STUDIES IN THE BIOLOGY OF THE LEECH.[1]

V. Behavior Following Nerve Cord Transection

JOHN A. MILLER
The Ohio State University

It is axiomatic that the central nervous system plays an essential part in the process of normal locomotion. The sequence of muscle contraction during locomotion has been described for the earthworm (Bovard, 1918). Similar studies have been reported for the leech (Miller, 1936). In this paper a number of reactions are presented which may be considered as traumatic and resulting directly from the complete transection of the ventral nerve cord. A partial explanation of these responses is to be found in the discussion later in this paper.

The procedure involved either the transection of the nerve cord by ventral section or the complete transection of the body. These incisions were made in the anterior, the middle, and the posterior regions. Observations were made over periods of two to twenty days following the operation. The results are recorded below.

Anterior Dissection.—1. (Fig. 3).

The ventral nerve cord was cut at the fifteenth annulus. Considering the extent of the cephalization this would place the cut between somite six and seven. It was found that this point of dissection was the anterior limit where recognized differential behavior of both the anterior and posterior portions could be classified. Giant fiber response was unimpaired in the region posterior to the cut. The response to tactile stimulation applied to either end of the posterior section was an end-to-end shortening. When stimulated near the center of the body, especially noted in water, there was an elongation followed by swimming. Tactile stimulation applied anterior to the cut was always followed by a shortening of that region. Crawling movements were expressed independently by both the anterior and posterior portions.

Forward locomotion on a wet slate was accomplished through the extension and subsequent contraction of that portion of the leech posterior to the cut. In this procedure the anterior segments were pushed forward. The random movements of the anterior tip and its subsequent extensions did not produce forward locomotion. Such anterior extensions were not necessarily followed by an extension of the large posterior section. Combined with the usual adherence of the posterior sucker and the extreme disproportionate relation of volume

[1]All leeches used in these experiments were *Haemopsis marmoratis* (Say).

between the anterior and posterior sections, it is understandable why forward locomotion by anterior section extension was not accomplished. The fact that this small anterior section was capable of independent forward locomotion was established when it was completely severed from the remainder of the leech.

In shallow water crawling movements did not result in forward locomotion. The failure of the anterior sucker, though functional, to make an adhesive contact following the extension of the posterior section together with the more frictionless substratum, combined to make forward locomotion by this method ineffective. The same limitations apply to the crawling efforts of the anterior section as listed above. Swimming and undulatory movements were not affected by this dissection to the same extent as were crawling movements. In swimming, as in crawling, the anterior end took no active part. Swimming and undulatory movements appeared to be nearly normal with the exception of that portion anterior to the cut. As in crawling, these anterior segments were turned under.

Anterior Dissection.—2.

The anterior fifteen annuli were severed from the body. This anterior tip expressed true crawling movements both on the wet slate and in the water. The oral sucker was functional. Actual forward progress was made. Undulatory movements were observed but did not result in forward locomotion.

That portion of the leech minus the six anterior segments remained alive for two days or more. On a moist slate crawling was an effective means of locomotion. In the water, swimming and undulatory movements were common and appeared to be nearly normal. Swimming was the usual response to tactile stimulation.

Mid-Body Dissection.—1. (Fig. 2).

The ventral nerve cord was cut in the mid-body region. This cut divides the central nervous system into two nearly equal portions. It was then possible to observe certain expressions of behavior not clearly evident in the preceding experiment. Under this condition the leech moved forward by crawling as well as swimming.

In crawling on the wet slate there were two alternatives. (1) Normal crawling movements of the anterior half up to the cut and the dragging of the posterior half. (2) Crawling movements originating posterior to the cut and proceeding in such a way that the anterior half was pushed ahead. Both methods were observed for the same animal, although they did not take place simultaneously.

In the water, crawling movements were observed only in that portion anterior to the cut. Frequently both suckers were attached following the forward extension of the anterior half. Forward movement occurred only after much twisting and pulling and finally the slipping of the posterior sucker over the substratum. It would appear that the posterior half was moved forward solely by the force of the contraction of the longitudinal muscles in that portion anterior to the cut. When the posterior sucker became unattached and the animal was engaged in crawling, the posterior half was dragged along.

Swimming movements and undulatory (breathing) movements were expressed either simultaneously or separately by both body sections. It is probable that each section acted independently. Crawling movement of the anterior section was frequently observed to take place

Haemopis marmoratis (Say)

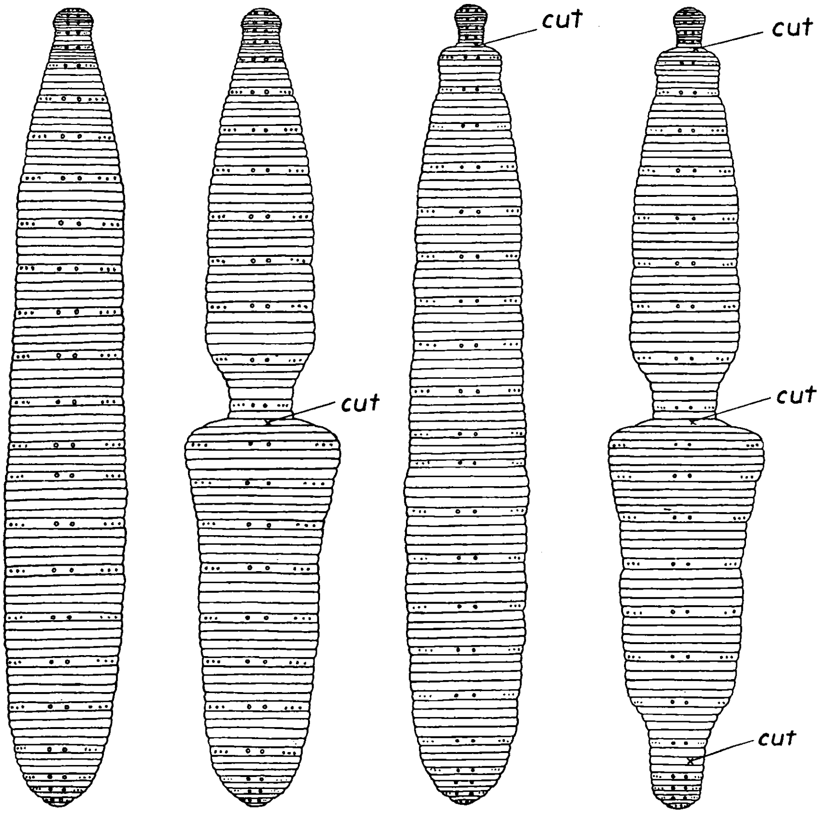

Fig. 1 Fig. 2 Fig. 3 Fig. 4

simultaneously with the swimming movement of the posterior section. Swimming movements of the posterior half alone often resulted in forward locomotion. The anterior half, in such instances, was inactive and folded back along the body. Other post-operative responses of an abnormal nature included the attachment of the anterior sucker at a time when the posterior half was engaged in undulatory movements.

Random movements were confined to that portion anterior to the cut. Tactile stimulation applied anterior to the cut usually resulted in a shortening followed by crawling movements of this region; similar stimulation applied posterior to the cut usually resulted in an extension followed by swimming movements of that region.

MID-BODY DISSECTION.—2.

The body of the leech was cut into two nearly equal parts both of which exhibited crawling and swimming movements. The anterior portion was more efficient in crawling, the posterior portion in swimming. Random movements were confined to the anterior section. The same responses to tactile stimulation were observed as stated previously under conditions of nerve cord transection only.

POSTERIOR DISSECTION.

The nerve cord was cut just anterior to the anal opening. Crawling movements were normal anterior to the cut. The attachment of the posterior sucker often delayed forward locomotion. The same pulling and slipping was observed as in previous experiments. Normal end-to-end contraction followed tactile stimulation anteriorly.

Swimming and undulatory movements under conditions just described presented a paradoxical procedure. In these instances a most unusual response was observed. Never before have backward swimming movements been observed in leeches by the author. Following the posterior cut in the nerve cord, the leech was dropped into a large crystallization dish containing an inch and a half of water. Swimming movements were initiated upon contact with the water. The leech swam a short distance backward, then while still undulating reversed its direction and swam forward. First one end and then the other took the lead in the initiation of the whip-like movements. For some time following the above dissection forward locomotion by swimming was ineffective. Later observations disclosed more frequent and successful forward movements. Normal undulatory movements were observed when the posterior sucker was attached. There were many instances, however, during this experiment when the anterior sucker became attached and the undulatory movements proceeded (contrary to normal) from posterior to anterior end. Throughout this experiment the leech remained abnormally extended.

ANTERIOR-POSTERIOR DISSECTION.—1. (Fig. 4, without mid-body cut in cord).

The ventral nerve cord was cut near the anterior end and near the posterior end. Crawling of the middle section was observed on the slate. The anterior tip was pushed forward and the posterior segments dragged. Each sucker retained its power of attachment. In the water this animal was much more active than on the slate.

Swimming activity following anterior-posterior cord transection was abnormal. Both anterior and posterior ends moved up and down simultaneously. The leech was abnormally elongated and progress was slow. The anterior end was usually foremost in locomotion. Undulatory movements continued with the whip-like action being initiated at either the anterior or posterior end. When the anterior end was attached, undulatory movements proceeded abnormally from the posterior to the anterior end. When the posterior end was attached, the whip-like movement proceeded from anterior to posterior as in the normal sequence. Undulatory movements were also observed when both anterior and posterior suckers were attached. The wave of undulation proceeded posteriorly. This anterior-posterior sucker attachment suggests that the middle portion only was involved in the undulation.

ANTERIOR-POSTERIOR DISSECTION.—2.

The anterior end and the posterior end were severed from the body. On the slate the middle section of the leech initiated normal crawling movements and some progress was made. In the water swimming and crawling movements were both exhibited. Swimming movements resulted in moderate progress.

At this point several additional segments were removed from both the anterior and the posterior ends. This additional reduction in the main body of the leech did not alter the basic reactions. Crawling and swimming were continued with proportionately less efficiency. This procedure was repeated with similar results until the remaining piece consisted of but a few segments. It was noted that each section thus removed also expressed movement essentially comparable to crawling or swimming.

DISCUSSION

In preceding papers of this series (Miller, 1933–36) the functional anatomy of the nervous and muscular systems, as well as certain normal responses of the leech have been described. The transection of the ventral nerve cord was noted as especially affecting the following activities.

Random movements are orientation activities. Such movements consist of a succession of extensions and contractions of the anterior end. Following nerve cord transection all random movements were confined to that region anterior to the cut.

Looping movements are modifications of crawling activity. Following the normal elongation of the animal the ventral longitudinal muscles contract in such a way that the animal forms a loop. In this arched position the anal sucker is attached just posterior to the oral sucker. Looping movements were not observed at any time after the ventral nerve cord was cut. Assuming that looping movements involve an anterior-posterior coordination, the cessation of this activity following nerve cord transection is understandable.

Crawling movements or movements of reptation as they are frequently called, are the result of coordinated contractions of body wall muscles. In forward locomotion a wave of circular muscle contraction proceeding from anterior to posterior is followed by a wave of longitudinal muscle contraction. Circular muscle contraction results in the elongation of the animal and the subsequent forward movement of the anterior end. During this phase of locomotion the posterior sucker normally remains attached. The anterior sucker becomes attached at the conclusion of the forward extension. The release of the posterior sucker and the contraction of the longitudinal muscles are followed by a shortening of the animal.

The cutting of the ventral nerve cord or the complete transection of the body were factors incident to modifications in crawling activity. As was pointed out in the main body of this paper, crawling movements were expressed independently by either the section anterior or the section posterior to the cut. Antagonistic action was often observed between the two sections. This was indicative not only of complete nerve separation, but of certain inherent behavior within isolated sections. Friedlander (1894) and Biederman (1904) in their discussion of locomotion in the earthworm emphasized the "pull" exerted by the elongating portion of the animal as a cause of successive contractions. It was suggested for the earthworm that this pull or stretch initiated impulses which were responsible for continued crawling movements throughout the length of the worm. This is not true for the leech. The observations and discussion presented under mid-body dissection, 1, in this paper is the basis for this statement.

Swimming and undulatory movements are essentially the same. The waving movements which occur while the leech is posteriorly attached to the substratum are referred to as undulatory or breathing in character. The same movements while the leech is unattached result in locomotion and are defined as swimming movements. The rhythmic wave of alternate contraction of the dorsal and ventral longitudinal muscles are responsible for this activity. The ventral longitudinal muscle area is larger and therefore probably capable of exerting greater force than the dorsal area. From observation it appears that the power stroke in this movement is largely produced by the ventral series. During undulatory or swimming activity the animal is extended and dorso-ventrally flattened. The latter is probably the result of the contraction of the dorso-ventral muscle fibers.

In swimming as in crawling the separate sections express independent action. In the various experiments the anterior half was observed in crawling at the same time that the posterior half was engaged in undulation. A previous study (Miller, 1934) has established a difference in rate between normal undulations while attached as compared with number (per min.) of undulations while swimming. The application of this information makes possible the present differentiation between swimming and undulatory (breathing) movements. On this basis it can be stated that operated animals expressed swimming movements while the posterior sucker remained attached. This activity was particularly evident following posterior cord transection. In this instance only the portion anterior to the cut was engaged in swimming activity, while that portion posterior to the cut, including the anal sucker, acted independently.

Swimming and undulatory movements were expressed by groups of segments cut from any body region. This indicates that this activity is not dependent upon any particular area such as anterior, middle, or posterior regions of the central nervous system. Transection of the nerve cord in the posterior region did, however, temporarily inhibit normal swimming. A temporary reversal in the direction of the undulatory wave produced backward swimming movements.

Deviations in behavior and body form not previously discussed are as follows. When the nerve cord is cut near the anterior end or in the mid-body region the portion of the leech anterior to the cut may fold back along the ventral surface. This was most frequently observed during crawling and swimming when the cut was made in the anterior region, and during swimming when the cut was made in the mid-body region.

This conspicuous ventral folding just anterior to the cut followed complete relaxation of the longitudinal muscles in that area. It has been established experimentally (Miller, 1936) that the motor neurons innervating the longitudinal muscles extend from posterior to anterior in the cord. The immediate contraction of the ventral longitudinal muscles anterior to the cut may be attributed to direct stimulation through sub-epidermal nerve innervation. During crawling or swimming activity in which that portion anterior to the cut is taking no part the animal literally bends in that region in which the longitudinal muscles are relaxed. The bend follows the line of least resistance. After the cutting of the cord, the following change in body shape was noted. The operated leech showed in the region of the cut (except near the posterior end, see Fig. 4), a conspicuous constriction extending anteriorly, and an equally obvious enlargement extending posteriorly. In the mid-body region a typical segment consists of five annuli. In the segment anterior to the cut, there was a loss of tone in the longitudinal muscles. Posterior to the cut there was a corresponding loss of tone in the circular muscles. The area thus affected, depending upon the relation of the cut to the segmental ganglia, extended from three to five annuli anteriorly and from four to six annuli posteriorly, Fig. 2.

These observations further substantiates previous experimental data relative to the position in the ventral nerve cord of the motor fibers innervating body wall muscles. It further suggests that certain motor fibers extend for only a short distance in the cord. As determined from these observations it would appear that the motor nerve cell bodies, the extensions of which innervate the circular muscles, are located in the ganglion anterior to the segment containing the muscles innervated. Further, that the motor nerve cell bodies, the extensions of which innervate longitudinal muscles, are located in the ganglion posterior to the segment containing the muscles innervated.

CONCLUSIONS

1. Abnormal behavior follows the complete transection of the ventral nerve cord.

2. Types of behavior known to be affected include crawling, looping, swimming, and undulatory movements.

3. A given region of the animal may respond normally, while in another section cessation or a reversal from normal behavior is observed.

4. Following the cutting of the ventral nerve cord, there is a loss of tone in the circular muscles immediately posterior to the cut.

5. Following the cutting of the ventral nerve cord, there is a loss of tone in the longitudinal muscles immediately anterior to the cut.

6. Swimming and undulatory movements may be carried on by either the anterior, the posterior, or middle section of the leech's body.

7. The cutting of the cord does not affect the functional capacity of either the anterior or posterior sucker.

8. Looping movements are not observed after a cut in the cord is made.

9. Giant fiber, or end-to-end, reaction is retained in sections just anterior or posterior to the cut.

10. Tactile stimulation produces an end-to-end contraction in the region anterior to the cut.

11. Random movements are confined to that portion of the animal anterior to the cut in the cord.

12. Backward swimming movement sometimes follows the cutting of the cord near the posterior end.

13. Undulatory movements originating posteriorly are expressed following the cutting of the cord near the posterior end.

14. An intact ventral nerve trunk is a necessary prerequisite to normal co-ordinated crawling, looping, swimming, and undulatory activity.

15. Certain motor fibers extend for only a short distance in the cord.

LITERATURE CITED

Biedermann, W. 1904. Studien zur vergleichenden Physiologie der peristaltischen Bewegungen der Würmer und der Tonus glatter Muskeln. Arch. gesam. Physiol., 102, 475–542.

Bovard, J. F. 1918. Univ. Calif. Pub. Zool. Vol. 18: 103–134.

Friedlander, B. 1894. Beitrage zur Physiologie des Centrolnervensystems und des Bewegungsmechanismus der Regenwürmer. Arch. gesam. Physiol., 58, 168–206.

Miller, John A. 1933. The Ohio Jour. of Sci. Vol. XXXIII. No. 6.

1934. The Ohio Jour. of Sci. Vol. XXXIV. No. 1 and No. 5.

1936. The Ohio Jour. of Sci. Vol. XXXVI. No. 6.