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THE RATE OF THE NERVOUS IMPULSE IN THE
VENTRAL NERVE-CORD OF CERTAIN WORMS.

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(From the Hopkins' Seaside Laboratory and the Physiological Laboratory of
Leland Stanford, Jr. University.)

With 14 Figures.

The physiological properties of the muscles in different species of worms have been investigated by BIEDERMAN (1, 1889), FÜRST (2, 1889), UEXKÜLL (3, 1896), BOTTAZZI (4, 1898), STRAUB (5, 1900), and BUDDINGTON (6, 1902), and the physiological effects of sectioning the ventral nerve cord, extirpation of portions of the same, and extirpation of the œsophageal ganglia have been studied by LOEB (7, 1894), FRIEDLÄNDER (8, 1894), and MAXWELL (9, 1897); but no observations on the rate of propagation of the nervous impulse appear to have been made in this phylum. In this paper we record some measurements, done by the graphic method, of the rate of nervous impulse in the following species:

Cerebratulus sp. ¹	Sthenelais fusca Johnson
Aulastomum lacustre	Eunice sp.
Cirratulus sp. ²	Nereis virens Sars = N. branti Ehlers
Arenicola sp.	Nereis sp.
Bispira polymorpha Johnson	Lumbriconereis sp. (a)
Aphrodite sp.	Lumbriconereis sp. (b)
Polynoe pulchra Johnson	Glycera rugosa Johnson

¹ The two nemertians worked on were identified for us by Professor R. W. Coz of Yale University as belonging to this genus, species probably new.

² The marine annelids were identified for us by Professor H. P. JOHNSON of Harvard University. Some of them are new species described by Professor

The work on the marine forms was done at the Hopkins' Seaside Laboratory, Pacific Grove.

A simple muscle-nerve preparation suitable to the graphic method is not obtainable in the worms. The preparation we employed consisted of the ventral nerve-cord in connection with an anterior or a posterior part of the worm serving as a reacting portion. This may be called a muscle-nerve-cord preparation to distinguish it from the simple muscle-nerve preparation. The length of the nerve-cord obtainable for this preparation is considerable in some members of the group, and the muscle part, especially if prepared from the anterior end of the animal, is strong enough to raise a light lever. The extreme posterior end of the worm can be used for a reacting portion in few forms only, owing to its greater fragility. The length of the reacting portion can be suited to any case; we found a length that gave a height of contraction of 10 to 20 mm. as magnified by the lever most convenient, but in worms with well developed chitinous epidermis a less height of contraction had to suffice.

The apparatus used in the present work was much the same as that used by us in the work on the determination of the rate of impulse in molluscs (17, 1903). Many difficulties were encountered in preparing the worms for experimentation, but after many unsuccessful attempts the following method was found most serviceable. The animal was securely fixed by dissecting needles, ventral side down, to the moveable floor of a large moist chamber supported on a universal stand, the point of fixation being sufficiently posterior or anterior to give the desired length of the reacting portion. In case it was desired to prepare the reacting portion from the anterior part of the animal the extreme posterior end was then secured in the same manner, care being taken that the anterior and posterior points of fixation were so close together that maximal longitudinal contraction of the worm between these two points exerted lit-

JOHNSON (Preliminary Account of the Pacific Coast Annelids, *Proc. Cal. Acad. Sci.*, 3rd ser. Vol. I, No. 5, 1897; the Polychaeta of the Puget Sound Region, *Proc. Bost. Soc. Nat. Hist.*, Vol. 29, No. 18, 1901); and the species not named are now in his hands for study.

tle or no pull on the needles, for when this is the case the worm breaks in two. The body of the worm was secured to the board as before in two places: one about 1 to 2 cm. anterior to the last and the other about the same distance posterior to the first point of fixation, care being taken in all cases not to injure the nerve cord. Between the two anterior and posterior fixed points the body of the animal was laid open by a longitudinal dorso-median incision through the body wall. The body wall was pinned out to either side and the exposed viscera were turned to one side or removed. The nerve cord was dissected free from the adjacent tissue and the entire musculature completely severed near the reacting portion, so that this was in connection with the rest of the body by the nerve cord only. The freed portions of the nerve cord were placed on the distal and the proximal pair of platinum electrodes respectively, and the muscle was connected with the lever by means of a hook and thread passing over a friction wheel at the end of the platform. This general account applies more especially to forms like the *Glyceridæ* and the *Lumbriconereidæ*, but numerous devices such as narcotics, decapitation, etc., had to be resorted to to meet the exigencies in other groups. Variations from the general method are noted with each group.

The complete freeing of the nerve cord from adjacent tissues without impairing its function is extremely difficult, if not practically impossible, in most worms, partly because of the small calibre of the cord, and partly because of its more or less complete investment by the ventral musculature. In *Nereis virens* the nerve cord is large and therefore comparatively easily freed; in *Aulastomum*, *Aphrodite* and, to some extent, in *Arenicola*, the cord runs free in the body cavity; but with these exceptions we never succeeded in completely freeing the cord from the ventral musculature.

The severing of the dorso-lateral musculature (the ventral musculature is severed by the dissecting out of the nerve cord) between the two points of fixation nearest the reacting portion was done to prevent complications by possible myelo-conduction. At the time, we were not acquainted with FRIEDLÄNDER'S obser-

vation (8, 1894) on *Lumbricus* that the contraction of the worm on stimulating any part of the body does not extend beyond the segment where the ventral nerve cord has been severed. But this severing of the musculature involves considerable injury, especially to worms like the *Sabellidæ* and *Aphroditæ*, and to avoid this we ascertained by severing the nerve cord and stimulating the worms anterior and posterior to the cut that the contraction with which we had to do in our experiments never passes beyond the segment where the cord is cut, either in the postero-anterior or the antero-posterior direction. This fact makes the operation unnecessary, and it was therefore dispensed with in the subsequent work.

Owing to the necessity of having the fixation points, that is, the points of application of the two pairs of electrodes, close enough together to prevent the preparation from breaking off when being stimulated, the actual distance between the electrodes could not be taken as a measure of the distance of nerve cord traversed by the impulse. At the end of the experimentation the segments were counted and the distance measured, or more properly estimated, the preparation being stretched as nearly as possible like the normally crawling worm or after it was killed in fresh water. The last method has this advantage that it gives uniform results but it may not approximate the true distance any closer. It goes without saying that neither method gives accuracy. This is especially true of forms with only slightly developed chitenoid epidermis like the *Sabellidæ* and *Glyceridæ* and therefore capable of great elongation and contraction. In the *Nereidæ* the distance can be measured more accurately. In *Aphrodite* and *Aulastomum* the entire length of the cord was dissected out and measured. In addition to this difficulty of obtaining accurate measurements of the nerve cord other difficulties and serious sources of error were encountered in the experimentation, chief among these the activity or "spontaneous" contractions of the reacting portion and its unequal degree of relaxation at the moment the records were obtained, and the fact that the same strength of stimulus usually caused greater contraction when applied by the prox-

imal electrodes to the nerve cord near the reacting musculature than when applied by the distal electrodes some centimeters away from the reacting portion. The incessant relaxation and contraction caused, no doubt, in part by the injury in the dissection and by the pull of the lever, are almost entirely absent in forms like *Bispira* and *Cirratulus*; they are quite pronounced in *Glycera* and *Lumbriconereis* and even more so in *Aulastomum*, while in *Lumbricus* they present difficulties which we have thus far been unable to surmount. The unequal relaxation of the musculature at the moment of stimulation caused variations in the height of contraction, which, together with the unequal efficiency of the distal and proximal stimuli, rendered comparison of the tracings very difficult, as little guidance could be had in the height of contraction. We found, however, that in many instances the height of contraction varied 50% without any appreciable variation of the latent time. But the latent time seemed to vary with the strength of the stimulus, and stronger stimuli were always used for the stimulation by the distal electrodes to secure approximately the same height of contraction as on proximal stimulation. The electrodes nearest the reacting musculature were always placed one to four centimeters from it and additional precautions were taken to insure against direct stimulation of the muscle by escape currents.

The measurements are tabulated in summaries for each species, but to give an idea of the make-up of these summaries the standard deviation and the coefficient of variability of individual measurements of one typical experiment are given. The figures present a representative pair of records from each species. The relaxation phase of the myograms is much prolonged and in many cases very irregular, but as this does not directly concern the present work only the part of the tracings showing the latent time and the height of contraction is given.

Most of the experiments on the marine forms were carried out during the summer of 1901 and 1902, but some records were also obtained during the winter seasons. In the winter the temperature of the aquarium varied from 11°C. to 20°C.,

in the summer from 12°C. to 14°C. The temperature recorded in the case of *Aulostomum* is that of the room.

***Cerebratulus* sp.**

Several species of Nemertians are found in abundance at Pacific Grove, but most of them are of too delicate a structure to be experimented with by the method employed by us.

Fig. 1. *Cerebratulus* sp. Postero-anterior. Length of nerve cord between distal and proximal electrodes: 5 cm. Rate: 8 cm. per sec. Time: 50 d. v. per sec.

We succeeded in securing but two specimens of *Cerebratulus* of sufficient strength. These specimens were about 30 cm. in length, but showed the same tendency to break into small fragments on irritation, that was manifested by their smaller relatives. Decapitation failed to quiet them. However, we secured an unbroken portion of a few centimeters in length from the anterior part of each specimen. The Nemertians possess one dorsal and two lateral longitudinal nerve cords, in which they resemble the *Platodes* rather than the *Annelids*. No attempt was made to isolate the nerve cords. The stimulus reached the cord by application of the electrodes to the ventral side of the body. Single induction shocks were not always sufficient for excitation from the distal point of stimulation. The required intensity of the stimulus is much greater in this species than in any of the *Annelids* included in this work.

The length of the portion of the nerve cord between the two points of stimulation was determined in the specimen while crawling in the aquarium.

EXPERIMENT NO. 1, Table I, Dec. 26, 1901.

	Distal	Proximal
No. of records	6	6
Mean latent time	1.76 sec.	0.29 Sec.
Standard deviation	0.174 sec.	0.06 sec.
Coefficient of variability	.10	.20

Length of cord : 8 cm. Rate : 5.44 cm. per sec.

TABLE I.

Summary of experiments on *Cerebratulus sp.* Postero-anterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	6	6	8	5.44
2	5	5	5	9.0

Aulastomum lacustre.*(Horse Leech.)*

Through the kindness of Mr. J. C. BROWN of the Department of Animal Biology of the University of Minnesota, we received a number of large individuals of this species from Lake Vermillion, Minn. They thrived well in the aquarium, some

Fig. 2. *Aulastomum lacustre.* Postero-anterior. Length of nerve cord between distal and proximal electrodes: 11 cm. Rate: 63.8 cm. per sec. Time: 50 d.v. per sec.

being kept for over three months. The preparations used may be therefore regarded as from individuals in good condition.

The muscle-nerve-cord preparation was made as in the other members of this series. It was found after experimenting with one specimen that the dissection of the cord for its whole length produced too great injury to it, and such extended dissection is unnecessary. The cord is fairly free and easily accessible to the electrodes. No precaution against its breaking itself in pieces is necessary with the leech. Unfortunately, the dissection necessary to make the preparation caused the posterior portion of the animal to contract so strongly that it would not react to further stimulus and hence could not be used to make records of contractions. Consequently we were unable to determine the antero-posterior rate in the cord. The head end, however, being free from this prolonged contraction allowed the determination of the postero-anterior rate. This was not without difficulties, for the almost incessant motion of the anterior part of the animal, thus continually displacing the lever attached to it, makes it necessary to watch very closely to catch the moment of rest of the animal, coinciding with proper adjustment of apparatus. Still, when all was right, the stimulus gave prompt and decisive reaction. These conditions made it obviously impossible to take the records at equal intervals.

It was found necessary to make use of the interrupted current, for, while single induction shocks were efficient as a stimulus when applied at the point of the cord nearest the musculature used, they failed to produce a definite contraction when applied at the distal point. This was true for both directions in the cord. However, a single induced shock applied to a point in the posterior end of the cord generally produced the indefinite motion of swimming or crawling.

At the conclusion of each experiment the worm was killed in 5 % alcohol, the cord dissected out, and measured after taking the precaution to straighten out the loops formed in the interganglionic portions produced by the contraction of the body of the leech.

The temperature of the room varied from 16°C. to 21°C.

EXPERIMENT NO. 2, Table II, Oct. 5, 1901.

	Distal	Proximal
No. of records	23	23
Mean latent time	0.28 sec.	0.11 sec.
Standard deviation	0.03 sec.	0.004 sec.
Coefficient of variability	.10	.036

Length of cord: 10.25 cm. Rate: 59.4 cm. per sec.

TABLE II.

Summary of experiments on *Aulastomum lacustre*.
Postero-anterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	14	17	10.50	42.0
2	23	23	10.25	59.4
3	7	4	10.50	39.9
4	28	27	10.50	57.7
5	15	18	10.25	48.2
6	8	9	10.50	45.1
7	29	25	11.00	47.0
8	18	21	10.50	87.1
9	11	15	11.00	57.2
10	12	6	10.50	80.8
11	26	16	11.00	91.3
12	16	19	11.00	37.5
13	18	26	10.50	52.5

Mean rate: 56 cm. per sec.

Standard deviation: 16.

Coefficient of variability: .28.

Cirratulus sp.

This species is very common at Pacific Grove where it is found under the rocks and in their crevices throughout the littoral zone. It reaches a length of fifteen to twenty cm. The posterior portion of the body is very slender and fragile and too

Fig. 3. *Cirratulus* sp. Postero-anterior. Length of nerve cord between distal and proximal electrodes: 9 cm. Rate: 100 cm. per sec. Time: 50 d.v. per sec.

feeble to raise the lever of the apparatus, consequently the antero-posterior rate was not determined. The head end, how-

ever, reacts well to stimuli to different points in the cord and allows the determination of a postero-anterior rate. On first making the preparation the head end contracts strongly, but in a few minutes it relaxes, and afterwards the preparation is fairly quiet, reacting only to the stimulus from the electrodes. A single induced shock applied to a point in the posterior portion of the cord usually produced contractions in its immediate vicinity which extended a short distance only, not reaching the head. However, a weak interrupted current of short duration produced a contraction which reached the anterior end.

The preparations fatigue quickly, so that only a few comparable tracings can be obtained in each case.

The length of the nerve cord was measured in the preparations after being killed in fresh water.

EXPERIMENT NO. 4, Table III, postero-anterior, Aug. 16, 1901.

	Distal	Proximal
No. of records	3	3
Mean latent time	0.28 sec.	0.17 sec.
Standard deviation	0.009 sec.	0.01 sec.
Coefficient of variability	.03	.05

Length of cord 10 cm. (105 segments). Rate: 90.9 cm. per sec.

TABLE III.

Summary of experiments on *Cirratulus* sp.

Postero-anterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	3	3	13	85.8
2	6	8	15	82.5
3	4	4	18	86.4
4	3	3	10	90.9
5	2	5	9	99.9
6	4	4	9.5	86.4

Mean rate: 90 cm. per sec.

Standard deviation: 1.66.

Coefficient of variability: .013.

Arenicola sp.

This worm as judged by the number of its egg masses seen during the breeding season is common in the vicinity of Pacific Grove. However, the sand in which it lives is so filled with large rocks that it is difficult to collect it. Only three workable specimens were obtained. It is very sluggish in its move-

ments. In attempting to make the nerve-cord-muscle preparation the musculature is thrown into strong and prolonged contraction. That of the circular musculature was the most marked especially at the points where the worm was fastened to the floor of the apparatus. This contraction of the circular musculature was so vigorous as to prevent the longitudinal musculature from shortening the body and thus acting on the lever. A

Fig. 4. *Arenicola* sp. Antero-posterior. Length of nerve cord between distal and proximal electrodes: 10 cm. Rate: 125 cm. per sec. Time: 50 d.v. per sec.

dorsal longitudinal slit throughout the preparation did not lessen the effect of the circular contraction, but put the preparation in such a condition that the contraction of the longitudinal layer on stimulation of the cord bent the preparation to the inner side and in this way gave opportunity to attach the recording lever. The nerve cord is about 0.7 mm. in diameter and easily separated from the adjoining tissue. The interrupted current was used, since single induction shocks proved inefficient.

EXPERIMENT NO. 3, Table IV, antero-posterior, temp. 14.5°C, July 9, 1902.

	Distal	Proximal
No. of records	12	7
Mean latent time	0.20 sec.	0.12 sec.
Standard deviation	0.01 sec.	0.007 sec.
Coefficient of variability	.05	.06

Length of cord: 10 cm. Rate: 126 cm. per sec.

TABLE IV.

Summary of experiments on *Arenicola* sp.

Antero-posterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	26	14	9	128.7
2	41	30	15	106.5
3	12	7	10	126.0

Mean rate: 120.6 cm. per sec.

Standard deviation: 9.

Coefficient of variability: .07.

***Bispira polymorpha*.**

This large tube inhabiting worm is very abundant near the lower limits of the tides. Their tubes are so well hidden in the crevices of the rocks and so firmly attached to them, that it is only with difficulty and great care that they can be removed without injury to the occupants. When undisturbed the head

Fig. 5. *Bispira polymorpha*. Postero-anterior. Length of nerve cord between distal and proximal electrodes: 28 cm. Rate: 700 cm. per sec. Time: 100 d.v. per sec.

of the worm with the mass of constantly moving tentacles is protruded from the tube. On being disturbed it suddenly retracts its head and tentacles into the tube. Conformably with its mode of life, the musculature of the anterior portion of the body is greatly developed, especially that of the longitudinal

layer, while that of the posterior portion is comparatively little developed and is feeble in its action. On the other hand, the contraction of the anterior portion was quick and powerful, readily lifting a weight of 1000 grams. Consequently while the preparations allowed the determination of the postero-anterior rate in the cord, the antero-posterior rate was not obtained.

On account of the difficulties in dissecting out the cord and the chances of injury to it on approaching it through the dorsal side, the nerve-cord preparation in this worm could not be made in the same way as was done in the other worms. It was treated as follows: The worm was pinned to the board dorsal side down; a longitudinal incision was made through the body wall on each side about one mm. from the median line on the ventral side; this ventral strip was further freed from all connection with the organs in the body cavity. This strip containing the uninjured ventral cord was raised and placed on the electrodes. While this method, used with care, kept the cord uninjured, it presented the apparent disadvantage of placing a comparatively large thickness of tissue between the cords and the electrodes. This did not, however, prove of any disadvantage, as vigorous responses were obtained from single break induction shocks even on stimulation at the posterior point, when the secondary coil was 24 cm. from the primary. The anterior 12 to 15 segments were used as the reacting portion, leaving from 17 to 20 cm. of nerve-cord between the points of stimulation. The lever was weighted with from 20 to 25 grams. A single break induction shock produces a single prolonged contraction. The preparation is not easily fatigued. Anaesthetics were found not to be necessary. The length of the nerve used was measured after the preparation was killed in fresh water. Their length, thus killed, corresponds to that of the animals undisturbed in the aquarium but freed from their tubes. In this condition the worm is from 12 to 15 cm. shorter than in its tube.

EXPERIMENT NO. 10, Table V, postero-anterior, temp. 14°C, Jan. 2, 1902.

	Distal	Proximal
No. of records	11	7
Mean latent time	0.057 sec.	0.024 sec.
Standard deviation	0.0022 sec.	0.002 sec.
Coefficient of variability	.04	.08

Length of cord: 20 cm. (150 segments). Rate: 606 cm. per sec.

TABLE V.

Summary of experiments on *Bispira polymorpha*.
Postero-anterior rate.

No of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	12	12	18	691
2	2	2	15	555
3	2	2	18	817
4	15	16	20	952
5	16	15	19	729
6	11	11	17	629
7	8	8	20	714
8	4	2	20	526
9	6	4	17	680
10	11	7	20	606

Mean rate: 694 cm. per sec.

Standard deviation: 93.

Coefficient of variability: .13.

Aphrodite sp.

An undetermined species, probably new, of this interesting Polychæte occurs in the vicinity of Pacific Grove. As it lives in rather deep water and seems not to be common it is only occasionally brought in by the fishermen. We have secured thus

Fig. 6. *Aphrodite* sp. Antero-posterior. Length of nerve cord between distal and proximal electrodes: 8 cm. Rate: 52.8 cm. per sec. Time: 50 d.v. per sec.

far but two uninjured specimens, the largest of which measured 12 cm. in length and 5 cm. in breadth. This worm is very slow in its movements and it was found to possess a rather low irritability since single induction shocks failed to procure a reaction when applied to the distal point of stimulation. The

complicated dorsal structures of this worm together with the powerful contractions on irritation contribute to render the making of nerve-cord-muscle preparations difficult. The red pigmented nerve cord is nearly free in the body cavity and when the body is contracted the cord is thrown into loops, which necessitated the taking the cord out and straightening it before measuring the length involved. The musculature of the posterior end was taken as the reacting portion, and the antero-posterior rate only was determined. Although single induction shocks were not efficient at the distal points of stimulation to produce contractions in the longitudinal muscles of the reacting portion, they were found to be sufficient to set up a progressive movement of the setæ from the point of stimulation posteriorly, indicating that their neuro-muscular apparatus is more irritable. This seemed to be further indicated by the fact that the animal could be quite roughly handled without producing contractions of the longitudinal muscles, while the setæ reacted to the treatment.

EXPERIMENT NO. 2, Table VI, antero-posterior, temp. 15°C, Jan. 19, 1902.

	Distal	Proximal
No. of records	25	18
Mean latent time	0.422 sec.	0.26 sec.
Standard deviation	0.045 sec.	0.03 sec.
Coefficient of variability	.10	.11

Length of cord: 9 cm. (17 segments). Rate: 56.25 cm. per sec.

TABLE VI.

Summary of Experiments on *Aphrodite* sp.

Antero-posterior rate.

No of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	34	31	8	52.8
2	26	18	9	56.25

Average rate: 54.5 cm. per sec.

Polynoe pulchra.

This worm lives on the surface of the oral tentacles of the large sea cucumber, *Holothuria californica*, and in the mouth cavity of the large key-hole limpet, *Lucopina crenulata*, both of which are common at Pacific Grove. This species of *Polynoe* reaches a length of from 4 to 5 cm. On account of the delicacy of its structure the nerve-cord is exposed with some difficulty. The worm also breaks in pieces very readily, neither chloralhy-

drate nor decapitation serving to quiet it. These obstacles prevented our obtaining satisfactory records from more than two specimens, although many specimens were attempted. The preparation fatigues quickly and single induction shocks, unless very strong, were not always efficient. Only the postero-anterior rate was determined. Another species of this genus, *Polynoe brevis*, is common at Pacific Grove, but as it reaches a length of only 2 or 3 cm. no records could be taken from it.

Fig. 7. *Polynoe pulchra*. Postero-anterior. Length of nerve cord between distal and proximal electrodes: 3.5 cm. Rate: 350 cm. per sec. Time: 50 d.v. per sec.

EXPERIMENT NO. 1, Table VII, postero-anterior, temp. 13°C, Aug. 16, 1901.

	Distal	Proximal
No. of records	2	2
Mean latent time	0.127 sec.	0.110 sec.
Standard deviation	0.004 sec.	none
Coefficient of variability	.03	none

Length of cord: 4 cm. (33 segments). Rate: 230 cm. per sec.

TABLE VII.

Summary of experiments on *Polynoe pulchra*.

Postero-anterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	2	2	4	236
2	2	2	3.5	350

Average rate: 293 cm. per sec.

Sthenelais fusca.

This worm seems to be rare at Pacific Grove. Satisfactory records for a single specimen only were obtained, and these are of the rate of the impulse in the postero-anterior direction.

Fig. 8. *Sthenelais fusca*. Postero-anterior. Length of nerve cord between distal and proximal electrodes: 5 cm. Rate: 250 cm. per sec. Time: 100 d.v. per sec.

TABLE VIII.

Detail of experiment on *Sthenelais fusca*. Dec. 31, 1902.

Postero-anterior.

Total latent time in sec.		
	Distal	Proximal
	.065	.025
	.045	.028
	.055	.028
	.050	.029
	.045	.028
	.048	.025
Average:	.051	.027
Transmission time: 0.024 sec.		
Length of cord: 5 cm. (53 segments).		
Rate: 205 cm. per sec.		

Eunice sp.

This worm, fairly abundant, lives under rocks in tubular passages formed by cementing particles of gravel together. It attains a considerable length, specimens 25 cm. long being taken. It breaks into pieces very readily. For this reason, and further, because of its violent struggling in being captured, an unbroken specimen was rarely secured.

When being prepared for experimentation in the usual manner, *Eunice* always broke in pieces unless it was previously

decapitated, but even the decapitated preparation would sometimes twist itself in two. Chlorhydrate had the same quieting effect as decapitation.

Eunice is very quick in its movements and compares in irritability with Polynoe and Nereis. Single induced shocks were efficient stimuli, the reacting portion responding generally with a single prolonged contraction.

Fig. 9. *Eunice* sp. Postero-anterior. Length of nerve cord between distal and proximal electrodes: 9 cm. Rate: 450 cm. per sec. Time: 100 d.v. per sec.

The measurements were made after the preparation had been killed in fresh water, which gives nearly the same extension as when the worm is lying quiet in the aquarium.

The antero-posterior rate alone was determined.

EXPERIMENT No. 3, Table IX, postero-anterior, Dec. 26, 1902.

	Distal	Proximal
No. of records	13	12
Mean latent time	0.050 sec.	0.038 sec.
Standard deviation	0.003 sec.	0.0023 sec.
Coefficient of variability	.060	.061

Length of cord: 5.7 cm. Rate: 474.8 cm. per sec.

TABLE IX.
Summary of experiments on *Eunice* sp.
Postero-anterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	2	2	9	473.4
2	3	3	4.5	409.0
3	14	12	5.7	474.8
4	13	12	13.0	520.0

Mean rate: 466 cm. per sec.

Standard deviation: 41.

Coefficient of variability: .09.

***Nereis* sp.**

This species is very common at this point. It is found under rocks and crevices, attaining a length of 15 cm. The posterior third of the body is too weak and fragile to raise the lever, hence the antero-posterior rate was not determined. Unless it was first decapitated the conditions of the experiment invariably threw the worm into violent contractions by which it broke into pieces. The activity and irritability of this worm

Fig. 10. *Nereis* sp. Postero-anterior. Length of nerve cord between distal and proximal electrodes: 12 cm. Rate: 133.2 cm. per sec. Time: 50 d.v. per sec.

is much the same as that of *Eunice* and *Glycera*. However it does not respond to single induction shocks as regularly as does *Glycera*. A single shock applied to the cord posteriorly produces a contraction anterior to the point of stimulation, the distance to which the contraction extends depending on the intensity of the stimulus. Still, the contraction does not always reach the head even with a high intensity of stimulus. The interrupted current is more sure of producing this effect.

The length of nerve-cord between the points of stimulation was measured after the preparation was killed in fresh water, in which the condition is very near the normal extension of the worm.

EXPERIMENT NO. 2, Table X, postero-anterior, Aug. 7, 1901.

	Distal	Proximal
No. of records	8	9
Mean latent time	0.095 sec.	0.061 sec.
Standard deviation	0.003 sec.	0.0046 sec.
Coefficient of variability	.031	.075

Length of cord: 55 cm. (45 segments).

Rate: 165 cm. per sec.

TABLE X.

Summary of experiments on *Nereis* sp.

Postero-anterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	4	4	10.0	164
2	8	8	5.5	165
3	9	9	12.0	223.2
4	3	3	5.0	156.0
5	4	4	12.0	123.6

Mean rate: 165 cm. per sec.

Standard deviation: 32.

Coefficient of variability: .19.

Nereis virens Sars (= *N. branti* Ehlers).

This species seems to be quite rare at Pacific Grove, since but one specimen was secured during extended collecting in the summers of 1901 and 1902. The specimen was about 100 cm. in length and from 1 to 1.5 cm. in diameter, but it unfortunately broke into several pieces through its contractions when being captured and the piece containing the head, which was the largest, broke up further in attempting to submit it to the experimental conditions. Decapitation served to quiet its motions, and, no doubt, a much longer portion could have been obtained if this treatment had been used at first. The ventral cord was from 1 mm. to 1.5 mm. in diameter, which large size together with its favorable position in the body allowed it to be easily dissected free. Two pieces were used, one with the head contained 85 segments and gave an available distance of cord of 20 cm. The other was from near the tail and contained 25 segments with 6.5 cm. of cord available. These dis-

tances were measured while the pieces were crawling in the aquarium and represent very nearly the length during the natural extension of the worm.

Single induction shocks applied to the distal point of stimulation produced a single prolonged contraction. After three or four reactions, single shocks failed at the distal point, then the break or make of the direct current was still efficient. Since the largest preparation was no more than one-fourth the length of the whole worm, it is impossible to say whether through the whole length of the cord a single induction shock would prove efficient.

Fig. 11. *Nereis virens*. Antero-posterior. Length of nerve cord between distal and proximal electrodes: 6.5 cm. Rate. 81.2 cm. per sec. Time: 56 d.v. per sec.

Good reactions were obtained from one portion 24 hours after its separation from the rest of the body; in other pieces 48 hours later only feeble responses were obtained; however one piece lived three weeks in the aquarium, when it was destroyed by an accident. In one piece the rate was taken in the antero-posterior direction, in the other postero-anterior direction. The rates 89 and 73.4 respectively, differing as they do, may not be taken, in the absence of other experiments, as conclusive evidence that the rates in the two directions differ.

EXPERIMENT NO. 1, Table XI, antero-posterior, July 20, 1901.

	Distal	Proximal
No. of records	27	19
Mean latent time	0.183 sec.	0.096 sec.
Standard deviation	0.016 sec.	0.007 sec.
Coefficient of variability	.08	.07

Length of cord: 6.5 cm. (25 segments).

Rate: 73.4 cm. per sec.

TABLE XI.

Summary of experiments on *Nereis virens*.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1 (antero-posterior)	27	19	6.5	73.4
2 (postero-anterior)	13	11	20.0	89.0

***Lumbriconereis* sp. (a).**

Small specimens of this species of 20 to 30 cm. and from 2 to 3 mm. in diameter are very abundant in the gravel at the lower limits of the tide, but only one large specimen was secured. This was 75 cm. in length and from 6 to 7 mm. in diameter, but the specimen was accidentally broken in two pieces in being captured. The anterior portion proved of great service since since 150 good records distributed over a period of three days were obtained from it. The posterior portion failed

Fig. 12. *Lumbriconereis* sp. (a) Postero-anterior. Length of nerve cord between distal and proximal electrodes: 21 cm. Rate: 262.5 cm. per sec. Time: 50 d.v. per sec.

to give equally good results from the fact that in attempting to prepare it for experimentation it went into a strongly contracted state which continued for three days, although left undisturbed in the aquarium. During this time it failed to react to any stimuli. This same phenomenon has been observed in some of the specimens of *Glycera* which had been injured. The smaller specimens of *Lumbriconereis* gave so much trouble in this way that but few records were obtained from them. These are the only free swimming polychaetes in which this phenomenon was observed.

The nerve-cord-muscle preparation can more easily be made from *Lumbriconereis* than from *Glycera* on account of its squirming less. Like *Glycera*, it is less easily broken than the rest of the series worked with. It is less active than *Glycera* but equally irritable; single induction shocks applied to the cord 20 cm. from the reacting portion produce good contractions. The measurements of the cord were taken after killing the preparation in fresh water.

EXPERIMENT NO. 1, Table XII, postero-anterior, July 24 to 27, 1901.

Length of cord: 21 cm. (114 segments).

July 24 3-9 p. m.	First four pairs of records, rate: 300 cm. per sec. Total No. of records (24 pairs), rate: 65 cm. per sec.
July 25 8-11 a. m.	First four pairs of records, rate: 221 cm. per sec. Total No. of records (16 pairs), rate: 65 cm. per sec.
July 25 4-6 p. m.	First three pairs of records, rate: 210 cm. per sec. Total No. of records (15 pairs), rate: 94 cm. per sec.
July 26 9 a. m.-5 p. m.	First three pairs of records, rate: 233 cm. per sec. Total No. of records (13 pairs), rate: 80 cm. per sec.
July 27 9 a. m.	First pair of records, rate: 42 cm. per sec.

The coefficient of variability of the transmission time of the fourteen pairs of records that show a rate above 200 cm. per sec. is .37.

TABLE XII.

Summary of experiments on *Lumbriconereis* sp. (a)
Postero-anterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	14	14	21	241
2	3	3	9	45
3	4	4	10	45

Lumbriconereis sp. (b)

This worm is very abundant in crevices and under rocks where it constructs for itself delicate tubular passages by debris and gravel cemented together. It is commonly 30 to 40 cm. in length and from 5 to 7 mm. in diameter, but owing to its great fragility generally only portions of the worm could be secured for the preparation. The worm is rather inactive, so anæsthetics were not necessary. Despite its sluggish habits it responds to single shocks almost as readily as *Glycera*, but the

preparation fatigues much sooner. The measurements of the cord were made on preparations killed in fresh water, with the exception of preparation No. 7, Table XIII A., which was extended during the experimentation to the length given.

Fig. 13. *Lumbriconereis* sp. (b) Postero-anterior. Length of nerve cord between distal and proximal electrodes: 30 cm. Rate: 681 cm. per sec. Time: 100 d.v. per sec.

EXPERIMENT NO. 4, Table XIII, postero-anterior, Aug. 7, 1902.

	Distal	Proximal
No. of records	6	6
Mean latent time	0.060 sec.	0.035 sec.
Standard deviation	0.004 sec.	0.004 sec.
Coefficient of variability	.07	.11

Length of cord: 15 cm. (125 segments). Rate: 600 cm. per sec.

TABLE XIII A.

Summary of experiments on *Lumbriconereis* sp. (b)

Postero-anterior rate.

No. of experiment	No. of records.		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	4	2	20	40
2	5	3	13	
3	3	3	16	1
4	6	6	15	6
5	4	4	12	52
6	5	5	15	937
7	9	8	30	768

TABLE XIII B.

Summary of experiments on *Lumbriconereis* sp. (b)

Antero-posterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	2	2	25	80
2	3	3	8	160
3	3	2	10	42

***Glycera rugosa* Johnson.**

This worm is fairly abundant in the sands of the lower tide limits at Pacific Grove. The largest specimen that we collected measured from 35 to 40 cm. in length and about 13 mm. in diameter, when killed in fresh water. It is very ferocious, even in the aquaria preying on *Eunice* and *Nereis*. It is also very active,

Fig. 14. *Glycera rugosa*. Antero-posterior. Length of nerve cord between distal and proximal electrodes: 30 cm. Rate: 441 cm. per sec. Time: 50 d.v. per sec.

making its way through the wet sand with great speed or gliding through the water by the graceful twistings of its whole body. This worm was selected for a beginning in this work because of its large size, high irritability and strength. *Glycera* is less fragile than any of other free swimming polychaetes worked excepting *Lumbriconereis* sp. (a) which equals it in this respect.

In most cases an anaesthetic, chlorhydrate, was necessary to quiet the violent squirming in making the preparation. Decapitation did not quiet these motions. The preparations responded with great regularity to single induction shocks of moderate intensity applied to the cord 20 to 30 cm. from the contracting portion; when the single shock became inefficient the interrupted current of short duration was used. The nerve-cord-preparation of this species is not easily fatigued and consequently allows a great number of records to be taken from each specimen. The preparation from one specimen, No. 2, Table XIV A, gave good responses 23 hours after it was made.

It frequently happened that an injury to any part of the body caused the musculature, both circular and longitudinal, to go into a strongly contracted state, in the immediate region of the injury. This condition in some cases continued for 24 hours, or even more, during which time it is practically impossible to send an impulse through the cord of the contracted portion. In the only case in which an impulse passed through so small a distance as 100 segments of the worm a strong interrupted current was necessary. Even in this case the responding contractions were feeble and very much delayed.

EXPERIMENT NO. 2, Table XIV A, postero-anterior, July 16, 1901.

	Distal	Proximal
No. of records	32	32
Mean latent time	0.18 sec.	0.10 sec.
Standard deviation	0.014 sec.	0.003 sec.
Coefficient of variability	.08	.03

Length of cord: 34 cm. (150 segments). Rate: 425 cm. per sec.

TABLE XIV A.

Summary of experiments on *Glycera rugosa*.
Antero-posterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	21	22	34	680
2	33	32	34	425
3	11	11	25	357
4	22	22	20	400
5	4	4	25	500
6	25	25	17	425
7	11	11	20	400
8	12	11	30	375
9	9	9	24	271

Mean rate: 433 cm. per sec.

Standard deviation: 87.

Coefficient of variability: .20.

TABLE XIV B.

Summary of experiments on *Glycera rugosa*.

Postero-anterior rate.

No. of experiment	No. of records		Length of cord in cm.	Rate in cm.
	Distal	Proximal		
1	7	7	15	420
2	2	2	18	514
3	7	7	13	540
4	3	3	18	265

Mean rate: 435 cm. per sec.

Standard deviation: 106.

Coefficient of variability: .24.

TABLE XV.

Summary of the rates in the fourteen species worked on.

Species	Direction	No. of individuals	Rate in cm.	Coefficient of variability
<i>Cerebratulus</i> sp.	Postero-anterior	2	5.4-9.0	
<i>Aulastomum lacustre</i>	" "	13	56.0	.28
<i>Cirratulus</i> sp.	" "	6	90.0	.013
<i>Arenicola</i> sp.	Antero-posterior	3	120.6	.07
<i>Bispira polymorpha</i>	Postero-anterior	10	694.0	.13
<i>Aphrodite</i> sp.	Antero-posterior	2	54.5	.04
<i>Polynoe pulchra</i>	Postero-anterior	2	293.0	.19
<i>Sihenelais fusca</i>	" "	1	205.0	
<i>Eunice</i> sp.	" "	4	466.0	.09
<i>Nereis</i> sp.	" "	5	165.0	.19
<i>Nereis virens</i>	" "	1	89.0	
" "	Antero-posterior	1	73.4	
<i>Lubriconereis</i> sp. (a)	Postero anterior	3	45-241	
" " (b)	" "	7	49-937	
" " (b)	Antero-posterior	3	42-160	
<i>Glycera rugosa</i>	" "	9	433.0	.20
" "	Postero-anterior	4	435.0	.24

In *Aulastomum* (table II, page 267), *Cirratulus* (table III, page 268), *Bispira* (table V, page 272), *Eunice* (table IX, page 277), *Nereis* sp. (table X, page 278), and *Glycera* (table XIV, page 284), the number of individuals worked and the relative constancy of the individual rates seem to allow the conclusion that the mean of the individual rates is representative for their respective species. The mean in the groups represented by by two or three individuals only is of less value, especially in the two species of *Lubriconereis* (tables XII and XIII) where the individual variations are so great. But in some species

thus scantily represented the individual rates show only slight variation, as in *Arenicola* (table IV, page 270), *Aphrodite* (table VI, page 273), *Polynoe* and *Sthenelais* (tables VII and VIII, pages 274 and 275), and *Nereis virens* (table XI, page 280), and their representative means may therefore not be far from the true rate in these species.

The rate of the nervous impulse in this series of worms is as varied as the structure and the habit of the worms themselves, the lowest being in *Cerebratulus* with a rate of only 5 to 9 centimeters per second and the highest in *Bispira* with a rate of 7 meters per second. But there seem also to be differences in rate between species in which little difference in structure and habits exists, as in the cases of *Eunice* and *Nereis* (tables IX, X and XI), the former showing a rate of 466 cm. per second, the latter a rate of 165 cm. per second.

In the species which permitted of determining the rate of the impulse in both directions of the cord (*Nereis*, table XI; *Lumbriconereis*, table XIII, and *Glycera*, table XIV) there seems to be no constant difference between the antero-posterior and the postero-anterior rates.

A question of considerable interest is whether the rate in the ventral nerve cord as determined in the present work represents the rate through continuous nerve fibers as in a vertebrate muscle-nerve preparation or whether the nervous paths are more complex. Our knowledge of the structure of the ventral nerve cord of the worms has been greatly advanced within the last few years through the researches of RETZIUS (10, 1891, 1892, 1894, 1898, 1900), RHODE (11, 1891), BIEDERMANN (12, 1891), LENHOSSÉK (13, 1892), FREIDLÄNDER (14, 1894), APÁTHY (15, 1897) and HAVET (16, 1899). But while many of the histological elements have thus been worked out and found to be markedly uniform throughout the phylum, it seems that the number of segments with which a motor neuron comes in direct relation and the extent and relation of the small sensory fibers in the longitudinal tracts and of the central or "association cells" are yet undetermined. Even the applicability of the neuron conception to the nervous system of the worms

is called in question by APÁTHY's work. On histological grounds we cannot therefore say whether the ventral nerve cord contains such a direct nervous path extending throughout its whole length.

Nor does the present work furnish anything conclusive on this point. It is true that the muscle-nerve-cord preparations of *Bispira*, *Glycera*, *Eunice*, *Nereis* and *Lumbriconereis* respond to a single induced shock of low intensity; and these responses on stimulating the cord 20 to 30 cm. from the muscle in *Bispira* and *Glycera* approached the uniformity of the responses of the frog's gastrocnemius on stimulation of the sciatic nerve. And such uniformity in the response to single induced shocks has not been found to obtain in the vertebrates when complex nervous mechanisms are involved. On the other hand, such great variation of the rate in the same preparation as was observed in *Lumbriconereis* (page 281) can not be reconciled with the physiology of simple muscle nerve preparations as it is known in vertebrates and molluscs. In *Cerebratulus*, *Aulastomum*, *Cirratulus*, *Arenicola*, and *Aphrodite* the muscular response to a single induced shock applied to the nerve cord subsides few centimeters in either direction from the point of stimulation. It requires a series of shocks to obtain the muscular response if the length of nerve cord involved comprises many segments; which fact suggests a complex nervous path. But while the response of the nerve cord to a single induced shock points in some species to a complex, in others to a simple nervous mechanism, the question remains yet undecided whether in the latter cases the nervous part of the muscle-nerve-cord preparation is as simple as that of an ordinary muscle-nerve preparation.

It is of some interest to know that the lowest rate in the Annelids, that of *Aphrodite*, or 54 cm. per sec., is higher than the rate in the pedal nerve of the slug, *Ariolimax*, which we found to be 40 cm. per sec., while the rate in *Glycera* (430 cm. per sec.), *Eunice* (460 cm. per sec.) and *Bispira* (694 cm. per sec.) is as high and even higher than the rate in the pallial nerve of the swift moving *Loligo* (17, 1903).

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