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THE TRANSMISSION OF NERVOUS IMPULSES
IN RELATION TO LOCOMOTION
IN THE EARTHWORM

A THESIS SUBMITTED IN PARTIAL SATISFACTION OF
THE REQUIREMENTS FOR THE DEGREE OF
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AT THE UNIVERSITY OF CALIFORNIA

BY

JOHN FREEMAN BOVARD

MAY, 1917

The Transmission of Nervous Impulses
in Relation to Locomotion
in the Earthworm

by

John F. Bovard

A thesis presented to the Faculty of the
College of Letters and Science
in the
University of California
in partial fulfillment of the requirements
for the degree of
Doctor of Philosophy.

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JOHN F. BOVARD

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INTRODUCTION

The normal creeping movements of the earthworm proceed as follows. The first movement is a contraction of the circular muscles of the first few segments. This causes an extension of the anterior end. The chaetae now become directed backwards and take hold on the substrate while the longitudinal muscles begin a contraction which draws the next few segments forward. The circular muscles in each segment contract, one segment after another beginning at the anterior end and proceeding posteriorly. Immediately following the circular muscle action the longitudinal muscles contract so that a wave of extension followed by a shortening can be seen to traverse the whole animal. After the first wave of muscular activity is well started posteriorly another may be initiated and at any one time several of these contraction waves may be seen in a normally creeping worm.

Some years ago Friedländer (1894) showed that in the normal creeping of an earthworm the nervous system played only a small part. When a section of the nerve cord containing ten to twelve ganglia was removed, the movements of the parts of the worm were still perfectly coördinated. The most important part of the activity was the "pull" which the contraction of each segment as the wave progresses gave to the succeeding segments. The wave-like motion of the contractions proceeding down the length of the animal was due, first, to the pull of segments on each other, and, secondly, to the sequence of reflex actions of the nerves in each segment, which are such that the longitudinal muscles follow the contractions of the circular muscles. This nervous mechanism is, according to Friedlander, concerned with each segment alone, and there is no passage of impulses up or down the cord. No attempt was made by him to analyze the matter of tension or pull, or to determine whether coördination would proceed without this factor.

In order to show that the nervous system was entirely secondary, Friedländer cut a worm into two pieces and then joined these two with a thread. The creeping movements of the anterior piece gave the necessary pull on the posterior piece through the thread, and the two parts crept along in perfect coördination. In certain special cases, when the nerve cord was destroyed for a short distance without transection of the body, the parts anterior and posterior to the cordless region moved together with perfect coördination. According to this

view, then, the nerve cord is supplementary and concerned only with those short reflex paths which are mediated by a single ganglion. Previous to the year in which Friedländer published his analysis of the movements of earthworms, Krukenberg (1881) showed, in some work on leeches, that the middle section of the animal could be anesthetized with the result that the parts anterior and posterior to this region still acted in perfect coördination. In these animals, however, the nervous system differs structurally from that of an oligochaete. In leeches the nerves run from the anterior to the posterior end, while in the oligochaetes the only long nerves are the giant fibers, the other fibers in the cord being those of short neurones extending at most from one ganglion to the next. The anesthesia in leeches affects only the peripheral nerve endings, while the trunks connecting anterior and posterior portions are not affected.

The more recent work of Biedermann (1904) becomes particularly interesting, however, as it gives some new light on the function of the nerve cord of the earthworm. In this work on the comparative physiology of peristaltic movements he compares the locomotor action in earthworms to the rhythmic movements found in smooth muscle. Biedermann discovered that if worms were placed in seven per cent alcohol for a few minutes until they became motionless and then the middle region of several segments was anesthetized with nitric acid or pure chloroform for a few seconds, the muscular activity of the section was destroyed and all response to stimulus failed. He then had a worm with active anterior and posterior parts connected through the anesthetized area by a nerve cord. In creeping movements, the anesthetized area, or dead area, acted as one piece. It transmitted no rhythmic movements, while the posterior part still acted in perfect coördination with the anterior part.

In further tests by Biedermann of the transmission of impulses through the cord over more than one segment, he pinned such anesthetized specimens to a cork plate by needles through the dead muscular area and found that the posterior part still moved in perfect coördination with the anterior part. With regard to the limits of this transmission through the cord, and the speed of the impulses, it is stated in his paper (1904, p. 493) that the transmission often runs 2-3 centimeters in 4-5 seconds.

In the interpretation of these experiments Biedermann accepts the theory proposed by Friedländer, except that in order to explain the coördinated movements of posterior pieces when a certain part was

anesthetized, it is necessary to assume that the impulses run through the cord for a considerable distance rather than through one ganglion as Friedländer supposed.

MATERIALS AND METHODS

Materials.—Several species of worm were used for these experiments. The large garden worm, *Helodrilus caliginosa*, was favorable material owing to its size. The small dung worm, *Allolobophora foetida*, was also very convenient material because of the ease of obtaining the material during the winter. No difference was observed in the reactions in these worms. Unless specially noted the experiments recorded will refer to the larger worm, *Helodrilus*.

Methods.—Biedermann's (1904) method of anesthetizing a certain portion of a worm by use of nitric acid or chloroform, as described, had the effect of killing any peripheral nerve endings present in the part and of impairing the muscle cells. It left the anterior and posterior portions connected, however, by a functioning nerve cord, still intact, except that no stimuli applied to the treated epithelium were effective in setting up reflexes.

It was suspected by Biedermann that as locomotion took place the posterior part was acting in coördination, not only because it was connected to the anterior, as Friedländer might have supposed from his string experiment, but that there was some real nervous influence transmitted by the cord in the inert middle section. In order to test this point fully, he pinned the middle anesthetized portion to a cork plate to remove the factor of tension, when it was found that the posterior portion still made movements coördinated with those of the anterior piece. This established beyond a doubt that transmission did take place over a longer section of the cord than the earlier investigators had deemed necessary and showed the more important part played by the nervous system.

In developing a method of anesthesia to test farther the matter of transmission, it seemed to me desirable to find some means of blocking reflexes in the *middle area*, and yet it was also quite necessary at the same time to leave the muscle tissue and the central nerve cord intact, only the peripheral nervous system being eliminated. The method developed was quite different from that of Biedermann. The worm was placed on a glass plate slightly moistened with water, so that it was slippery. A small four-drahm homeopathic vial containing some

cotton soaked with ether, was then turned down over the worm so that the mouth of the bottle covered the middle section of the worm. It was possible to hold this in place over the squirming worm until the middle part was anesthetized. Owing to the slipperiness of the plate, the worm could get no hold and autotomy was very rare. When, however, as occurred in early experiments, this method was tried on a cork plate, autotomy of the anterior or posterior part was frequent because of the hold the chaetae were able to take on the cork and so the worm could pull itself in two. Exposure of two minutes to ether fumes was sufficient for complete anesthesia, but had little effect on the muscle tissue itself. The worms usually recovered completely from the effects of the treatment in from ten minutes to an hour. During this time a stimulus to the muscle in the anesthetized area called forth a direct response but started no reactions in the untreated parts of the worm.

In using some of the larger worms this simple method was varied by treating the etherized area with six per cent nitric acid for ten seconds, then washing the whole worm in water; this made certain that the sensory nerve endings, of this part, were rendered functionless. In cases where nitric acid was used the worm never recovered from the treatment, and in a few cases where the worms were kept for a few days they autotomized the posterior and middle sections. This method was used where only a nerve bridge was desired between the active anterior and posterior parts, as in measuring the speed of transmission of impulses in the nerve cord.

STATE OF THE ANESTHETIZED AREA

For a very short period after treatment, the anesthetized section looks whitish and gives off a great deal of mucous, but later the appearance is much the same as that of the rest of the worm, except for an increase in diameter. As the worm begins active movement, this middle piece decreases in diameter, due to stretching, for it acts much like a rubber band, extending and then contracting with each creeping movement. However, no waves of muscular contraction run along its length, as in the anterior and in the posterior parts, or from the former to the latter.

Stimulation of a quiescent worm in the anesthetized and live regions respectively gives a marked difference in response. If the anterior part is touched lightly the response is an increase in diameter due to a reflex stimulation of the longitudinal muscles, but a stimu-

lation of the middle area results in a constriction, due to the contraction of the circular muscles with no reflex to the longitudinal muscles. In recovery from the ether treatment the longitudinal muscles recover and reassume normal functions first and the circular some minutes later. In creeping movements the middle section shows that the longitudinal muscles recover their nervous connection first, for they begin to contract in coördination with the anterior part, some time before the circular muscles begin any active participation in the general movement. This condition is due no doubt to the fact that the longitudinal muscles lie deeper than the circulars and so are less affected by the anesthesia. In addition to this the position of the longitudinal muscle is closer to the general blood supply, which would be advantageous in the removal of waste products and the bringing in of new materials.

THE PROBLEM

The problem then suggests itself: how is this transmission through a number of segments accomplished? (1) Does Biedermann's discovery necessitate the existence of long fiber tracts in the cord? or, (2) Can it be explained on present knowledge of the neurones? (3) Are there any limits to the transmission through anesthetized areas? (4) Can the speed of such impulses be measured, and how do they compare with the speed of nerve impulses in other annelids?

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The greater part of the experimental work was done at Harvard University during the year 1914-1915, under the general direction of Dr. G. H. Parker, to whom I am greatly indebted for his very kindly interest and his many suggestions. Later the work of bringing together the results of the experimentation was done at the University of California. I wish to acknowledge and express my appreciation for the helpful criticism and advice of Dr. S. S. Maxwell, of the Department of Physiology, and to Dr. C. A. Kofoed, of the Department of Zoology, for the general supervision of the work and the revision of this paper.

EXPERIMENTS WITH ETHERIZED WORMS

Problem.—Will it be possible to get transmission of locomotor impulses through an anesthetized area in both directions, from anterior to posterior and also from posterior to anterior?

Discussion.—If a worm is etherized by the vial method and allowed to creep on a damp surface, such as moist filter paper, it will be seen to act like a normal worm in every way, except that the middle or etherized portion takes no part in the contractions. With each pull of the anterior piece it will stretch and passively contract as the posterior piece moves up, without showing the normal waves of muscular contraction seen in the active portions.

A worm, that is moving anteriorly, will reverse its direction and creep posteriorly if stimulated on the anterior end. Stimulation of the posterior end reverses the direction again. This indicates that nerve impulses may pass up or down the nerve cord and that these impulses may change the direction of the creeping movement, but it does not indicate that the impulses responsible for the actual creeping pass through the nerve bridge. There is still the fact that the muscles in the etherized section attaching the anterior to the posterior part may act as the "string" in Friedländer's experiment and give the necessary pull which keeps the two parts working in coördination.

Conclusion.—These simple experiments only show that there may be transmission of locomotor impulses in both directions through the nerve cord in an anesthetized region of the worm.

TENSION

(a) *Experiments with Etherized Worms*

Problem.—To what extent is the factor of tension or pull responsible for normal locomotor reactions?

Method.—By the use of ether in anesthesia we are able to test out the importance of the matter of tension or pull in the transmission of locomotor impulses. It will be remembered that the etherized part acts as one piece. No waves of contraction pass up or down this part. A small piece of cork was glued to a glass plate and the glass plate kept wet. A worm prepared by etherizing ten segments in the middle portion was pinned to the cork so that the anterior and posterior parts were free to move, but the middle part was fixed.

Discussion.—Under these conditions no movements of the anterior part could exert any pull on the posterior piece. In all such experiments the worms behaved as Biedermann (1904) reported, the posterior piece responding with locomotor reactions in perfect coördination to all attempts of the anterior piece to make creeping movements. These movements could not be accomplished because of the slippery

glass surface and the pinning down of the middle section, but the wave of contraction, as in normal creeping, can be easily observed (fig. 1).

Fig. 1. This shows the method of pinning the anesthetized region of the worm. Region *A* has just made an anterior creeping movement and region *C* can be seen making a coordinated movement. On account of being pinned through region *B*, the anterior part of *C* is forced to buckle.

The reversal of the direction of these movements is also possible. Stimulation of the anterior end will cause the posterior end to attempt creeping posteriorly with the anterior piece acting in perfect coordination.

If, now, the nerve cord be severed in the middle region without disturbing the muscular connections a great deal, the coordinated movements of the two ends cease and become independent each of the other. It is possible when a worm is pinned and the continuity of nerve in the anesthetized area is broken, that the anterior and posterior ends may each be making locomotor movements in opposite directions, showing an independence of action even though joined by a muscular connection. There can be, therefore, no doubt that the nerve cord carries, for some distance, impulses which are responsible for locomotor movements. By pinning the worm to the cork, the matter of tension has been eliminated and by cutting the nerve, the transmission through the nerve cord has been removed and coordinated movements cease entirely.

When such a worm with transected nerve cord and anesthetized middle section is released from its cork plate and allowed to creep freely, it is found that the coordination of anterior and posterior parts is perfect. In this case, however, there is an entirely different explanation. The coordination of the posterior end can not be due to any nerve impulses from the anterior end, but each forward movement of the anterior section causes a pull on the posterior piece and this starts a chain of reflexes at the anterior end of the posterior piece which run the length of this part of the worm and give rise to the muscular contractions which normally would give rise to locomotion.

In worms in which the entire dorsal wall, the lateral muscles, and the intestine of the etherized part were dissected away and the nerve cord freed from the ventral muscle by cutting the lateral roots, the coördination continued perfect in function between the anterior and posterior portions. It was observed that such specimens, in creeping, did not move with the middle section tense, as a string connecting the two parts, but that often the posterior part moved along rapidly, causing the middle part to buckle so that under these circumstances no pull could possibly have been exerted on the posterior part. When the anterior part was pinned down, the posterior piece still continued its coördinated movements and "telescoped" anteriorly into other parts.

Conclusion.—Tension or pull, while important in normal creeping movements, may be eliminated and the locomotor stimulus will still pass on down the nerve cord for some distance.

(b) Autotomy

In the course of administering the anesthesia to the middle portion of the worms, it sometimes followed that the strong contractions would break the muscular walls of the body, a condition of incomplete autotomy. If the animal was released in time the anterior and posterior ends would remain connected by the intestine and the nerve cord (fig. 2).

Fig. 2. This shows the nervous bridge as made in an incompletely autotomized worm. The break in the musculature occurs between the segments. The intestine (*int.*), with the dorsal and ventral blood vessels (*d.bl.v.* and *v.bl.v.*) and a portion of the ventral nerve cord (*n.*), may be seen.

Problem.—Is the nervous bridge made by incomplete autotomy between anterior and posterior ends of the worm capable of transmitting locomotor impulses in both directions as in the etherized worms?

Discussion.—Under these circumstances the reactions of the partially autotomized worms are the same as in etherized ones; creeping anteriorly and posteriorly can be induced by stimulation. If the anterior end is pinned, the posterior part will still act in coördination; in this case the only possible way for the transmission to take place would be through the nerve cord. Microscopical sections of such cases as these showed that the nerve cord was quite normal in structure and still intact.

Friedländer (1894) laid such stress on the matter of tension, the pull of one part on the next succeeding segment, that the behavior of the worm under these conditions of anesthesia becomes particularly important as bearing on the correctness and completeness of his explanation (fig. 3).

Fig. 3. An illustration of Friedländer's experiment which shows the anterior and posterior parts of the worm tied together with a thread. The movement of the anterior piece pulls on the anterior end of the posterior piece and starts the locomotor reactions which are coördinated with those of the anterior half.

Conclusion.—In cases where the tension is eliminated by pinning the worm to a cork on glass, the posterior part can be seen to begin rhythmical movements of contraction coördinated with those of the anterior part. If this anesthetized portion is composed of but few segments, then the coördination is most perfect and the beginning of the movement of the posterior section follows in shorter time than when this portion of the worm includes many segments. It is possible to anesthetize a section of such length that no coördination is carried on and the posterior part lies entirely inert. In *Helodrilus* transmission of impulses was effective through 20 segments, rarely through 28, and never through more than 30 segments.

NERVE FREE PREPARATIONS

Problem.—The fact that the worms perform autotomy and that the anterior and posterior parts are then connected with each other only by a simple nerve bridge and the intestine, suggested the possibility of dissecting away all the connecting muscle between the anterior and posterior parts. Could the nerve cord be dissected free for a distance exposing several ganglia and could locomotor impulses be transmitted through such a cord?

Methods.—(a) *Dissection.* All the muscle in the anesthetized region was cut away after the worm had been pinned to a cork plate. Owing to the fragility of the nerve, it was easily broken and in cases where it was not broken it was easily impaired by stretching, so that particular care had to be taken with the preparations made. Here, as in the experiments discussed above, where transmission was over a few segments, the coördination was good and as the nerve bridge was lengthened the coördination was less complete and finally failed. Such an operation must have a decided “shock” effect on the animal and it does not behave as would be expected under more normal conditions, consequently the length of the nerve does not represent the limits of transmission, as will be shown in some experiments to be discussed later.

In all these cases it was necessary to keep the worm pinned, for if allowed free creeping the anterior part would move more rapidly than the posterior, the nerve was not strong enough to drag the weight of the posterior part and so the nerve was promptly broken.

In my first dissections all of the musculature in the anesthetized region was removed, so that the nerve cord was the only connection between the anterior and posterior parts of the worm. Later I modified this so that the nerve cord, while entirely free for several segments, was not allowed to touch the cork plate but was kept in its own body fluids on a piece of muscle (fig. 4). All the muscle on the dorsal and

Fig. 4. Type of dissection used in nerve free preparations. (n.) nerve cord with lateral roots cut (l.r.), intestine (int.) and blood vessels (d.bl.v. and v.bl.v.) cut away.

lateral walls was dissected off. The intestine was removed. This left the nerve cord attached to the ventral plate of muscle. A sharp flat stylet was introduced under the nerve cord and all the lateral roots severed. A transverse cut was then made across the ventral muscle so that no muscular connection remained between the two parts of the worm. When this type of operation was used much more uniform

results were obtained than where the nerve was allowed to come in contact with the cork of the dissecting tray. Garrey and Moore (1916) used a method similar to the earlier method that I used with the same general results.

(b) *Graphic Records. Apparatus.* As a check on the observations just described, it became desirable to find some way in which to make a graphic record showing the part the nerve cord plays in the transmission of locomotor impulses. The movements of the anterior and posterior ends of the worm, while the middle part was fixed to a cork plate glued on glass, suggested that if levers were attached to these moving parts a record could be obtained on a kymograph. It was necessary in order to obtain good records to have the levers as light as possible and to have them move with very little friction. This was accomplished by making the levers of aluminum wire, number 22. A desired length was inserted in a cube of cork. Through the cork a small glass capillary tube was thrust which made the bearing for the axle of the lever. A very fine needle was then fitted into the glass capillary and the needle stuck into a firm support. This sort of a bearing allowed the lever to move with little friction and also was

Fig. 5. The general arrangement of the apparatus for recording movements of the anterior and posterior parts of the worms. Method used at Harvard, 1914-1915.

a.l.—Aluminum wire lever connected to anterior end of worm by hook and thread; *c.*—Cork plate glued to glass for pinning the middle anesthetized portion; *c.c.*—Cork cubes through which aluminum wires run; *g.pl.*—Glass plate to which a little water was added to allow the worm to slide back and forth when pinned; *p.l.*—Aluminum wire lever connected to posterior end of worm by hook and thread; *ky.*—Drum of kymograph for taking tracings on smoked paper; *wt.*—Counter balance weights.

advantageous in that it allowed little side lash. Various forms of levers could be built up by means of extra cork cubes and short sections of aluminum wire, as in figure 5, *a.l.* and *p.l.*

The levers had to be weighted slightly so that the worm would be kept in a straight line on the glass plate or else the curves recorded would be exceedingly irregular (fig. 5).

If now a worm is prepared with the middle part anesthetized and arranged to record movements, the movements of the posterior part should show a perfect coördination with those of the anterior part (fig. 6).

Fig. 6. Experiment 143. A record showing perfect coördination between anterior and posterior parts with a middle area of eight segments anesthetized and musculature cut away. The upper curve represents the movements of the anterior end and the lower that of the posterior end. Transmission of impulses mediated through the nerve cord only.

The method of preparation of the middle portion varied. In some cases the worm was treated with ether by the vial method, and then triple-pinned to the cork plate. In other cases, in addition, the dorsal musculature was cut away, the intestine removed, exposing the nerve cord, and the lateral branches of the nerve cord transected. In still other cases the musculature was cut in the middle region but not

removed, so the nerve could rest on its own body fluids. In all these cases coördinated movements of anterior and posterior portions were shown. The best records were obtained when the least dissection was used.

The clinching argument, however, was obtained when during the course of such experiments the nerve cord is cut. In all such cases, no matter what type of dissection was used, non-coördinated movements were shown when the cord was transected (fig. 7).

Fig. 7. Experiment 143. Explanation of the curves here the same as in figure 6. The nerve cord connection between anterior and posterior has been cut. Notice the lack of coördination between the movements of two portions of the worm.

(c) *Stovaine*. Should any doubts still remain concerning transmission of impulses for locomotor movements over long sections of the nerve cord, the action of stovaine will set these completely at rest. If stovaine be injected into the body cavity of the worm it acts as a block to the nerve cord over four or five segments and allows no impulses to pass up or down through the segments containing the anesthetic. The records will show that there is a lack of coördination and suppression of movements of the posterior end while the drug is effective (fig. 8),

Numbers refer to time of day animals were tested.
Arrow indicates stimulus given to the anterior end.

Fig. 8. Experiment 190. Stovaine injected into middle section of worm, four segments affected. Lower curve registers the movements of anterior end and upper curve those of the posterior end. At 2:41 P.M. the coördination between anterior and posterior parts is not normal, and at 2:50 P.M. the giant fiber action is lost. Stimulation at the arrow fails to give a reaction in the posterior part.

A represents ordinary locomotor activities.

B represents giant fiber action.

but as soon as the effects begin to wear off, the coördination between the two parts becomes more and more complete until finally the anterior and posterior parts are again acting in perfect rhythm (fig. 9).

The supposition in this case is that stovaine acts on tissue of earthworm as it does in the vertebrates, where it has no effect on muscle or nerve endings but acts only as a "block" on nerve fibers. The effects of the drug were kept localized to small sections while anteriorly and posteriorly all the normal reactions could be obtained.

Conclusion.—The nerve-free preparations, the graphic records of movements before and after the nerve was cut, and the physiological block established by stovaine, all go to show that the locomotor impulses travel considerable distances in the cord. This work confirms the results obtained by Biedermann but by quite different methods. The most important aspect of these results is the demonstration that

locomotor impulses are not "short relays" depending on a stimulus from each segment, but are capable of running a number of segments with no stimulus from the outside.

Fig. 9. Experiment 190. Continuation of experiment shown in figure 8. At 6:20 P.M. the worm had recovered from the effects of the stavaine. Normal coördinated movements are being made (A) and the giant fiber action has returned (B). Stimulation of the anterior end at the arrow shows a response in the posterior end.

LIMITS OF TRANSMISSION

Problem.—How far will these locomotor impulses travel in the cord? Can a middle area of sufficient length be anesthetized so that no impulses from the anterior piece can get through to start locomotion in the posterior part?

Discussion.—It was soon discovered that transmission was best shown when it was concerned with few segments and that, as the number of ganglia through which the impulse must pass was increased, the coördination became less and less perfect. No sharp limits could be determined. When the nerve cord was dissected free from muscle, the most severe type of dissection, the transmission seemed to be limited to eight free ganglia. In one case, coördinated movements were obtained when ten ganglia had been freed, but this was unique.

When the length of the free nerve contained four ganglia, transmission was easily demonstrated.

In those cases where the dissection included the removal of the dorsal wall, intestine, and the transection of lateral nerves, the transmission easily ran for more than ten segments, but never for more than twenty-eight.

It has been demonstrated by Biedermann (1904) and confirmed by my own experiments, that the impulses run long distances in the cord when the worms are anesthetized in the middle region which is afterwards treated with six per cent nitric acid. In such cases, records of transmission were obtained when twenty segments intervened between the still active anterior and posterior ends. Failures came more often as the length of this etherized part was increased. One record was obtained with the large *Helodrilus* where coördinated movements appeared in the posterior part when twenty-eight segments were etherized and their muscles killed with nitric acid.

These results fall somewhat short of the cases reported by Biedermann, where coördinated movements were obtained through anesthetized parts two to three centimeters long, but the number of segments is not stated. The greater part of my records were obtained on *Helodrilus*, where twenty segments of the body, in the part measured, approximated two centimeters. While this does not show a great discrepancy, my results are apparently nearer the lower figure quoted by Biedermann.

We can establish, then, no absolute limits, except to say that transmission is fairly well accomplished over ten segments, may run to twenty and even to twenty-eight, but that the longer the nervous bridge the greater the difficulty. No records have been obtained where thirty segments were concerned.

One factor which makes the determination of any such records very difficult is that impulses from normal stimuli in normal worms starting down the length of the worm do not necessarily continue to the end. The dying out of an impulse is quite a usual phenomenon seen in the contraction waves that run only part way down the animal. One of these impulses may start into the cord of the etherized part and never reach the other end of the etherized part of the worm. This does not mean that no impulses can come through, and so no limit can be determined by this failure, but it does indicate a dying out of this particular impulse somewhere in transit. Therefore, in the experimental determination of the limits to transmission, as long as impulses

come through the etherized part we are still within the limits of transmission, but as soon as failures become frequent it is evident that the limits have been approached. More refined methods may be able to determine these limits closely. My records can be considered only as approximations.

One other difficulty arises in making these determinations. Summation of stimuli has been shown by both Straub (1900) and Budington (1902) for annelid muscle. Weak stimuli adding themselves together will sooner or later give a contraction. There is the possibility that, in observations on these reactions, failures have been recorded, where, in reality, weak stimuli did get through. However, any errors so made would be on the conservative side.

Conclusions.—The results of these experiments show that no absolute limits can be set, the impulses travel short distances in the cord very readily and that the longer the section of cord to be traversed the greater the difficulty. In *Helodrilus* twenty-eight segments was the limit for the distance locomotor impulses would travel in the cord when the superficial nerves were anesthetized.

DEPENDENCE ON NERVOUS SYSTEM FOR TRANSMISSION

Problem.—While the nerve cord is capable of transmitting locomotor impulses for considerable distances is it possible for the muscles to carry on rhythmical movements without the aid of the nervous system?

Discussion.—If a short section of a worm containing about twenty to thirty segments is prepared in such a way that it will give a record of contractions of the longitudinal muscles on a moving drum, and the lever is slightly weighted so the piece will be kept straight but not stretched, it will be found to make rhythmic contractions. Straub (1900) and Budington (1902) show this characteristic of annelid muscle but disagree in the interpretation. Straub claims that strips of the muscles, both with and without nerve, will give rhythmic contractions. However, regions of the worm from which the nerve had been removed must be given several (eight) days for recuperation and then they would give contractions comparable to those of the regions of worm with nerve intact. Budington found that when care was used to remove all nervous tissue by using only pieces of worm in which the whole ventral muscle had been removed, that such pieces gave no rhythm; while pieces containing even a small amount of nerve gave a regular rhythmic curve (fig. 10).

Fig. 10. Experiment 104. Curve *A* is made by a short piece of worm attached to a writing lever. The piece was normal in every way and gave rhythmical contractions. Curve *B* represents a curve made by the dorsal half of a short piece of a worm that had been split in two longitudinally. This piece contained no nerve cord. Curve *C* was made by the ventral half of a short piece of a worm that had been split in two longitudinally. This piece did contain the ventral nerve cord and did give rhythmic contractions.

My results agree entirely with those of Budington. It is quite possible that the findings of Straub may be due to a factor that he overlooked, the matter of regeneration. As I shall show in a later paper, regeneration is exceedingly rapid and there is a possibility that nerves have grown into the operated portion, and the probability is that Straub was really dealing with pieces in which nerve fibers and cells had regenerated.

As further evidence of this dependence upon the *nerve cord* for transmission it will be noted that when a worm is pinned in the middle portion to a cork plate and the anterior and posterior ends are registering coördinated movements on a revolving drum, if the nerve be cut in the pinned region the rates of contraction of the two parts will be immediately changed. In this case, the muscle is disturbed as little as possible and only the nerve cord is cut (fig. 11).

Fig. 11. Shows how the posterior half of the worm changed its rhythm after the nerve cord had been cut. The upper line represents the movements of the anterior (*A*) half and the lower line the posterior (*B*) half. The nerve cord was cut without cutting any but a small portion of the ventral muscle.

Conclusion.—From the work just cited, it is quite certain that spontaneous movements are dependent on the nervous tissue and that

the muscle has no property of rhythmic contractility. While this does not show that transmission of impulse passes over many ganglia in locomotion it strengthens the work of Biedermann (1904) and Budington (1902) who hold the theory of nervous control.

RATES OF TRANSMISSION OF LOCOMOTOR IMPULSES

Problem.—The fact that locomotor impulses could be transmitted through a portion of the nerve cord isolated from segmental muscle connections led to the query, what is the speed of these impulses? If the speed were rapid it would mean that there were some fairly long neurones in the cord, and if the speed were slow it could be interpreted on the basis of short neurones and many synapses. This study should throw some light on the structural basis of transmission.

Discussion.—Jenkins and Carlson (1903) measured the rate of nerve impulses in several species of annelids. The rates were found to be exceedingly variable, from 89 centimeters in *Nereis* sp. to 694 centimeters per second in *Bispira polymorpha*. The question these investigators raised was whether they were dealing with simple continuous nerve fibers or with a very complex nervous tract. While the anatomical connections of neurones in the cord have been worked out to some fair degree of certainty, no long connections have been established in the cord, except by the giant fibers. Jenkins and Carlson left the question open as to whether their measurements were those of a direct nervous path or an indirect one.

After observing a very large number of experiments on the transmission of the impulses as they pass through the etherized section of the worm, and noting the slow progress of these as compared to the quick end to end jerk of the worm when stimulated, there is little doubt in my own mind but that the cord has two kinds of transmission of nerve impulses. First, the very rapid impulses through giant fibers, which result in vigorous contractions, as in the jerking back into their burrows of the worms when strongly stimulated; and the second type, the impulses in the short fibers in the middle of the nerve cord, which offer a complex path and so transmit impulses slowly down the cord.

My records for the speed of impulses in the giant fibers agree quite well with the speed recorded by Jenkins and Carlson (1903). The method which these workers used was such that only the action of quick contractions was recorded and no attempt was made to separate this phenomenon from that of the locomotor impulses. As has been shown, these latter impulses run but short distances in the cord unless

reinforced by outside reflexes; and so, unless special methods are used, the reactions of these short fiber systems would not be observed.

A frequent observation on the locomotor habits of worms is that the wave of contraction runs for a short distance and then disappears. This was a source of great inconvenience in determining the rate of impulse down the cord. A method was devised whereby electric contacts were successively made as the wave of contraction passed along the worm. These were recorded on a drum from which measurements were easily made and speeds computed (fig. 12).

Fig. 12. The apparatus for measuring the speed of nervous impulses through the nerve cord in an anesthetized region was as follows: *a.l.* and *p.l.* are levers pivoted at *piv.* The lower part of the lever *n.* is a sharp, very fine needle. One of these is thrust into the muscles of the first segment in front of the anesthetized part *m.* and the other into the muscles just behind this region *m.* The upper ends of these levers is quite long so that very slight movements of the lower part will produce considerable movement in the upper part. Platinum contacts were provided at *pt.c.* and each lever was connected by battery to signal magnets, *a.s.* and *p.s.*, which gave a record on a smoked drum of a kymograph. When the locomotor movement of the anterior part of the worm had reached the muscles at *x.* the electrical contact would be made in lever *a.l.*, which registered on a fast revolving drum at *a.s.* Now when the nervous impulses had passed through the anesthetized area *m.* and reached the muscle *y.* another electrical contact was made by lever *p.l.* and registered by signal magnet *p.s.* The speed of the drum being measured, the speed of the impulse could be calculated.

The very noticeable result of this series of experiments was the great variability in the speed, which seemed to depend on the state of irritability in the worm.

Another important fact seemed evident from these measurements; namely, the longer the section of nerve measured the slower the rate recorded.

TIME TAKEN TO TRAVEL OVER CERTAIN LENGTHS OF NORMAL AND ANESTHETIZED WORMS

	EXPERIMENT 180 3 live, 20 etherized segments	EXPERIMENT 162 11 live, 20 etherized segments	EXPERIMENT 162 19 live, 20 etherized segments
1	.26 seconds	.90 seconds	.68 seconds
2	.44	.50	.65
3	.24	.64	.70
4	.21	.60	.90
5	.25	.34	.70
6	.35	.34	.82
7	1.02	.30	.92
8	.72	.25	.75
9	.13	.40	.72
10	.08	.25	.72
Average	.370	.452	.760

¹These figures are calculated from experiment 180, a series different from that in columns 2 and 3.

The method for making these records was not refined and the times recorded can only be approximations. The table will show that where the length of the portion of the worm measured is increased the time of transmission increases, but not proportionately. The full significance of this fact and its relation to transmission and a new theory of locomotion will be brought out in a later part of this paper.

In measuring the speed of the impulse through the nerve cord in a section where the muscle had been anesthetized, the electric method of measurement was quite effective. Records of slight movements of the segments just anterior to the inert section were followed by the registration of movements beginning in the part immediately behind this portion. Here again we meet great variability, depending on the state of excitement in the worm. If the etherized section is greatly increased in length the point will eventually be reached when no impulse comes through. Records through more than twenty segments were frequent, but when more than twenty segments were used, failure resulted more often than in fewer than twenty. Measurements were recorded over twenty-eight segments but these seemed to be exceptional

cases. For the most part, impulses passed along the cord at the rate of about 25 millimeters per second. This represents the mode of a series of ninety-one measurements. Several observations showed good transmission at the rate of 60 millimeters per second, and a few were recorded in which the rate was very low, 10 millimeters per second (fig. 13).

Fig. 13. The frequency polygon which shows results of ninety-one measurements of the speed of locomotor impulses through the nerve cord when the peripheral nerves have been anesthetized. The mode lies between 20 and 30 millimeters per second.

Conclusion.—The locomotor impulses show no definite speed. The most interesting feature is the extreme variability of this movement. In those cases where strength of stimulus is sufficient and other conditions are right the speed may be as fast, as 100 millimeters per second, and again the speed may be so slow that it will die out in the nerve cord without ever emerging from the anesthetized region. I have taken the mode of the frequency polygon as against the average which shows that ordinarily the speed is about 25 millimeters per second. The slowness and variableness are the two main characteristics.

RATE OF IMPULSES IN THE GIANT FIBERS

Problem.—How does the rate of transmission of locomotor impulses compare with that of the giant fiber? Are the rates such that these two phenomena can be ascribed to quite different systems of neurones?

Discussion.—The method used to measure the rate of transmission of impulses in the giant fibers was practically the same as that used in measuring locomotor transmission, except that in this case it was

possible to use the full length of the worm. One characteristic of this type of action is that it seems to be related solely to the longitudinal muscles in contrast to that of the locomotor nerve fibers which set up complex reactions in both circular and longitudinal muscles.

Responses resulting from stimulation of these large fibers are always exceedingly rapid as compared with other movements of the worms. The reaction may be slight or violent, according to the amount of stimulus applied, but any response travels the length of the worm in a very short time. It is interesting to note the antagonistic relations of the innervation of muscles when a quiescent worm is stimulated lightly, with a sharp needle, at the anterior end; immediately there is a response by a relaxation of the circular muscles near the posterior tip so that this part is flattened and enlarged. If the stimulus is made stronger, this reaction will be followed by a jerk of the longitudinal muscle and when the stimulus is moderately strong the contraction of the longitudinal muscle is so quick and extensive that no reactions of the circular muscle can be detected.

A number of determinations for speed of this rapid action are recorded in the accompanying table. The range of variation is large, due in part at least to the methods of measurement and the inaccuracies of the apparatus (fig. 14).

Fig. 14. Frequency polygon which shows the speed of impulse through giant fibers. The figures represent millimeters per second. The mode is between 1000 and 1500 millimeters per second.

All of these measurements were made on the large garden worm, *Helodrilus caliginosa*, and as nearly as possible under the same conditions. The interesting feature of this array of figures is that they are high compared to those obtained in locomotor transmission. Ordinarily they can be said to be fifty times faster, and may even be one hundred times faster, than the other type of transmission. The mode for these few measurements is around 1500 millimeters per second. While this is not so rapid as some recorded by Carlson and Jenkins (1903) (table 1), in measurements on marine annelids, it is certain that it belongs in the same class of phenomena as they were

TABLE 1

SUMMARY OF RATES IN WORMS—CARLSON AND JENKINS

Species	Direction		Centimeters per sec.
<i>Cerebratulus</i>	P	A	5.4- 9.0
<i>Aulastoma lacustre</i>	P	A	56.0
<i>Cirratulus</i> sp.	P	A	90.0
<i>Arenicola</i> sp.	A	P	120.0
<i>Bispira polymorpha</i>	P	A	694.0
<i>Aphrodite</i> sp.	A	P	54.0
<i>Polynoe pulchra</i>	P	A	293.0
<i>Sthenelais fusca</i>	P	A	205.0
<i>Eunice</i> sp.	P	A	466.0
<i>Nereis</i> sp.	P	A	165.0
<i>Nereis virens</i>	P	A	89.0
<i>Nereis virens</i>	A	P	73.0
<i>Lumbriconereis</i> sp. (a)	P	A	45-241.0
<i>Lumbriconereis</i> sp. (b)	P	A	49-937.0
<i>Lumbriconereis</i> sp. (c)	A	P	42-160.0
<i>Glycera rugosa</i>	A	P	433.0
<i>Glycera rugosa</i>	P	A	435.0

measuring. None of my measurements approached the highest speeds in these marine forms, such as that in *Bispira polymorpha*, viz., 6940 millimeters per second, or even in *Lumbriconereis* sp., viz., 9370 millimeters per second, nor on the other hand did I find any as slow as that in *Cerebratulus* at 54 to 90 millimeters. Several worms, *Nereis*, *Arenicola*, *Sthenelais*, give averages about the same as that which I found for *Helodrilus*.

Jenkins and Carlson used *averages* in obtaining the figures above, when it would seem such a variation in measurements occurred that the mode is more nearly the correct expression. I have used this in both series, that on locomotor transmission and on giant fiber action.

One feature of giant fiber action that is easily noticed is, that, once started, it always goes through to the posterior end; it never dies out in transit as the locomotor waves do. In cases where the nerve cord has been severed, the impulse runs as far as the cut, and never beyond.

Krawany (1905) in his discussion of the elements in the central nerve cord describes the relations of the giant fibers to the association cells in the cord. These large fibers pass from end to end of the nerve cord and in each ganglion send out branches which are intimately in connection with processes from association cells in the middle group. These cells which thus synapse with the direct fibers never have cross-over connections but seem to be entirely homolateral.

The physiology of these reactions is correlated with the anatomy of these fibers. The path is a direct one and the speed of their impulses is fast, 1500 millimeters per second compared with 25 millimeters per second for locomotor reflexes. The connections are simple and the reactions are concerned largely with the contractions of but one set of muscles, the longitudinal muscles. The fibers run the full length of the cord and so reactions are concerned with the whole animal. They are single fibers and produce a single action. There is no wave motion nor evidences of loss as the stimulus passes down the cord.

There is no reason to suppose that these fibers have anything to do with locomotor reflexes or transmission; everything points to a separate function for these large long fibers.

Conclusion.—We have taken for granted that Friedländer's (1894) suggestion that the end to end movements are due to impulses carried by the giant fibers. The results of this work on rates of transmission seem to justify this supposition. No theory allows a nerve to have for itself more than one rate of transmission. The speed of one type of action and the slowness of the other would necessitate two kinds of fibers. The anatomical conditions and the physiological reaction are easily correlated. The large giant fibers are continuous structures running the full length of the worm and capable of carrying the impulses swiftly from end to end at a normal rate of 1500 millimeters per second, while in the center of the nerve cord are numerous short neurones running short distances up and down the cord, giving a complex path, with slow speed of transmission, normally 25 millimeters per second, such as would be expected on account of the multiplicity of synapses.

THEORETICAL CONSIDERATIONS

The Nervous Mechanism.—Some of the most salient facts brought out in the study of transmission are: the nervous system plays an essential part in the movements of locomotion; the impulses responsible for the waves of contraction are capable of running for considerable distances in the cord and are not confined to one or two segments, as indicated by Friedländer; transmission may extend over as many as twenty segments without intervening muscular activity, the rate of transmission is a variable one becoming slower as it pro-

ceeds. The giant fibers have little to do with locomotion and are specialized for rapid, end to end contractions.]

The excellent work of Krawany (1905) on the neurones of the central system of the worm and the researches of Dechant (1906) on the peripheral nervous system, together with the great amount of work done by the older writers, such as Bethe (1903), Rhode (1887), Apathy (1897), Retzius (1900), Biedermann (1904), Smirnow (1894), and others, have demonstrated that the nervous system is compounded of many short neurones. The longest elements are some few large fibers from the anterior end of the cord which arise in the sub-esophageal ganglion and run posteriorly to the terminal segment, but Krawany (1905) shows that for the most part the other nerve fibers run only from one ganglion to the next.]

Sensory nerve fibers originating in the epidermis pass down through the main nerve trunks to the ganglion where they branch as T- or Y-shaped bifurcations immediately on entering. These run but short distances before ending in fine arborizations. Krawany (1905) was unable to demonstrate that these passed into ganglia anterior or posterior to the segments of entrance, but was inclined to think that they remained within the ganglion entered. No demonstration of neuro-muscular end organs has ever been made in the smooth muscle of earthworms. Retzius (1895) and Langdon (1900) have shown, by using Golgi methods, that nerve fibers are in among the muscle cells, but Dechant (1906) by using methylene blue was unable to differentiate any definite end organs. Many nerve fibers parallel to muscle can be seen, showing the presence of abundant nervous tissue, but all fibers which looked like end organs proved to run only short distances and could not therefore be true nerves. While free sensory endings in the subepithelial regions are not yet demonstrated, Dechant believes they are undoubtedly there.

After entering the cord the sensory nerves bifurcate, one branch passing up and another down the cord on the same side as they enter. They may then form synapses with neurones of motor ganglia in the anterior, middle, or posterior groups of nerve cells. These large cells send out neuraxes which may or may not cross to the opposite side, where they leave by one of the three lateral roots.

Within the cord, however, there are still other paths open to impulses entering by the sensory paths. The large multipolar cells are the association cells which show an arrangement into three groups, an anterior, a middle, and a posterior group. Their function is to connect

more or less distant parts of the ganglion and to interpolate themselves between the sensory and motor elements. Many of these are homolateral and some are contralateral. The greater number of these association cells are intraganglionic, i.e., never leaving the segment; but a few in the anterior and posterior groups send processes into the next ganglion and so connect up the ganglia segment to segment.

The most interesting feature is that in this nervous system there are no long nerve tracts, the giant fibers excepted. Impulses that run the length of the cord must find their way over a complex route and be necessarily slow. We have then a nervous system made up of many short units. Each ganglion is a complete relay station capable of receiving sensory and giving out the motor impulses necessary for the functions of each particular segment. The only connections between the succeeding segments are association fibers in the nerve cord and a few motor fibers which Dechant (1906) shows. These motor fibers take their origin from a nerve arising from the posterior root and pass laterally around the muscular wall near the intersegmental furrow and at intervals give off five branches which pass into the segment behind. Without these two connections, one in the cord and one peripheral, there would be no nervous connection from segment to segment of the worm.

Friedländer (1894) laid particular emphasis on the "pull" of one segment on the succeeding ones and that coördination was accomplished even though the nerve cord were cut. The experiment of cutting a worm in two and attaching a string to each part resulting in coördinated movements indicates that pull certainly does play an important part. Undoubtedly the tension or stretching stimulates the nerve and starts the reflex movement. The succeeding movements then are due to both pull and nerve impulse. If part is etherized, it ceases contractions although it responds to direct stimulus. The nerve reflex has been broken. Again, if tension be eliminated by pinning experiments, coördinated movement proceeds; but if now the nerve be cut, coördination ceases. So while tension is important in supplying a stimulus to the nerve mechanism, it is not wholly sufficient.

Biedermann (1904) showed that these reflexes can travel considerable distances in the cord. The interpretation of this might demand that there be present in the nerve cord longer systems of neurones than had been previously reported. However, it can be shown that no such supposition is necessary. The present knowledge of the neurones can be used to explain the facts at hand.]

TRANSMISSION BY REINFORCED STIMULI

There is one other point of great importance in the analysis of locomotion in the earthworms and one which has not been heretofore mentioned. This is the variability in the rate of the impulse along the cord. Experiments have shown that the transmissions over short distances are much faster than those over longer distances, and this agrees with a phenomenon easily observable in the movements of worms, i.e., the dying out of waves of contraction. One can watch a wave of contraction start down the length of the worm and become more and more feeble until it is lost at the middle region. The distance the wave runs seems to depend on the force of the wave at the start. A strong wave runs further than one with a weak start. A glance back at the charts of the speeds of impulses passing through the etherized portion of a worm will show that there is a great variability. One has but to observe a single worm under the experimental conditions to become convinced of this without the figures.

Any theory that accounts for locomotion must take into consideration the short unit system of the nervous system, the transmission of locomotor impulses over long sections of the cord, and the variability in rate of the speed of these impulses.

Friendländer (1894) likened the locomotor mechanism to a system of telegraphic relays. Each contraction of the circular muscle elongated the segment and stretched the longitudinal muscle. This stretching caused a stimulus to pass along the nerves to the cord, where a reflex gave a contraction of the longitudinal muscle. The contraction of the longitudinal gave the pull which caused the circular muscle to contract and so on down the length of the worm, each segment with its own reflex, but progression of the wave of contraction due to the pull of contracting parts on succeeding segments.

A short unit nervous system is all that is necessary for such an explanation. But when transmission of locomotor impulses can pass along the cord this relay system in each segment is not sufficient. If, however, we suppose that the association fibers transfer stimuli from one ganglion to the next, then we have a means for explaining Biedermann's experiment. One of the characteristics of this transmission was that it varied considerably in rate. When the worm was in an excited state or stimulated, the impulses passed through an etherized section faster than otherwise. If we suppose that with each contraction reflexes are set up in each segment and that these stimuli entering the cord reinforce the locomotor stimuli passing along in the short

association tracts, and that if these stimuli are heavy they add to the strength of stimulus passing along, or if weak add little or nothing at all, then we have a basis for explaining the variations in rate. In each ganglion there will be at least one and maybe two synapses to be passed, each with a certain resistance which will tend to cut down the force of the stimulus and its power to get through. Each synapse in each segment resists the passage of the locomotor impulse but in ordinary locomotion each well coördinated contraction wave reinforces the loss and the movement runs the full length of the worm. The uncertain limit of such transmission then can be understood for many factors may come in to change the force of the stimulus; the stimulus may have started in a weak contraction—outside conditions may have altered the amount of reinforcement—internal conditions in the cord itself may have demanded a more complex path in one case than in another, or even the physiological condition of the worm may have had some effect on the resistance in the synapses.

SUMMARY

1. When a worm is anesthetized in the middle area and the peripheral nerves are rendered useless, locomotor impulses may be transmitted in both directions through the nerve cord of this middle region from anterior to posterior, and posterior to anterior.

2. Tension or pull, while important in normal creeping movements, may be eliminated and the locomotor stimuli will still pass up and down the cord for some distance.

3. Nerve free preparations show that locomotor impulses may travel considerable distances in the cord. Under such conditions the anterior and posterior parts act in perfect coördination. When the nerve is cut such coördination ceases. Stovaine when applied to the nerve cord blocks the passage of locomotor impulses up and down and the coördination of anterior and posterior parts is lost; as soon, however, as the effects of the drug are removed impulses again pass freely in the cord and coördination returns.

4. The results of measuring the limits of transmission of the locomotor impulses shows that no absolute limits can be set. The impulses travel short distances of ten segments very readily but when required to traverse a longer section of twenty-eight segments the difficulty is great. No records show impulses passing through as many as thirty segments.

5. Spontaneous rhythmical movements are dependent on the nervous system and the muscle tissues do not possess the property of rhythmic contractility. This strengthens the theory that locomotion is under nervous control.

6. The speed of locomotor impulses is quite variable. The mode that expresses the normal rate is about 25 millimeters per second. The rate may be increased or decreased in transit from segment to segment.

7. The rate of the transmission of giant fiber action is very rapid when compared to that of the locomotor impulses. The mode for a number of measurements shows the speed to be about the rate of 1500 millimeters per second. The wide gap between these two types of nervous activity, the slow locomotor on the one hand and the rapid giant fiber action on the other, indicates that these impulses are mediated by two quite different kinds of nerve elements.

8. The anatomy of the nerve cord as shown by Krawany and Deschant has in it no long neurones. The processes may join successive ganglia but none extend through the cord for a great distance except the larger giant fibers, which run the full length of the cord.

9. The peculiarities of the locomotor impulses in transmission, such as the variability in rate of speed, and the slowness of it, can be accounted for on the basis of the structure. The impulse to make its way down the cord must pass in each ganglion at least one synapse, and the possibility is that there would be more than this. Each synapse would not only cut down the strength of the impulse but would also slow down the speed because of the time consumed to cross the gap between neurones. In normal creeping the impulses travel regularly down the cord because each contraction of circular and longitudinal muscle in each segment sends in locomotor impulses which reinforce the impulse passing down the central nerve cord, and any loss through the synapse is made up in this way. If for any reason the muscular activity fail or if the nervous connections to the cord be destroyed the locomotor impulse traveling down the cord in this region would decrease in strength and decrease in rate because of the lack of reinforcement.

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THE FUNCTION OF THE GIANT FIBERS IN EARTHWORMS

BY

JOHN F. BOVARD

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INTRODUCTION

In the analysis of the locomotion of the earthworm Friedländer (1894) showed that worms made well co-ordinated movements even after considerable portions of their nerve cords had been removed. He concluded that the nervous system served simply as a medium for very short relayed reflexes and played a secondary part in locomotion. Biedermann (1904) extended this idea by showing that stimuli could run long distances in the cord, and in my recent paper (1918) I was able to show something concerning the limits of this transmission and also the rate at which such impulses travel in the cord when not reinforced from without.

Straub (1900) claimed that the spontaneous contractions of short sections of earthworm were due to inherent qualities of the muscle; at least they were not due to the nervous system present. My own experiments seemed to show a contrary result, and in all cases rhythmic movements were only in pieces containing nerve cord.

The results of these experiments just cited were obtained on worms from which the nerve cord had been entirely taken away. It occurred to me, therefore, to study the effects of regenerating nerve cord on locomotor movements. It is well known that the nerves do not all regenerate in the same time, and this, then, would give me some clue as to which fibers carried locomotor responses and which the end to end collapsing movements. Friedländer (1894) suggested that the quick jerks which take the animal back into its burrow were due to impulses carried by the giant fibers. This has been accepted as most probable, but has not been demonstrated. If, then, a regeneration of the nerve cord would give a differential healing, it would be probable that the giant fibers would unite sooner or later than the transmission nerves, and we would have some definite proof for Friedländer's contention.

The effects of simple transverse sections of the ventral cord were studied and later short portions of the cord were removed. Drugs, such as stovaine, were also tested, because they have the effect of "blocking" the nerve cord, which is practically the same as removal of ganglia for a brief time. Drugs have the added advantage of losing their effect quickly, and so the changes in nerve reactions during development and recovery from the anesthesia could be watched.

MATERIALS AND METHODS

Material.—Both the common *Allolobophora foetida* and *Helodrilus caliginosa* were used in these experiments. Similar results were obtained with each, but in general the larger worm was the easier to work with, especially when operations were made for the removal of sections of cord.

Methods.—In all cases where operations were to be performed the worms were kept for at least twenty-four hours in clean moist cloths, so they would clear themselves of dirt and grit. Worms that were kept in moist filter paper usually ate large quantities of this, which made the cutting of sections quite difficult.

The transecting of the nerve cord was a simple operation. The worm was held tightly on a moist surface and a transverse cut made with a safety razor blade. A single stroke was usually sufficient to cut both ventral muscle and the nerve, and if care were exercised there was little danger of cutting too deep. The cut was examined with a hand-lens to make certain that the cord had been cut.

A simple physiological method of determining whether the cord had been sectioned, and a method that proved a check on all experiments, was as follows: Examination of the worm immediately after the operation showed that the muscles posterior to the cut had lost their tone, giving an increase in the diameter of the part. This condition did not extend for any great distance, but was usually confined to from three to five segments. If the nerve had not been severed, this effect wore off after the first day of regeneration; otherwise it remained enlarged until physiological continuity was re-established.

In operating on *Helodrilus*, a simple transverse cut with a razor blade usually only severed the musculature. The cord adheres very closely to the intestine and comes away from its ventral muscles very readily. In these cases it was necessary to cut the cord with a pair of fine scissors, making a simple snip. Where care was not used and the ventral blood vessels were cut also, the animal bled profusely, and in many cases died or autotomized the posterior piece.

When necessary to remove two ganglia, the worms were anesthetized in a 5 per cent alcohol solution for fifteen minutes to one-half hour, in all cases until they were motionless. Under a dissecting microscope, a transverse cut was made in the ventral muscles. The opening was stretched and pinned back with clean, fine needles. The nerve cord and bloodvessels then could be easily seen. Great care

had to be exercised to prevent cutting any blood vessels. The cord was lifted up with fine forceps, and a cut made anteriorly. The cord could then be pulled forwards and a cut made posteriorly. The segment, which was removed, was then put into 95 per cent alcohol and examined later to ascertain the exact amount of nerve substance removed.

After the operation the worms were placed in small 8-ounce jars with some moist cloths over them and put away in a dark cabinet. It was not found necessary to keep the worms in a particularly cool place as long as the jars and cloths were kept scrupulously clean. The temperature was the ordinary room temperature during April and May in the Harvard laboratories. The only cases where worms died during these experiments were those which bled profusely after the operation due to rupture of the large ventral blood vessel. The loss was surprisingly small.

By the following day the worms appeared normal, the wound had healed over and they could be seen creeping about in the jars. Usually, however, they were not very active in the cramped quarters of their jars.

EFFECT OF TRANSVERSE SECTIONS OF THE CORD

The result of simply transecting the cord was the loss of transmission and of the animal's power to reverse its direction of creeping on stimulation. Stimuli applied at either end ran as far as the cut, but failed to pass across the break in the cord. Earthworms often respond to strong stimuli given to the anterior end by certain lashing movements and side to side jerks. When the cord was severed these lashing movements could be induced in the anterior portion of the worm without producing any effect on the posterior part behind the cut, which might lie quiet during this movement. Giant fiber action induced either from the anterior or the posterior direction was effective as far as the cut only. The quick, end to end action never succeeded in starting the same kind of a movement in the portion of the worm on the other side of the break opposite to the point stimulated.

The effects on the musculature were particularly noticeable. Immediately behind the cut region the worm showed an enlargement of the segments. Here the circular muscles seemed to have lost their tone. As the worm crept along the posterior part acted in co-ordination with the anterior, but these few segments behind the cut took no part. The length of this inactive part varies from three to five

segments. Behind this, normal creeping movements were seen as the nerve regenerated and the lost function was restored. This appearance of the cut region disappeared as the normal reactions returned.

REGENERATION

The regeneration of the nerve was remarkably rapid. Sections of a worm (*Allolobophora foetida*) prepared after two days of regeneration showed that the nerve fibers had penetrated into the regenerating tissue and had formed across the gap. And on the third day the physiological reactions were being transmitted up and down the cord. The reversal of the direction of creeping was easily possible on stimulation. The giant fiber reactions, however, were not yet possible. Any stimuli which called out such reactions in the anterior part of the worm ran only as far as the cut, and the same is true of reactions started in the posterior part. However, on the fourth day and fifth day the giant fiber action was restored for the entire worm, which in all respects gave normal reactions.

In the large *Helodrilus*, the same relations were found, except that the period of regeneration was a little longer. The return of the locomotor transmission occurred usually from the fourth to sixth day after the operation and the giant fiber action on the following day. The regeneration of nerve cord in this large worm shows a very interesting thing in this return of the activity of the giant fibers. Twenty-four hours after the return of locomotor transmission, one can look for giant fiber action. This makes its first appearance as an impulse traveling from anterior to posterior, and it is not until some hours later, usually the following day, that this action is transmitted in the opposite or postero-anterior direction.

In testing worms for the return of locomotor transmission through the cut area it will be noticed that in the early stages posterior creeping may not be the response on stimulating the anterior part. However, if several stimuli are given, summation takes place and a posterior movement takes place. At other times the result of a stimulation may be shown in the contraction of the circular muscles and elongation of the posterior tip, a movement preparatory to creeping, without the movement being completed by a well organized reaction.

The first indication of the return of giant fiber transmission is a condition that shows the antagonistic innervation of muscles that has been shown for vertebrates.

The following table, no. 182, shows a series of worms and regeneration of nerve cord as expressed by the return of physiological activity.

EXPERIMENT 182—REGENERATION OF NERVE CORD AFTER A SIMPLE TRANSVERSE SECTION

Time in days when impulses are again possible in Transmission Fibers and Giant Fibers

Worm	Locomotor trans.		Locomotor trans.		Giant fiber		Giant fiber	
	A	P	P	A	A	P	P	A
A	3		3		3		---	
B	3		3		---		---	
C	3		3		4		5	
D	3		3		5		6	
E	3		3		4		5	
F	4		4		5		6	
G	4		4		5		7	
H	4		4		5		6	
I	4		4		5		5	
J	4		5		8		10	
K	4		4		5		5	
L	5		5		6		6	
M	5		7		10		---	
N	5		5		6		8	

A P = transmission from anterior end to posterior end.

P A = transmission from posterior end to anterior end.

Stimulation of the anterior end causes the end to end jerk of muscles as far as the cut, but behind this no such movement arises. With each stimulus there will be seen, in the posterior tip, a relaxation of the circular muscles and a dorso-ventral flattening. The chaetae will be projected and directed forwards, but there is no movement of the longitudinal muscles. A few hours later the same movement will be accompanied by a distinct jerk of the longitudinal muscle, and the next day a well co-ordinated, end to end contraction will be added to the reaction.

REMOVAL OF SECTIONS OF THE CORD

When small sections of the cord were removed, as shown in the following table, the return of physiological activity was in the same order as when simple transverse sections were made. The time for regeneration and complete recovery was lengthened, but was still surprisingly short.

EXPERIMENT 191—REGENERATION OF NERVE CORD AFTER REMOVAL OF SHORT

Worm	No. of ganglia removed	SECTIONS OF CORD		Giant fiber A P	Giant fiber P A
		Trans. locomotor A P	Locomotor trans. P A		
A	2	6	6	9	9
B	1½	4	4	10	11
C	2	----	Dead	----	----
D	2½	----	Dead	----	----
E	1½	4	4	5	6(?)9
F	2	4	4	9	9
G	1½	----	Dead	----	----
H	1	9	9	12	13
I	1½	4	4	5	6
J	1	----	Dead	----	----
K	1	----	Dead	----	----
L	2	9	9	10	11
N	2	4	4	5	6(?)9

A P refers to locomotor impulses passing from anterior to posterior.

P A refers to locomotor impulses passing from posterior to anterior.

Fig. 1—A camera lucida drawing showing the union of the cut ends of the ventral nerve cord. $\times 42$. Experiment 191, line 1. In this worm two ganglia had been removed and nine days given for regeneration. Normal locomotor transmission and giant fiber action had returned. *ch. sh.*, chaeta sheath; *cir. m.*, circular muscle; *ctx.*, cicatrix tissue; *epi.*, epidermis; *g. f.*, giant fiber; *int. epith.*, intestinal epithelium; *l. m.*, longitudinal muscle; *n. c.*, nerve cord; *n. sh.*, nerve sheath.

Figure 1 shows a longitudinal section of a worm that showed normal locomotor transmission and giant fiber action after nine days of regeneration. Two ganglia had been removed. In some cases the regeneration was more rapid and in some slower, so this figure represents a typical case.

It was expected that the removal of short sections of the cord would lengthen the time between recovery for locomotor transmission and giant fiber action. But this was found not to be the case, for, in general, the responses of end to end contractions recur about twenty-four hours after the locomotor transmission reappears. Here, as in the regeneration from simple transection, the giant fibers gave impulses in the antero-posterior direction in advance of those in the opposite direction. While removal of short pieces of cord lengthens that period of regeneration in which no transmission of impulses is possible, it changes very little the order and time of events after the union of the cord is established.

The remarkable facility with which these worms regenerate lost sections of nerve cord has an interesting bearing in the experiments of Friedländer (1894) and Straub (1900).

After the removal of ten to twelve ganglia from the nerve cord, Friedländer (1894) allowed the worm two to four weeks before he discarded them for use in his experiments. My results would indicate that he was not dealing with segments entirely free from nervous transmission, for, while the nerve cord may not have entirely regenerated, it is certain that it could have grown considerable distances into the region, even if it had not grown across the gap. This would make a marked difference in interpreting experiments of co-ordination of anterior and posterior pieces, especially if nearly four weeks had been given for regeneration.

Straub (1900) claimed that annelid muscle would give rhythmic contraction if the nerve cord were dissected out. In this case, sections of twenty to thirty ganglia were removed and the worms given eight days to recuperate. In this short time the nerve probably could not grow the length of such a gap, but could grow into the area for a considerable distance from the end of the nerve stump. When he cut out the operated part and used this to show rhythmic contractions, it is just possible these segments may have contained some regenerated nerve elements. Budington (1902) has shown that segments of worms containing even small fragments of nerve will give these rhythmic contractions, but when the ventral wall is removed no such contractions can be induced.

EFFECT OF DRUGS

If small quantities of cocaine or stovaine are injected into the body cavity of the worm the drugs act as a block on the nerve and affect the transmission through the nerve cord. Cocaine has a more general effect on the worm and produces in many cases very irregular behavior, but stovaine gives very consistent results. The first effect was the loss of giant fiber action through the region. Transmission was perfect above and below the point of injection. As the effect of the drug worked deeper into the cord the transmission of locomotor impulses became more irregular and in some cases was lost altogether. As recovery took place the return of activity was just the reverse. The locomotor impulses became more and more regular until perfect co-ordination was set up. Then the giant fiber action began to show transmissions. Here, too, the same phenomena were seen as in the case of regeneration. Just before giant fiber impulses showed normal, end to end responses, the stimulation of the anterior end showed the characteristic relaxation of the circular muscles in the posterior tip. Very soon after this the end to end movements occur in response to stimuli.

A record is given below of an experiment with stovaine, which shows the course of events and the relation between giant fiber and locomotor fibers.

EXPERIMENT 188—EFFECT OF STOVAINE ON TRANSMISSION

May 18, 1915, 4:45 p.m.—The worm (*Helodrilus caliginosa*), doubly pinned to a cork plate on a glass, was injected with a small quantity of stovaine in the body cavity of the middle region.

Almost immediately giant fiber action is lost and locomotor transmission not normal.

5:00 p.m.—Locomotor impulses pass through block, but do not run full length of posterior part.

Locomotor co-ordination between anterior and posterior parts.

As time goes on locomotor movements run further down the posterior part.

5:10 p.m.—Any stimulus to the anterior end results in locomotor movements in posterior end. Wave contractions run to posterior tip more frequently. No giant fiber action.

5:35 p.m.—Stimulation of anterior end gives increased activity of posterior end. No giant fiber action. Animal apparently normal except no end to end contractions.

5:48 p.m.—Giant fiber action returned. Animal fully recovered.

SUMMARY

1. After transverse section of nerve cord, locomotor transmission fibers regenerate before giant fibers.
2. The period of regeneration after a simple transection is very short, from three to four days.
3. Removal of short pieces of the cord gives the same results as simple transverse section, except that the period of regeneration is prolonged.
4. The effect of drugs, such as stovaine, on the cord shows that the transmission fibers may be active, while the giant fibers are still under the anesthetic. Recovery is in the same order as is shown in regeneration.
5. The general result of this study shows that the giant fibers are concerned with other functions than locomotion, and that locomotor transmission fibers lie deep in the cord.

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