation is not the outcome of trial and error, but "is as direct as the locomotor mechanism of the organism will allow."

Baunacke (5) gives a general discussion of the function of the statocyst in various invertebrates and describes several experiments showing the relation of the statocysts to the preservation of the normal position in various mollusks.

Bohn (6) has given a discussion of modifiability of behavior in lower organisms and its relation to certain physical and chemical processes. That he is correct in ascribing associative memory to protozoans and coelenterates may be questioned by many comparative psychologists, but all will find his treatment of the topic suggestive.

The experiments of Miss Brundin (7) on some terrestrial amphipods from California showed that the more terrestrial of the two species studied, *Orchestia pugettensis*, is the more strongly positive to light. This species commonly lives in holes in the sand above high tide mark, while *Orchestia traskiana* lives in cooler and moister conditions under sea weeds and rubbish nearer the water's edge. It was found that both dryness and heat tend to make negative *Orchestias* positive. Enforced activity also produces the same effect. *Orchestias* compelled to lie on one side by being compressed between two glass plates would nevertheless manage to go toward the light. Specimens with one eye blackened over would at first perform circus movements toward the normal side, but after a time they would go to the light in a more direct course. There is a discussion of the relation of the behavior of the two species to the choice of their respective habitats.

Brunelli (8) has given a resumé of the behavior of hermit crabs and adds a detailed description of how *Pagurus arrosor* detaches the anemone *Adamsia* and then places it, base down-

ward, on the shell which this crab inhabits. The author discusses the origin and significance of the symbiotic relations of these two forms

Buddenrock (9) finds that in *Branchiomma* and certain other annelids that bore into the mud or sand, the statocyst does not serve for the perception of jars, but affords stimuli causing the side of the tail end in contact with the substratum to bend downward; *i.e.*, the statocyst is the organ of geotaxis. Extirpation of both statocysts destroys the power of boring straight into the earth.

Car (10) gives a not very illuminating discussion of ciliary movement in general and the locomotion of the ciliate infusoria, he also touches upon the movements of gregarines.

After section of the ventral cord of diplopods, Clement (11) finds that co-ordinated movements between the appendages in front of and behind the incision continue to occur. Stimuli afforded by muscular strains are probably instrumental in effecting this co-ordination. Reactions of particular appendages were studied and their influence on the movements of other appendages. Rolling into a spiral, which persists after decapitation, no longer occurs if the first three metameres are removed.

Cole (12) finds that the starfish *Asterias forbesi* locomotes most frequently with the madreporite or one of the adjacent rays in front. This "physiological anterior" of the starfish "corresponds to the anterior of the spatangoids with respect to the position of the madreporite." Starfishes tend to crawl in the same general direction in successive trials, but when changes of direction occur there is a tendency for the locomotor impulse to "shift or rotate gradually around the body in one direction or the other."

In experiments on co-ordination and righting in the starfish, Cole (13) found that individuals with the radial nerves cut near the circum-oral nerve ring were nevertheless able to right themselves. The operation was accomplished only with difficulty owing to the lack of co-ordinated activity in the different arms. Specimens with one or more arms amputated were found to right themselves as were also the individual arms.

Cowles (14) describes the method by which *Cryptodromia tuberculata* St., a sponge-carrying crab, snips loose a piece of sponge, pushes its body under it and carries it off while holding

it with the posterior pair of legs. *Alpheus pachychirus* St. has the curious habit of forming a tube of an alga which grows in the form of a sheet of threads. The *Alpheus* lies on its back, draws the folds of the alga together on either side, then, by pulling the threads through holes made by its feet, actually sews together the folds of the alga to form a complete tube.

By throwing light from various differently colored surfaces on the daphnid *Simocephalus*, Erhard (16) noted that the eye reacted in the same way as to changes in the intensity of any one color. He concludes, like Hess, that daphnids are color blind.

The behavior of the parasitic copepod *Lernaeopoda edwardsii* has been studied by Fasten (17) who finds that the free swimming young habitually move in a spiral course, thus increasing their opportunities of coming into contact with their host. The larvae are positive even in strong light and swim near the surface during the day, but sink toward the bottom at night. Observations were made on thigmotaxis, geotaxis, reactions to temperature changes, and to various chemicals, and also on the method by which the larvae attach themselves to the gills of their host, the trout.

According to Franz (18) phototaxis is either a device for scattering the species, as when it occurs in the larvae of animals inhabiting the bottom of waters, or in a movement of flight (Fluchtbewegung) by which the animal escapes unfavorable or threatening conditions. For the arguments supporting this unique standpoint reference must be made to the original paper. Franz (19) has also given a more or less popular account of the behavior of snails.

Frisch and Kupelweiser (20), from a series of experiments on *Daphnia* and *Artemia*, conclude that these animals have the power of distinguishing different colors. If *Daphnias* which have become indifferent to a certain intensity of light are exposed to a light of less intensity they become positive, whereas if the intensity of light is increased they become negative. However, if one interposes a blue screen, the daphnids in spite of the diminution of light intensity become negative. If one adds yellow light to the white light to which *Daphnids* have become indifferent there is evoked a positive reaction notwithstanding

the fact that the intensity of the light is increased. *Artemia* reacts in much the same way as *Daphnia*, and the author concludes that lights of different wave lengths produce different effects.

Frölich (21) has experimented on the isolated eyes of *Octopus*, noting fluctuations in the current of action under constant stimulation by light. Rhythmical fluctuations of the current were noted which varied in frequency and extent with the intensity and wave length of light.

Gee (22) has made a thorough investigation of the behavior of two species of leeches, *Dina microstoma* Moore and *Glossiphonia stagnalis* L. His paper includes a description of the general habits of the two species; their various movements; food and feeding; reactions to light, heat, currents of water, and chemicals; daily changes of behavior; the behavior of the young, and various other features of the normal activities of these animals, thus affording a foundation for the analytical work which follows. Under the head of modifiability of behavior are treated the various responses of the animal to repetitions of the same stimulus and their different determining factors, acclimatization to stimuli, fatigue, depression induced by various chemicals and its relation to fatigue, and the influence of hunger and satiety on various reactions. Of particular interest is the parallelism between the effects of fatigue and influence of those substances, sarco-lactic acid, carbon dioxide, etc., which are supposed to cause fatigue in higher forms.

Gee's paper (23) on the modifiability of behavior in the sea anemone *Cribrina* embodies an attempt to account for the changes of behavior in this form in terms of certain physiological processes. Food produces a copious secretion of mucus and after a certain amount of food has been taken in the animal refuses to take more. Why does the surfeited anemone reject the food? It is not due to fatigue of the muscles involved in prehension or swallowing. If the anemones are stimulated by beef extract or oyster juice they secrete mucus copiously and soon reject solid food. Various salts were found to cause the anemone to reject food. The refusal of food is not the result of conditions of assimilation; apparently it is the effect of conditions brought about by the secretion of mucus. *Cribrina*

remains expanded in the light and contracted in the dark, and shows no diurnal or tidal rhythms independently of the changes of the stimuli directly affecting it.

In the course of an investigation of the alleged color sense of the lower animals Hess (24) has experimented on various fishes, the larvae of *Culex*, and the anemones *Cerianthus* and *Bunodes*. The general results are confirmatory of his contention that the lower animals are color blind, *i.e.*, they are affected only by the intensity and direction of the light rays.

In the course of a general account of the biology of *Asellus aquaticus* Kaulbersz (26) describes many features of the behavior of this isopod, and especially its reaction to chemical, photic and tactile stimuli. Observations were also made on the reactions of *Gammarus* and *Niphargus*.

Kechschowsky (27) has studied the effect of the constant electric current on various cestodes, nemerteans and annelids. Most forms reacted by a contraction of the longitudinal muscles when the anode was placed at the head end and the cathode near the tail.

Following a description of the histology of the sensory epithelium of *Microstoma caudatum*, Kepner and Taliaferro (28) have given an account of the reactions of the animal to various chemicals. The reactions were markedly influenced by variations in its "physiological tone." Removal of the ciliated pit of one side of the head caused circus movements toward the intact side. "The bilateral disposition of the ciliated pits serves to direct the animal in its movements." The same authors (29) have investigated the food taking of *Amoeba proteus*. They find much variability in the reactions to food, depending upon the condition of the animal and various external influences.

Lillie and Just (30) have made several interesting observations on the breeding habits of *Nereis* at Woods Hole, Mass. Breeding occurs at certain periods which are influenced mainly by lunar cycles, but which are also affected by several other factors, such as time of day, weather, light and possibly temperature. During the breeding time swarms of both sexes are found swimming near the surface and when the females discharge their eggs the males discharge their sperm. The exciting factor which stimulates the males to the discharge of their sperm was shown to be some substance discharged by the egg-bearing females.

Spent females had little influence on the sperm discharge of the males, but water which had contained an egg-bearing female would quickly provoke discharge of the sperm. The substance inducing the discharge of the sperm is quite labile as it is destroyed by heat or by standing a few days in sea water.

Lillie (31) has made a study of the behavior of the spermatozoa of *Nereis* and *Arbacia*. The sperm cells of *Nereis* are positively chemotactic to weak solutions of CO_2 and various other acids, but they show no response to alkalis. "In contact with any solid object *Nereis* spermatozoa tend to carry out circus movements in an anti-clockwise direction, when fresh, but soon come to rest." They are especially attracted by substances given off by the eggs. The same is true for the sperm of *Arbacia*, whose general behavior resembles that of the sperm of *Nereis*. Chemotaxis to egg substances is probably an important factor in bringing about the fertilization of the egg.

MacCurdy (32) has shown that *Asterias forbesi* is negatively phototactic. He finds that light produces chemical changes in the starfish which were studied by examining the sea water containing specimens exposed to the light.

Metalnikow (33) finds that *Paramoecia* which at first ingested injurious substances came after a few hours to reject them. In another communication (34) experiments are reported on feeding infusoria with sepia and carmine. At first both sepia and carmine were ingested; after a few days the carmine was ingested in very small quantities, but the sepia was engulfed in considerable quantity.

Moore (35) finds that *Diaptomus bakeri* ordinarily indifferent to daylight becomes negative upon the addition of small amounts of caffeine, strychnin, and atropin, while acids, alcohol and ether evoke a positive response.

Morse (36), who has made a detailed study of the habits of *Solenomya*, finds that this primitive bivalve burrows with the posterior end downward, thereby forming an exception to all other known lamellibranchs. *Solenomya* swims actively through the water by the combined action of the foot and valves of the shell.

Like several previous investigators, Mrázek (37) finds that *Branchipus* is positively phototactic and ordinarily swims on its back. This orientation was preserved after the removal of the eyes.

Orton (38, 39) has given a detailed account of the feeding mechanism and mode of feeding in *Crepidula* with observations on the feeding activities of various other mollusks.

Eubbranchipus dadayi was found by Pearse (40) to be positively phototactic and in general positively geotactic in the light and negatively so in the dark. After mating the females resist seizure by the males and usually leave the surface and keep quiet near the bottom.

By means of several experiments on the starfish Plessner (41) has brought out several differences between the functions of the ocelli and the general photodermic sensitivity of the body. The latter serves only as a means of reaction to variations in the intensity of light. The ocelli do not enable the starfish to see images nor to detect movement, but by their means the starfish is able to direct its movements toward a slit of light or a dark object. Removal of the ocelli involves destruction of the power of locomotion to special regions of light or shade.

H. Przibram and Matula (42) have studied the functions of the branches of an abnormal antenna of the spiny lobster *Palimnurus*. The antenna was furnished with three flagella. Two of these conveyed sensory stimuli but did not respond by movement, but the third responded by movement to the application of stimuli.

K. Przibram (43) has pointed out certain analogies between the random movements of some of the Protozoa and Brownian movements.

Sexton and Mathews (45) have described the food habits, mating and general behavior of the young in *Gammarus chevreuxi*, a species inhabiting fresh and brackish waters around Plymouth, England.

Oregonia gracilis, like many other spider crabs, was found by Stevens (46) to possess the curious habit of decking itself with various foreign growths. Contrary to the results of Minkiewicz there was no tendency on the part of the crabs to select materials that correspond to the prevailing color of the environment. Blinded crabs decorate themselves but they show no reaction to light. Crabs which had been previously exposed to white, yellow, blue, green or red light show a manifest tendency to go toward the same kind of light when they are free to move toward any one of these colors.

By stroking gently various parts of the body of a snail in much the same way as these parts are stimulated during the mating activities Szymanski (47) has succeeded in evoking reactions which closely simulate those of mating. The studies of Szymanski (48) on the relation of tropisms to rapidity of movement were made partly on insect larvae and partly on leeches and earthworms. When the animals studied were in a condition of relative inactivity they progressed with less rapidity and made many trial movements in their sinuous course. When more active they become oriented more directly and progress with greater rapidity and in a straighter path. The author discusses different interpretations of the relation of trial movements to locomotor activity.

Torrey (50) has given a discussion of the rôle of trial movements in orientation, especially in the case of *Euglena*, which, it is contended, contrary to the views of Jennings and Mast, orients itself by direct responses to stimuli instead of by the method of trial and error.

Yung (51) has reached the unexpected conclusion that the eyes of snails despite their considerable degree of development are not light percipient organs. Other parts of the body, however, possess a photodermic sensibility.

Zimmermann (52) describes the movements and respiratory activities of the *Galatheidea* with especial reference to the structural adaptations involved.

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