

CONTRIBUTIONS TO THE PHYSIOLOGY OF THE  
VENTRAL NERVE-CORD OF MYRIAPODA  
(CENTIPEDES AND MILLIPEDES)

(Six Figures.)

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*I. The Rate of Propagation of the Nervous Impulse in the Ventral Nerve-Cord.*

The measurements of the rate of propagation of the nervous impulse were made in the fall of 1902. Their publication has been delayed with the view of obtaining large centipedes from the tropics for the work, so as to exclude a possible source of error in the measurements when smaller specimens are made use of. The attempts to obtain larger centipedes than those available here in California have not proved successful, and the further work must therefore be postponed till more favorable material becomes available.

The structure and relations of the central nervous system of the centipedes and millipedes are essentially the same as in the annelid worms. Each segment is provided with a pair of ganglia, which are connected by transverse commissures and by longitudinal commissures with the neighboring anterior and posterior pairs of ganglia. This nerve-cord is situated ventral to the gut. In the anterior or head segment it is connected by a commissure on either side of the œsophagus with the supra-œsophageal ganglion or "brain."

The method of measuring the rate of propagation of the nervous impulse through this nerve-cord was essentially the same as that employed by Dr. Jenkins and myself in the similar work on the ventral nerve-cord of worms.<sup>1</sup> The preparation and arrangement of the animal for the experiment are shown in the diagram in Fig. 1. The centipede was placed with its dorsal side next to the platform or removable floor of the moist-chamber and se-

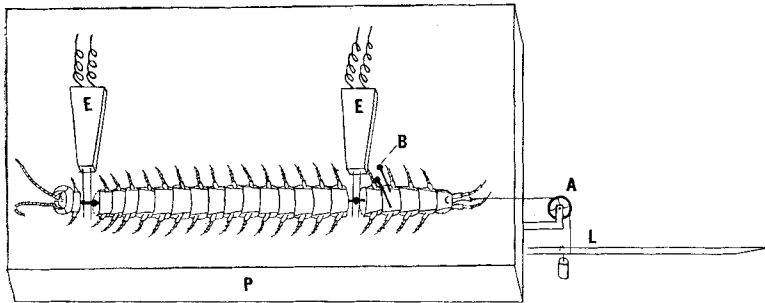


FIG. 1.

Diagram illustrating the method of measuring the rate of propagation of the nervous impulse in the ventral nerve-cord of centipedes. A, friction wheel; B, pins fixing one end of the reacting portion to the platform; E, electrodes; L, recording-lever; P, platform or floor of moist-chamber.

cured to the board by pins, care being taken not to injure the nerve-cord. In *Scolopendra morsitans* and *Scolopocryptops sexpinosus* three or four segments are sufficient as reacting or contracting portion, in the long and very slender centipede *Himantarium taeniopse*<sup>2</sup> eight to ten segments must be used, while in the millipede (*Jules* sp.), in which the actual lengthening or shortening of any part of the body is very slight, eight to ten segments must be employed in order to give sufficient amplitude to the excursion of the recording-lever. The segment next to the reacting portion was fixed to the board by means of two pins in the manner shown

<sup>1</sup>Jenkins and Carlson, Journal of Comparative Neurology, XIII, p. 259, 1903.

<sup>2</sup>These centipedes were identified for me by Mr. R. V. Chamberlin, of Cornell University. The centipede *Stylolemmus*, sp., made use of in studying the reflexes, was identified by Mr. R. E. Snodgrass, of Stanford University.

in Fig. 1, so that the contractions of the body anterior to this point could not be communicated to the lever. The freeing of the nerve-cord for the application of the distal and proximal electrodes is a very difficult undertaking, and in no instance was it done as completely as indicated in Fig. 1, especially in the slender *Himantarium*, in which the nerve-cord is correspondingly slender, and in the millipede, in which the dissection is rendered difficult by the very thick chitenoid epidermis. The dissection for the proximal electrodes was in every case made at least two or three segments from the reacting portion of the body, to avoid escape of the current directly to the reacting musculature. In *Himan-*

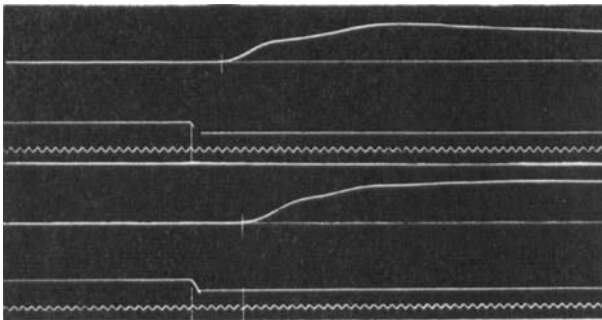


FIG. 2.—*Scolopendra*.

Tracings of the contraction of the posterior segments on stimulation of the cord at the distal and the proximal points. Length of cord, 5cm. Transmission time of the impulse, 0.02 sec. Rate, 2.50m. per sec. Time, 100 d v. per sec.

*tarium* six to ten segments were allowed to intervene between the point of stimulation and the reacting portion.

No anæsthetics were used, but prior to fixing the animal to the platform the head segment, including the cerebral ganglion, was usually removed.

The posterior or tail segments of the decapitated centipede which has been fixed to the board and prepared in this manner usually become quiescent after a few minutes, and remain quiescent during the intervals between the stimulation of the cord, provided the tension from the recording-lever is not too great.

When the tension due to the weight of the lever is considerable the segments are kept in constant motion until exhausted. And the same is true if the segmental appendages or legs are able to reach or touch any object. The contact of the legs with any solid object evidently starts reflex movements of locomotion, and for that reason the preparation does not become quiescent until nearly exhausted when fixed to the platform ventral side down so that the ambulatory appendages are in contact with the board. When the anterior end of the centipede serves as the reacting portion the reflex restlessness is much greater than when the posterior segments are employed. This is true whether the head segment is removed or not. The measurements of the rapidity of conduction of the postero-anterior impulses in the cord by the present method is therefore attended with greater difficulties than the

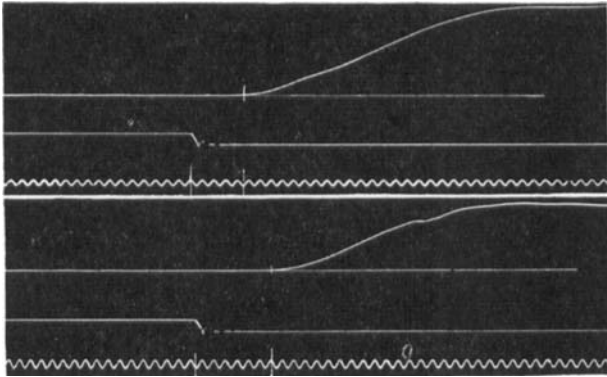


FIG. 3.—*Scolopendra*.

Tracings of the contraction of the posterior segments on distal and proximal stimulation of the cord. Length of cord, 6 cm. Transmission time of the impulse, 0.022 sec. Rate, 2.70 m. per sec. Time, 100 d. v. per sec.

measurement of the antero-posterior rate. In the millipede the union of the segments admits of only slight elongation and contraction of the body, but the body may be coiled by contraction of the ventral muscles in the segments. The amplitude of this contraction is much greater in the posterior than in the anterior

portion of the body, and for that reason the postero-anterior rate of the nervous impulse cannot very well be determined with the present method.

In the centipedes *Scolopendra* and *Scolopocryptops* a single induced shock of moderate intensity applied to the nerve-cord either at the anterior or at the posterior end of the body produces contraction of every segment in the body. In the work on these animals the break induced shock was therefore used as the stimulus. This reaction to the single induced shock is not obtained in the long and slender centipede *Himantarium* or in the millipede. In

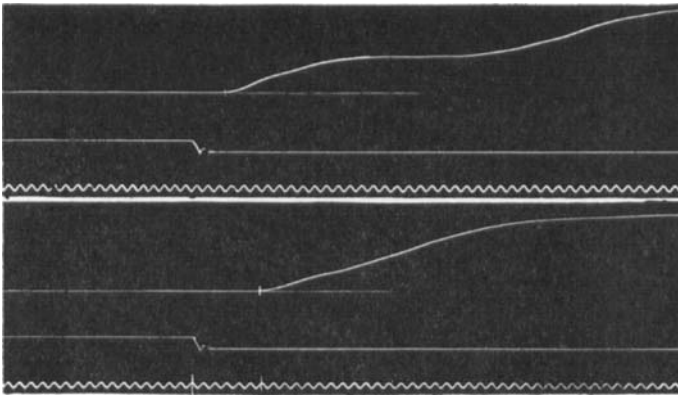


FIG. 4.—*Scolopendra*.

Tracings of the contraction of the anterior segments on proximal and distal stimulation of the cord. Length of cord, 4.5 cm. Transmission time of the impulse, 0.03 sec. Rate, 1.50 m. per sec. Time, 100 d. v. per sec.

*Himantarium* a single induced shock even of very great intensity applied to the anterior or posterior end of the nerve-cord does not always produce a contraction that extends over the whole animal. The contraction extends further from the point of stimulation the stronger the induced shock, but rarely from one end of the animal to the other. When the cord is stimulated with three or four weak induced shocks that follow one another in rapid succession the contraction involves every segment in the body. In the experiments on this centipede short series of the interrupted

current was therefore used as stimuli. A single induced shock applied at one end of the nerve-cord of the millipede *Jules* produces progressive movements of the ambulatory appendages or legs from the point of stimulation to the opposite end of the animal, but the contraction of the muscles moving the body segments is confined to the immediate vicinity of the point of stimulation; but a short series of the tetanizing current produces contraction of these muscles in all the segments of the body. A similar condition was found by Dr. Jenkins and myself to obtain in the marine annelid *Aphrodite*, in which a single induced shock applied to the ventral nerve-cord produced contraction of the muscles that move the setæ, but a tetanizing current was required to produce contraction of the muscles moving the segments. It is therefore probable that the nervous mechanism of the setæ in *Aphrodite* and of the legs in the millipede is less complex and more readily excited than is the nervous mechanism in connection with the muscles that move the segments. If one of the setæ in the worm and one of the legs of the millipede could be used for raising the lever and the rapidity of transmission of the impulse in this nervous mechanism thus measured, it would undoubtedly be found to be several times greater than that in the nervous mechanism to the segmental muscles.

The character of the records produced by the contraction of the reacting portion on stimulation of the nerve-cord may be gathered from the typical tracings reproduced in Figs. 2 to 6. Only the first part of the tracings showing the latent period and the amplitude of contraction is given, as these are the only points with which we are concerned. In the records from the millipede (Fig. 6) the rising curves represent the gradual bending ventralwards of the reacting portion, the movements of each segment fusing into one, apparently continuous, contraction. Each stimulation of the cord by a tetanizing current of short duration usually produces but one such movement. The records from the centipedes are more irregular from the fact that each stimulation of the cord usually starts a series of movements or rather contractions and relaxations which may last for a minute or two in the fresh preparations.

Because of the very complex nature of the muscular part of the preparation the character of the curves, that is, the rapidity and the amplitude of the contraction is not a very accurate guide in determining the admissability of individual records. For example, two successive tracings produced by stimulation of the cord at the distal or at the proximal point may show great divergence in the amplitude of the contraction and yet exhibit the same latent period or they may be nearly identical in the amplitude and rapidity of the contraction and yet show a difference in the latent period of from 15 to 25%. The tracings that showed a greater difference in the amplitude of the contractions than is exhibited by the records in Fig. 3 were usually excluded.

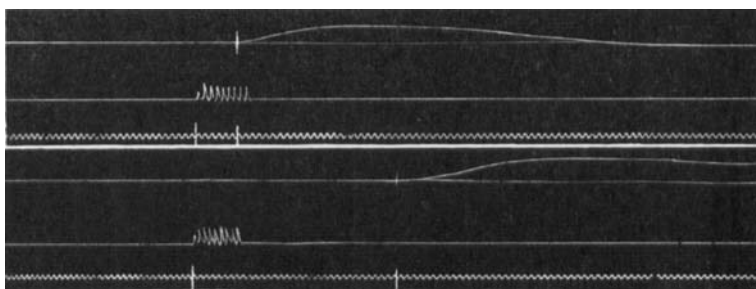


FIG. 5.—*Himantarium*.

Tracings of the contraction of the posterior segments on distal and proximal stimulation of the cord. Length of cord, 14 cm. (120 segments). Transmission time of the impulse, 0.52 sec. Rate, 27 cm. per sec. Time, 50 d. v per sec.

Of the centipedes worked on the best preparation for these experiments is obtained from *Scolopendra*. The largest specimens yield a length of nerve-cord between the distal and the proximal points of stimulation of from 5 to 6 cm. This centipede is relatively stout and the reacting segments amply able to lift the recording-lever. *Himantarium* is more than twice as long as *Scolopendra*, but is so slender that it is even difficult to fix the specimen to the platform without injuring the nerve-cord with the pins. For the experiments on this centipede the recording-lever had to be very light.

It was stated that the point of application of the proximal electrodes to the cord was always three or more segments distant from the reacting portion. This was done with two ends in view, namely, to prevent escape of the current directly on to the muscle and to prevent errors in the measurements from stimulation of a more direct nervous mechanism on proximal than on distal stimulation. In the annelids the cell bodies of the motor neurones to the musculature of any one segment are situated in the ganglia of the same segment as well as in the ganglia of the adjoining anterior and posterior segments. The conditions are in all probability the same in the nerve-cord of the centipedes and

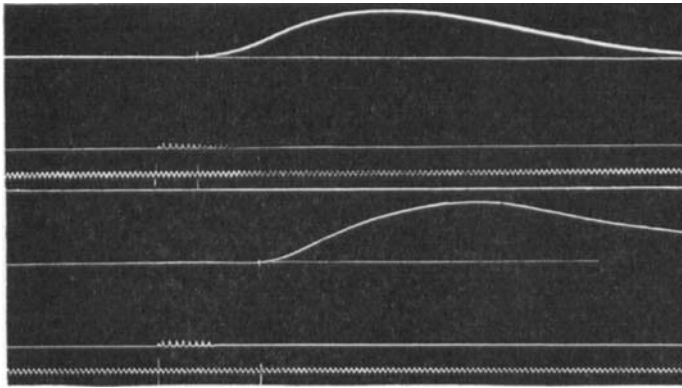


FIG. 6—*Jules*.

Tracings of the contraction of the posterior segments on distal and proximal stimulation of the cord. Length of cord, 5 cm. Transmission time of the impulse, 0.24 sec. Rate, 21 cm. per sec. Time, 50 d. v. per sec.

the millipedes. Now, if the cord is stimulated in the segment next to the reacting portion it is probable that some of the neurones to the reacting musculature are stimulated directly, while when the cord is stimulated at a point 5 to 14 cm. further away these neurones are probably stimulated indirectly; in other words, there is probably "synapses" at the junction of the longitudinal conducting paths in the cord and the motor cells to each segment. At such junctions the propagation of the nervous impulse is in all probability retarded. If therefore the latent time in the records



on distal stimulation includes this delay while the records obtained on proximal stimulation do not, it is obvious that the rate of propagation of the impulse as calculated from the latent periods of these records would be less than the actual. For that reason it would be desirable to check up the measurements on these comparatively short centipedes by experiments on larger representatives from the tropics, as in larger specimens this possible source of error can be practically excluded.

To give an idea of the variability of the latent time in the records obtained by this method, three series of experiments are given in detail in Tables I, IV, and V. All of the experiments are summarized in Tables II, III, V and VII. The character of the tracings has already been referred to. It is amply illustrated in figs. 2 to 6.

TABLE I.

*Scolopendra morsitans*. Antero-posterior. Detail of experiment No. 2, Table II, October 17, 1902. Temperature, 16° C.

TOTAL LATENT TIME IN SECONDS.

<i>Distal.</i>	<i>Proximal.</i>
0.045	0.028
0.047	0.025
0.048	0.027
0.047	0.026
0.045	0.025
0.047	0.025
Average . . . 0.046	0.026
Transmission time . . . . .	0.02 sec.
Length of nerve-cord . . . . .	5 cm.
Rate . . . . .	2.50 m. per sec.

TABLE II.

Summary of the measurements of the antero-posterior rate in the nerve-cord of *Scolopendra* (No. 1-8) and *Scolopocryptops* (No. 9-13). The length of nerve-cord involves from 13 to 17 segments.

	No. of pairs of records.	Transmission time in sec.	Length of cord in cm.	Rate in cm.
1.....	8	0.020	5	2.50
2.....	6	0.020	5	2.50
3.....	11	0.030	6.5	2.16
4.....	13	0.023	5	2.15
5.....	4	0.025	6.5	2.60
6.....	2	0.020	5	2.50
7.....	3	0.019	6	3.15
8.....	2	0.026	5	1.94
9.....	4	0.015	5	3.33
10.....	4	0.015	4	2.64
11.....	3	0.016	4	2.40
12.....	8	0.017	4.5	2.60
13.....	3	0.024	6	2.46

Mean rate..... 2.50 m. per sec.

TABLE III.

Summary of measurements of the postero-anterior rate in the nerve-cord of *Scolopendra*.

	No. of pairs of records.	Transmission time in sec.	Length of cord in cm.	Rate in cm.
1.....	5	0.040	6	1.50
2.....	4	0.032	4.5	1.40
3.....	4	0.040	7	1.75
4.....	3	0.037	4	1.08
5.....	4	0.040	6	1.50

Mean rate..... 1.40 m. per sec.

TABLE IV

*Himantarium taeniopse*. Antero-posterior. Detail of experiment No. 2, Table V, November 5, 1902. Temperature 18° C.

TOTAL LATENT TIME IN SECONDS.	
<i>Distal.</i>	<i>Proximal.</i>
0.46	0.10
0.48	0.11
0.51	0.13
0.40	0.10
0.42	0.09
0.46	0.11
0.45	0.09
0.45	0.13
0.43	0.13
0.45	0.11
0.46	0.13
Average... 0.45	0.11
Transmission time .....	0.34 sec.
Length of cord (100 segm.) .....	10 cm.
Rate .....	26.4 cm. per sec.

TABLE V.

Summary of the measurements of the antero-posterior rate in the nerve-cord of *Himantarium*.

	No. of pairs of records.	Transmission time in sec.	Length of cord in cm.	Rate in cm.
1.....	9	0.43	12 (100 segm.)	27.6
2.....	11	0.34	10 (100 segm.)	26.4
3.....	7	0.46	14 (110 segm.)	29.4
4.....	8	0.37	12 (115 segm.)	32.5
5.....	8	0.52	14 (120 segm.)	28.0
6.....	18	0.49	13 (125 segm.)	27.0
Mean rate.....				28.5 cm. per sec.

TABLE VI.

*Jules sp.* Antero-posterior. Detail of experiment No. 1, Table VII, November 16, 1902. Temperature 16° C.

<i>Distal.</i>	<i>Proximal.</i>
0.40	0.16
0.37	0.18
0.37	0.17
0.36	0.14
0.36	0.15
0.37	0.14
0.39	0.13
0.37	0.12
0.40	0.16
0.40	0.12
0.42	0.16
0.44	0.15
Average . . . 0.38	0.15

TOTAL LATENT TIME IN SECONDS.

Transmission time . . . . .	0.23 sec.
Length of nerve-cord . . . . .	6 cm.
Rate . . . . .	25.8 cm. per sec.

TABLE VII.

Summary of the measurements of the antero-posterior rate in the nerve cord of the millipede *Jules*. The length of cord involves 32 to 37 segments.

	No. of pairs of records.	Transmission time in sec.	Length of cord in cm.	Rate in cm.
1 . . . . .	12	0.23	6	25.8
2 . . . . .	15	0.36	6	16.8
3 . . . . .	4	0.28	5.5	19.8
4 . . . . .	2	0.38	6	16.2
5 . . . . .	5	0.35	6	17.4
6 . . . . .	7	0.17	5	30.0
7 . . . . .	6	0.22	5.5	24.7
8 . . . . .	6	0.30	6	20.0
9 . . . . .	7	0.29	6	20.4
10 . . . . .	2	0.30	5.5	18.1
Mean rate . . . . .				20 cm. per sec.

The rapidity of propagation of the antero-posterior nervous impulse in the cord is the same in the two centipedes *Scolopendra* and *Scolopocryptops*. These two centipedes are also closely alike in the number of segments and in the swiftness of their reactions and movements. The rate is lower than one might have expected, judging by the quick movements of these animals. While it is higher than the rate in the ventral nerve-cord of some of the worms, it is only about one-half that in the nerve-cord of the higher marine annelids *Glycera*, *Eunice* and *Bispira* (one of the *Sabel-lidae*).

The great difference between the rate in *Scolopendra* and *Scolopocryptops* on the one hand and that in *Himantarium* on the other is probably due to a greater number of "synapses," that is, a greater complexity of the conducting path in the cord of the latter. *Himantarium* exhibits a much greater segmental independence than do the other two centipedes. In *Himantarium* the progression of the contraction from the point of stimulation is slow enough to be observed by the eye, while in *Scolopendra* every segment of the body seems to contract at the same time on stimulation of the nerve-cord at any one point. In view of the relatively low rate even in *Scolopendra* it seems to me probable that the conducting path in the cord is not made up of a system of uninterrupted nerve-fibers, although it is evidently less complex than the corresponding conducting path in *Himantarium*.

The rate in the nerve-cord of the millipede is the lowest of all, or only 20 cm. per sec. This is only one-third that of the lowest rate recorded in the nerve-cord of the annelids, namely in the leech (56 cm. pr sec.), and in the marine worm *Aphrodite* (55 cm. per sec.). The reactions and movements of *Jules* are also much slower than those of *Scolopendra* or *Scolopocryptops*. From the fact that the rate of conduction of the impulse in the nerve appears to stand in direct relation to the rapidity of the processes of contraction in the muscle supplied by the nerve,<sup>1</sup> it seems probable that the difference in the rate in *Scolopendra* and *Jules* is not solely apparent and due to the greater complexity of the conducting path in the latter animal.

<sup>1</sup>Carlson, American Journal of Physiology, 1904, IX, p. 401.

A comparison of Tables II and III leaves no doubt that in *Scolopendra* the rapidity of conduction of the impulse through the cord is greater in the antero-posterior than in the postero-anterior direction. A similar condition exists in the case of the spinal cord of the California Hagfish (*Bdellostoma*) and there are indications of the same condition in the spinal cord of the snake.<sup>1</sup> In the annelid *Glycera*, on the other hand, the rate in the ventral nerve-cord is the same in both directions.<sup>2</sup> It is difficult to understand how this difference in the rate of conduction of the postero-anterior and the antero-posterior nervous impulses has come about in the course of development. For the preservation of the individual it would seem that a rapid transmission of the nervous impulse is just as essential over the sensory part of the reflex arch as over the motor part.

## II. *The Reflex Functions of the Ventral Nerve-Cord and the Segmental Ganglia.*

The great difference in the rate of propagation of the nervous impulse in the cord of *Scolopendra* and *Himantarium* lead to the study of the reactions and locomotions of these animals under natural conditions as well as of the reflexes exhibited after severance of the head segment, together with the supra-œsophageal ganglion or "brain," in order to determine whether these animals exhibit other differences in conformity with the difference in the rate of the nervous impulse.

*Himantarium* has two modes of locomotion, namely, by means of its legs and by means of series of contraction waves passing from one end of the body to the other exactly as in the worms. These movements are so identical with those of the worms that the muscular mechanisms are probably the same or at least similar. The centipede works its legs at the same time that it resorts to the other method of getting over the ground. The worm method of locomotion comes into play only when the animal is in a hurry to get away from an enemy. It is made use of with

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<sup>1</sup>Carlson, Archiv für die gesammte Physiologie, 1904, C1, p. 231.

<sup>2</sup>Jenkins and Carlson, loc. cit.

equal adaptation in moving either forwards or backwards, just as in the worms. In *Scolopendra* and *Scolopocryptops* the legs are the exclusive means of locomotion, whether the progression is hurried or slow. The chitenoid epidermis attains also a greater development in these centipedes.

*Himantarium* moves backwards or forwards with equal facility and rapidity. When at rest and touched anteriorly it runs backwards; on being touched posteriorly it proceeds forwards. *Scolopendra* or *Scolopocryptops* does not move backwards for any length of time, and never when making haste to escape from danger, as their backward locomotion is much slower than their progression. When *Himantarium* is beheaded its body keeps running backwards continuously for ten to fifteen min. before it starts to move in either direction, while the decapitated *Scolopendra* keeps running forwards, no matter what obstacles are placed in its way, and it is very difficult to induce it to walk backwards, even after the excitation from the injury has partly subsided. It is therefore plain that *Himantarium* and related genera exhibit a less degree of antero-posterior differentiation than do the shorter and stouter centipedes. This is further shown by the fact that when the quiescent *Himantarium*, which is usually coiled up in a bunch, is gently disturbed by light or by touching it, the two ends of the animal will often be found to crawl or move in opposite directions at the same time, that is, the head end walks forwards, the hind end backwards, till the body is straightened out, when either end may take the lead. This was never observed in *Scolopendra* or *Scolopocryptops*.

When *Scolopendra* or *Scolopocryptops* are decapitated by removing the anterior segment, inflicting as little injury as possible to the body, the body usually continues to move forwards incessantly and rapidly for five to ten min., lifting the anterior three or four segments next to the wound high up from the ground. After the elapse of a few minutes the body becomes relatively quiescent, usually moving only when stimulated or touched. If placed on its dorsal side, the decapitated animal straightway turns over on its legs. When the posterior part of the body is touched, it either springs forwards or brings the anterior end of

the body around as if to bite, reactions identically the same as those of the intact animal. When these centipedes are cut in two in the middle the posterior half exhibits the reactions just described, with the exception that it does not turn over on its ventral side so readily when placed on its back, but it attempts to do so in every case. The number of segments may be further reduced without destroying the coördinating mechanism of locomotion. If the sections are made with a razor or a pair of sharp scissors, the whole body may be divided into portions of three or four segments in length, each portion still retaining coördination to the extent that it walks across the table and keeps up locomotion for three to four minutes, but it exhibits no sense of equilibrium—that is, attempting to turn over on its ventral side when placed on its back. The direction of the locomotion in these small portions of the body is almost invariably forwards. The beheaded *Scolopendra* or *Scolopocryptops* live and react in this manner for three to four days. After the initial restlessness, evidently due to the stimulation from the lesion, it scarcely stirs if left undisturbed, although its excitability is retained apparently unimpaired for 24 to 48 hours. It does not react to light. When placed in a glass jar provided with sand or moist earth in one corner it usually comes to rest on these places rather than on the glass.

The beheaded *Himantarium* lives and reacts for seven to eight days, showing much more “spontaneous” activity than the decapitated *Scolopendra*. An 8 to 10 mm. long portion of the body usually exhibits the same reflexes and degree of coördination as the *Scolopendra* deprived of only its head segment. A portion of that length walks forwards or backwards with apparently perfect coordination of its legs, and it turns over on its ventral side when placed on its back, keeping up these reactions for 24 to 48 hours after being isolated from the rest of the body. A portion of three segments walks in either direction, the usual tendency being to forward progression. A portion of five to six segments exhibits the equilibrium reflex in attempting to regain its natural position when placed on its back. Longer portions turn over promptly.



The loss of excitability and death of the decapitated *Himantarium* proceeds antero-posteriorly. When the animal is simply cut in two in the middle the anterior half with the head intact dies sooner than the posterior half. The same is true when this centipede has been bitten in the middle by a *Scolopendra* or a *Scolopocryptops*, in which case the posterior half of the body usually lives for from 12 to 24 hours while the head end ceases to react to stimuli within 2 to 6 hours. The poison of these centipedes is also fatal when introduced into their own bodies. When a *Scolopendra* is seized at its middle by a pair of forceps it usually turns about and bites the forceps, but occasionally it will bite the posterior part of its own body, and always with fatal results, the symptoms of the poisoning appearing in gradual loss of coördination and power of locomotion, death following within 10 to 15 hours.

The decapitated *Stylolaemus* lives and reacts even longer than *Himantarium*, or for 12 to 14 days. The only difference in the behavior of the decapitated and the intact *Stylolaemus* seems to be the absence of the reaction to light in the former. The wounds of the decapitated *Himantarium* and *Stylolaemus* that lived for 8 to 14 days healed in some cases completely. There was no indication of a regeneration of the lost part. The death was probably due to starvation rather than to infection from the wound.

When a number of specimens of *Himantarium* and *Scolopendra* or *Scolopocryptops* are confined together where they can be readily observed, it will be seen that *Himantarium* jerks back and makes haste to get away whenever any portion of its body comes in contact with the other two centipedes. And it has good reasons to do so, as it is an easy prey for these strong and ferocious centipedes. A similar but much less pronounced jerking back of the body is exhibited by all the centipedes studied when they come in contact with the bodies of other individuals of even their own species, especially when the animals are much excited and moving about rapidly, but in no case is it as pronounced as in *Himantarium* on coming in contact with the aforementioned species. The decapitated *Himantarium* exhibits this very same reaction. Especially if the posterior end of the headless body comes in con-

tact with the centipedes, the body jerks back, and both modes of locomotion are usually employed in getting away. That the reaction is more pronounced when the posterior end of the body makes the contact is probably due to reduced excitability of the anterior segments next to the wound. The decapitated animal continues to react in this manner for several days.

The decapitated *Himantarium* retreats from water just as the intact individual, but on coming in contact with other objects in its path it simply walks over or around them. When, however, a solid object, like a pencil or a pair of forceps, is moved towards the crawling centipede and the contact thus made, the decapitated animal usually retreats. When the body comes in contact with an object which is moving towards it, the impact is necessarily stronger than when the object is stationary and the centipede alone moving, hence the difference in the motor reaction is probably due to the *quantitative* difference in the sensory impulses. But the decapitated *Himantarium* jerks back and retreats from *Scolopendra* and *Scolopocryptops* even when these latter lie perfectly dormant, so that the reaction cannot be explained on that ground. One further possibility must be investigated before this reaction can be ascribed to a *qualitative discrimination in the motor reactions to touch impressions on the part of the decapitated centipede*. The touch impressions may namely be supplemented by those of temperature. I have made no measurements of the body temperature of these animals, and until such determinations are made this interesting point must be left undecided.

Cross-section of the ventral nerve-cord in any part of the body destroys the coordination between the two ends of the body on either side of the lesion just as effectively as when the whole body is cut transversely and the two parts rejoined by a thread or a wire. The lesion does not destroy the coördinated locomotion of either half, but the direction of the locomotion of the anterior half may or may not be the same as that of the posterior half. When the direction is not the same, a "tug of war" ensues, in which the portion having the greatest number of segments or having the most favorable ground for contact for its legs comes out victorious. *Scolopendra* usually turns about and bites its refractory hind body repeatedly.

When the millipede *Jules* is cut transversely in the middle the coördination is destroyed in the posterior half. The anterior portion continues to move about for a short time but loss of coördination and death ensue within 10 to 20 min., and the same is true when the animal is decapitated. This animal is therefore not suited for the study of the reflexes and the relative independence of the coordinating mechanisms of the segmental ganglia.

To recapitulate: *Locomotion, movements to regain normal posture, as well as all contact reactions in the centipedes are obviously reflex movements not dependent on the œsophageal nervous complex or "brain," as the decapitated centipede exhibits the same reactions and movements as the intact animal, save that it does not avoid light and cannot feed or make passages for itself in the ground. The decapitated centipede is not abnormally restless, so that any inhibitory functions can be ascribed to the œsophageal nervous complex, nor is it quiescent to the extent that so-called "spontaneous" movements may be said to be wanting. The bending of the anterior part of the body preparatory to bite the object touching the posterior part is a reflex not dependent on the "brain." The maintenance of the body ventral side down is also a reflex through the segmental ganglia, the turning of the body to the ventral side when placed on its back probably depending not so much on the touch impressions on the dorsal side as the absence of the normal touch impressions from the contact of the legs with the ground. The relatively great segmental independence of this equilibrium reflex and especially of the reflex and co-ordinating mechanisms of locomotion is shown by the fact that these are exhibited by any portion of the body measuring not less than three intact segments in length.*

*The short and stout centipedes (Scolopendra, Scolopocryptops) exhibit a greater antero-posterior differentiation and a less degree of segmental independence than do the long and slender centipedes (Himantarium, Stylolaemus). These latter centipedes retain the annelid mode of locomotion, and the transmission of the nervous impulse through their ventral nerve-cord is slower.*