

STUDIES IN THE BIOLOGY OF THE LEECH. IV  
AN EXPLANATION OF CERTAIN PHASES OF LEECH BEHAVIOR

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In the study of natural phenomena man is confronted with a three-fold problem. First, what occurs; second, how does it occur; third, how can one account for its occurrence. In answering the first two of these questions it is only necessary to make careful observations and to give accurate descriptions of the phenomena. The solution to the third, however, enjoys the distinction of being the product of careful analysis of causal factors and the application of established principles. The study of animal behavior not only involves an analysis of the action systems and the responses of the organism, but it demands a physical explanation of these responses.

I regard the knowledge of the nervous and muscular systems essential to an understanding and explanation of the behavior of any animal. Each species has its characteristic mode of reaction to changes in its environment. Its behavior is determined primarily by the nature of the behavior pattern which is a recognized part of its inherited organization. The morphology of the nervous and muscular system of the leech *Haemopsis marmoratis* has been previously described, so that for the purposes of this paper we do not need to deal with it further.

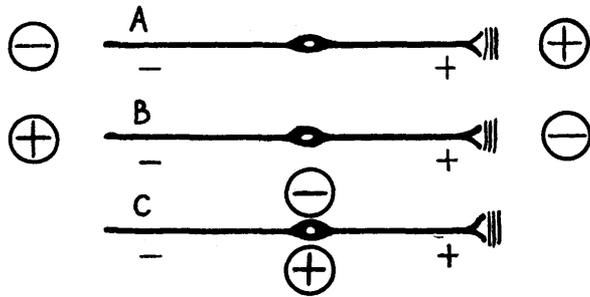
Through a knowledge of the nervous and muscular system, and through the treatment of this behavior pattern as a basis, we are able to describe and explain certain phases of leech (*Haemopsis marmoratis* (Say)) behavior. It is the object of this paper to interpret certain characteristic movements in terms of the stimuli and the intrinsic behavior patterns.

DISCUSSION OF RESPONSES TO ELECTRICAL STIMULATION

The behavior of an animal consists of acts which are the ultimate effects of stimuli upon its particular type of anatomical structures. These stimuli originate either from the environmental forces of the outer world or from causes operating within the body of the animal. The usual reactions to external stimuli are movements.

As described in preceding publications (Miller, '33-'34) there are distinct differences in behavior when the leech is subjected to different stimuli. These differences in behavior are due to the contraction of different combinations of body wall muscles. These muscles contract only upon stimulation. Direct current of low voltage stimulates motor neurons directly. (Loeb, Lillie, Shensa and Barrows).

Shensa and Barrows (1932) applied the "Law of Polar Stimulation," Lillie (1923) to the neurons of the subepidermal nerve plexus in the earthworm. In so doing they explained the behavior of the worm to lateral electrical stimulation.



**FIG. 1**

FIG. 1. Diagram illustrating the arrangement of electrodes in relation to the nerve cells and muscles. The electrodes are shown inside circles. A, the current direction which causes muscular contraction; B, the current direction which causes muscular relaxation; C, the current direction which does not affect the polarity of the neuron.

Experimental evidence, obtained by the author, demonstrates the same polarity of motor neurons in the leech. The references to galvanotropic responses on the part of some of the Annelida is to be found in the literature. The use, however, of this law or principle directed to a better understanding of the minute nervous structure and behavior of the leech has not previously appeared in the literature.

#### ANTERIOR POSTERIOR STIMULATION

Figure 1 illustrates neuron polarity and the effect upon the muscle of electrodes placed in a variety of relations to the neuron. It has been previously stated (Miller, '34) that when the negative electrode is placed in front of the anterior end of the leech and the positive electrode behind the posterior end, the leech elongates and crawls toward the cathode. With the

poles reversed, from the above stated situation, the leech shortens and eventually orients itself by turning completely around and crawls toward the cathode.

The only reasonable explanation of this orientation is found in the application of the principle of neuron polarity to a system in which certain neurons extend parallel to the current of negative electrons when the electrodes are placed as described

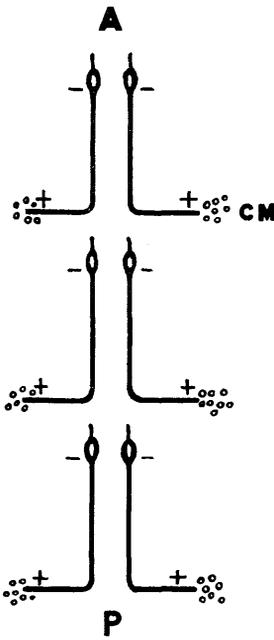


FIG. 2

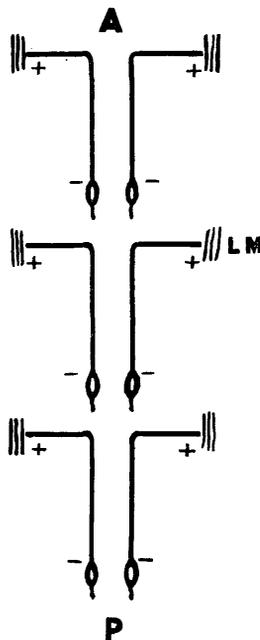


FIG. 3

FIGS. 2 and 3 illustrate the polarity of motor neurons within the ventral nerve cord and their relation to the body wall muscles. A, anterior; P, posterior; C. M., circular muscles; L. M., longitudinal muscles.

above. The impulses instigated by the current travel directly over the neurons in the cord. Herein lies the experimental proof of the position of the motor neurons within the cord. (See Figs. 2, 3.)

Figure 2 illustrates the position of that group of motor neurons within the cord which innervate circular muscles. This group of neurons have their origin and highest region of gradient anteriorly. The placing of the negative electrode near

the anterior end brings about a contraction of the circular muscles. As a result of this contraction the leech elongates. This elongation is easily seen and facilitates forward locomotion. The influence of the positive electrode at the posterior end has an inhibitory effect on the longitudinal muscles. This makes shortening difficult and to some extent delays forward locomotion.

With the negative electrode near the posterior end the impulses so incited are conducted over neurons innervating the longitudinal muscles. The current running lengthwise through the longitudinal muscles as well as the neurons probably intensifies the contraction. The contraction of these muscles (longitudinal) results in a shortening of the leech. The contraction of the circular muscles is inhibited by the action of the positive electrode at the anterior end. (The turning toward the negative electrodes is explained below.)

This electrotactic response on the part of the leech can now be explained entirely on a cause and effect basis. Locomotion, by reptation, is the result of co-ordinated contractions of circular and longitudinal muscles. The contraction of these muscles is intensified or inhibited as a result of the increase in polarity of the motor neurons innervating them.

#### LATERAL STIMULATION

To understand the behavior of the leech when the electrodes are placed a few inches to the right and left of the mid-body region involves an understanding of the subepidermal nerve plexus.

Until recently this system was not taken into account in explaining Annelid behavior. Following the description of this system in the earthworm by Hess (1925), Shensa and Barrows (1932), applied it to the explanation of certain phases of earthworm behavior. The subepidermal nerve plexus of the leech was described by the author in 1933, making possible this explanation of leech behavior to lateral electrical stimulation.

Experiments conducted by Miller (1934) demonstrate that the longitudinal muscles on the side facing the negative electrode are stimulated directly through the motor neurons in the subepidermal plexus. The motor neurons of this plexus lie at right angles to the surface of the skin. These neurons are polarized in such a way that the longitudinal muscles on the negative are stimulated while those on the positive side are

relaxed or inhibited. Stimulation in this manner results in the leech assuming a position like that of a "C," with the anterior and posterior ends toward the negative. Prolonged stimulation in this manner results in the extension of the anterior end toward the negative electrode but does not cause the posterior end to elongate. This elongation and movement of the anterior end is explained in a preceding paragraph.

#### DORSAL VENTRAL STIMULATION

In response to dorso-ventral electrical stimulation the leech orients itself in the following manner. The anterior and posterior ends point toward the negative, the middle region contracts and the dorsal surface orients toward the negative. (For details see Miller, 1934.)

The negative current stimulates the longitudinal muscles through the subepidermal nerve plexus on the surface facing this electrode. This results in the leech assuming a "U" shaped position pointing the anterior and posterior ends toward the negative electrode. In this position the anterior end elongates. This elongation is the result of circular muscle contraction. The circular muscles are stimulated through impulses conducted by motor fibres in the ventral nerve cord. These neurons, as in preceding experiments, are directly influenced by the polarized field in which they lie.

The orientation of the dorsal surface toward the negative electrode is, in my opinion, a combined neuro-motor and mechanical response. The fact that the ventral series of longitudinal muscles is much stronger than the dorsal series results in a higher arching of the animal when the negative electrode is below than when the negative electrode is above. As a result of this high arching the animal rolls over bringing the dorsal surface next to the negative electrode. In the latter position the dorsal longitudinal muscles contract. The contraction of these muscles does not bring about sufficient arching to cause the animal to roll over. Hence, the animal remains oriented with the dorsal surface toward the negative electrode.

#### SUMMARY AND CONCLUSIONS

To complete a study of animal behavior the physical explanation of the responses of the organism is necessary. To be able to do this it is imperative that the nervous and muscular systems be well understood. Direct current of low

voltage acts as an excellent source of stimulation. Our knowledge of the polarity of motor neurons makes it possible to interpret the contraction of certain muscles as a result of the increase in polarity of the neurons innervating them. This not only reduces the understanding of behavior to cause and effect but makes possible a better understanding of the exact arrangement of the minute motor neurons within the cord, and the principles which apply to this type of behavior study.

1. The leech has a specific neuro-muscular pattern; this mechanism can be stimulated directly; the behavior of this organism is understandable (as far as these experiments permit) as the joint product of the stimulus and the reaction pattern.
2. Different expressions of behavior are due to the ultimate effects of stimuli upon different combinations of body wall muscles.
3. The behavior pattern of an organism is a recognized part of its inherited organization.
4. Animal behavior is the ultimate result of stimuli upon a particular arrangement of anatomical structures.
5. Experimental evidence obtained here demonstrates for the leech the same polarity of motor neurons as previously demonstrated for other organisms.
6. The electrotactic responses of the leech can now be explained entirely on a cause and effect basis.
7. There is an understandable physical explanation of animal behavior that becomes apparent upon the analysis of the action systems of the organism.
8. Whereas all animals may not lend themselves to behavior studies, there are forms, such as the leech, from which certain of the fundamental principles of behavior may be derived.

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