

STRETCH-SENSITIVE NEURAL
UNITS IN THE BODY WALL OF THE EARTHWORM,
LUMBRICUS TERRESTRIS L.

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SUMMARY

1. Sensory neural units responding to sinusoidal longitudinal stretching of the body wall were studied in the earthworm, *Lumbricus terrestris* L.
2. A phasic stretch-sensitive unit found in segmental nerve I responded optimally to stretching at frequencies of 4–6/min.
3. The number of spikes per stretch and the spike frequency in the unit were directly related to the amplitude of the applied stretch within a range of 0.2–0.7 mm stretch/segment.
4. The ranges of amplitude and frequency sensitivity for the unit in isolated preparations corresponded closely to stretch parameters seen during peristaltic locomotion in intact animals.
5. Stretch-sensitive responses in segmental nerve II–III were more variable; some units responded to longitudinal stretch while others responded to relaxation.

INTRODUCTION

The importance of mechanoreception (touch, pressure and stretch) in annelid reflexes and locomotory behaviour has long been recognized (for reviews see Prosser, 1934; Bullock & Horridge, 1965). Although there have been a variety of electrophysiological investigations of mechanoreception in annelids, these investigations have primarily focussed on touch and pressure reception rather than stretch reception.

In the polychaete worm, *Harmothoe* sp., Horridge (1963) identified several types of mechanoreceptors; these include touch and bristle receptors scattered over the body and proprioceptors associated with the parapodia. The touch and bristle receptors are highly sensitive to tactile stimulation and show rapid adaptation. The proprioceptors respond with rapidly adapting trains of spikes to deformation or strain of the cuticle at the base of the parapodium. Similar types of mechanoreceptive responses were described by Dorsett (1964) in the polychaete, *Nereis virens*. Dorsett (1966) also described a small-amplitude sensory unit in segmental nerve IV which fired tonically for several seconds in response to stretching of the longitudinal muscle.

In leeches, Nicholls & Baylor (1968) and Nicholls & Van Essen (1974) have described responses of three types of mechanoreceptor neurones: touch, pressure and nociceptive. Touch neurones respond to light touch of the skin and show very rapid adaptation. Pressure neurones respond to marked deformation of the skin; these units may fire for 10–20 s in response to sustained stimulation, the firing frequency being proportional to stimulus intensity. Nociceptive neurones require stronger mechanical stimulation, such as pinching or scratching; these fire steadily during stimulation and often continue to fire after cessation of the stimulus. Mechanoreceptors have also been found in the sheath surrounding the ventral nerve cord of the leech. Smith & Page (1974) identified units in the sheath which respond to direct tactile stimulation or to indirect tactile stimulation via the skin in intact segments. The presence of peripheral stretch-sensitive units in leeches is indicated by the studies of Gray, Lissmann & Pumphrey (1938) in which slight passive longitudinal stretch of the body wall resulted in rapid rhythmic discharges in individual segmental nerves.

There have been numerous studies of mechanoreception in oligochaete earthworms. Prosser (1935) recorded sensory impulses in segmental nerves in response to tactile and proprioceptive stimuli. Tactile stimulation of the skin with a fine glass needle resulted in a rapidly adapting, asynchronous burst of impulses. Proprioceptive stimulation, such as pushing and pulling on the epidermis with a glass needle, produced rhythmic spiking at frequencies up to 18 spikes/s. Activity in these receptors was also seen during peristaltic contraction. Laverack (1960) confirmed Prosser's findings and found another type of unit, presumably a mechanoreceptor, which fires rhythmically for several seconds after cessation of tactile stimulation. Mill & Knapp (1967) also confirmed Prosser's findings and mapped out sensory fields for touch receptors in the body wall. In addition, they described a slowly adapting sensory unit in segmental nerve II–III which occasionally fired spontaneously but usually responded to deformation of the body surface. Similar slowly adapting firing occurred in segmental nerves I and II–III as waves of contraction passed over the segment.

Although some of the electrophysiological studies of annelid mechanoreceptors suggest the presence of stretch-sensitive units in the body wall, there have been no detailed or quantitative studies of the responses to stretching. In the light of the hypothetical importance of stretch-sensitivity in annelid reflexes and locomotion and the lack of electrophysiological information concerning such sensitivity, we have studied electrophysiological responses of stretch-sensitive neural units in the body wall of the earthworm, *Lumbricus terrestris*.

MATERIALS AND METHODS

Earthworms, *Lumbricus terrestris* L., were collected in western New York. Animals were maintained at 15 °C on a mixture of peat and Buss Bed-ting (Buss Mfg Co., Lanark, Ill., U.S.A.). During dissection and experimentation the tissue was maintained at 16–18 °C and bathed in a saline which consisted of 77 mM-Na⁺, 4 mM-K⁺, 6 mM-Ca²⁺, 1 mM-Mg²⁺, 95 mM-Cl⁻, 40 mM sucrose and 2 mM Tris at pH 7.4 (modified from Drewes & Pax, 1974). The primary modification in the saline was the replacement of SO₄²⁻ with Cl⁻ because sensory responses to stretch were more consistent in saline in which chloride was the only major anion. In the modified saline sensory responses were stable for at least 3 h.

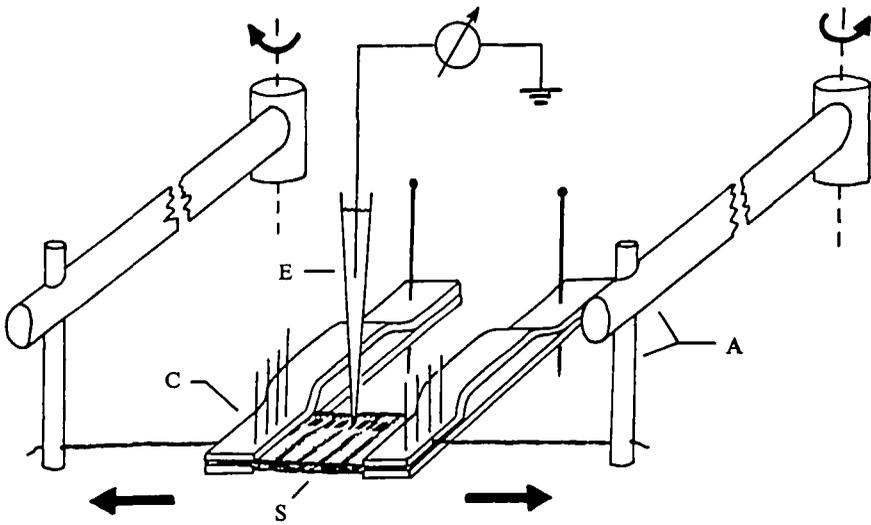


Fig. 1. Diagram of earthworm body wall preparation and stretching apparatus. The anterior and posterior ends of a strip of body wall (S) five segments in length are attached to two Plexiglass muscle clamps (C). Each clamp rotates freely on an insect pin and is connected by a thread to the arm (A) of a pen driver motor. As the shafts of the two pen motors turn in opposite directions (upper arrows) the pen motor arms move apart, stretching the preparation in a longitudinal direction. A suction electrode (E) applied to a single segmental nerve records the sensory response to stretch.

For dissection the animal was pinned dorsal side up to a shallow paraffin dish. A dorsal mid-line incision was made extending 10 or 12 segments posterior to the clitellum. Septa connecting the body wall to the gut were severed and the body wall was pinned flat. Transverse cuts were made completely through the body wall and ventral nerve cord at the anterior and posterior limits of the dissected region. The undissected anterior and posterior ends of the worm along with the entire digestive tract were removed *in toto*. Nephridia were dissected away to fully expose the body wall muscle and the segmental nerves. Segmental nerves were then severed at their connexions to the ventral nerve cord. Next, two parallel incisions approximately five or six segments apart, were made beginning at the dorsolateral edge of the preparation and continuing to the ventral mid line. A rectangular strip of body wall was freed by cutting along the ventral mid line between the parallel transverse incisions. This strip consisted of the lateral halves of five to six segments of body wall and segmental nerves.

The strip of body wall was then attached to two Plexiglass muscle clamps as shown in Fig. 1. Each clamp was mechanically coupled to a Plexiglass arm mounted to the shaft of an electrically shielded pen driver motor (Beckman Type 872-208654). With equal but opposing movements of these arms the preparation could be stretched in a longitudinal direction. Stretch was bidirectional and the middle segments of the dissected preparation displayed little or no movement. This technique therefore provided the opportunity to record from a segmental nerve via a suction electrode without mechanically stressing or stretching the nerve. Since in most preparations the amount of applied stretch was small, one clamp could be held stationary and stretch applied by moving the second clamp. Results were similar using either arrangement.

Stretching movements were generated using a Tektronix FG 501 function generator. Output from this was led into two channel amplifiers (Beckman Type 474A) of a chart recorder (Beckman Type RB Dynagraph) and then into the above pen driver motors. Stretch parameters such as amplitude, frequency and wave function could then be varied. A sine wave was routinely employed since it produced the most easily measured stretch. Other functions, such as saw-tooth and rectangular functions, produced very rapid stretching or relaxing phases and produced considerable overshoot in the desired muscle length due to the inertia of the pen motor arms.

At the beginning of each experiment the resting lengths of individual segments were determined, after stretching the preparation just enough to take up slack in the tissue. Resting length for a segment varied from 0.8 to 1.0 mm depending on the size of the animal. During sinusoidal stretching the length of the segment was measured at peak stretch. Some difficulty was encountered in obtaining uniform stretch across the entire segment; segments tended to stretch least near the dorsal and ventral edges and most in the middle of the segment. All measurements of stretch were made in this middle region of the segment using the septal boundaries of segments as reference points. Either the d.c. offset of the FG 501 or the pen position of the driver amplifier was set so that the muscle returned to resting length at the most negative portion of the sine wave.

Recordings of sensory activity in response to stretch were obtained by drawing individual nerves into the tip of a polyethylene suction recording electrode (O.D. of tip 75–100 μm). All segments chosen for recording were located near the middle of the preparation, and all segments were elevated well above the floor of the recording dish, thus avoiding the possibility of recording responses to tactile stimulation. Recordings were made with reference to a grounded Ag-AgCl electrode in the bath. Activity was amplified with a Grass P15 preamplifier and monitored on a Tektronix 5103N storage oscilloscope. Records were also stored on tape (Ampex SP 300) for later analysis and photography with a Grass C4 kymograph camera.

RESULTS

Stretch-sensitive units in segmental nerve I

In every segment of nine preparations a single neural unit which responded to longitudinal stretch was found in segmental nerve I (SN I). A typical response to sinusoidal stretch consisted of a series of spikes, each spike being less than 2 ms in duration (Fig. 2). The relatively consistent spike amplitude and interspike intervals suggest that a single neural unit is involved. Activity in the stretch-sensitive unit may be distinguished in several ways from activity in tactile units (Prosser, 1935; Laverack, 1960; Mill & Knapp, 1967). Weak touch or brushing of the cuticle produces spikes which are usually twice the amplitude of the stretch-sensitive unit. The response to touch consists of a rapidly adapting, high-frequency, and asynchronous burst lasting less than one-half second. This contrasts with the relatively long, low-frequency, and regular series of spikes in the stretch-sensitive unit.

Within the response to stretch two distinct features were seen (Fig. 2). The first was a gradual change in the spike frequency. Generally, maximum frequency of spiking was seen near the beginning or middle of the series. This corresponded to the period

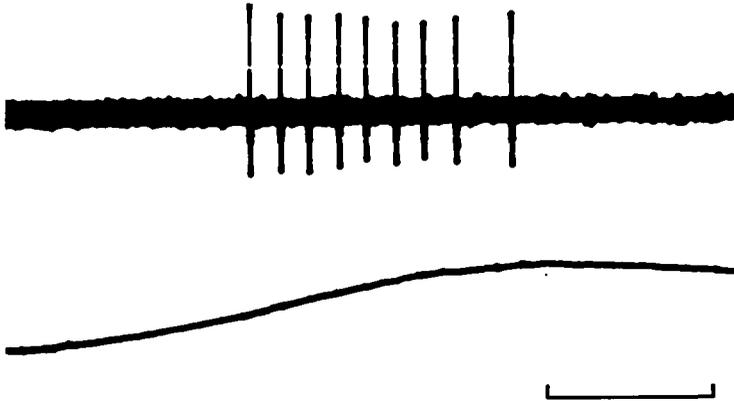


Fig. 2. Response of a single unit in SN I to longitudinal stretch. Spiking activity of the stretch-sensitive unit (upper trace) begins shortly after the onset of stretch (lower trace). Time: 2 s.

of most rapidly changing sinusoidal stretch. The last few spikes in the series were usually separated by longer interspike intervals. This decrease in spike frequency corresponded to a more slowly changing stretch as maximum stretch was approached. If stretch was maintained no tonic spiking was seen. Thus these responses were essentially phasic, signalling only increases in longitudinal stretch.

The second feature of the response was a decrease in spike amplitude (up to 50% in some cases) seen especially near the middle of the series during high frequency spiking. This was not due to a change in contact of the electrode with the nerve, because decreases in spike amplitude were also seen when there was no movement of the electrode relative to the nerve. One possible explanation for the decrease is that spikes occurring at the electrode were actually riding on a slowly developing depolarization, such as a receptor potential, across the sensory fibre membrane. Near peak stretch the decrease in stretch rate could have resulted in decay of the depolarization, causing an increase in spike amplitude. Essentially the same interpretation has been given for similar observations in the vertebrate muscle spindle (Katz, 1950). An alternative explanation is that the sensory fibre has an extremely long refractory period. During the highest frequency of firing, which rarely exceeds 5–6 spikes/s, spike amplitude may have diminished because spikes were occurring during the relative refractory period of preceding spikes. Similar responses have been reported in the earthworm circulatory system (Fournier & Pax, 1972). Without measurements of the transmembrane events in the stretch-sensitive fibre it is difficult to decide between the above alternatives.

Effects of changing stretch frequency

To further characterize the stretch-sensitive unit in SN I we studied the effects of varying the frequency of sinusoidal stretch in four animals. Such variations involved changes in the rate of stretching during each cycle. The results in Fig. 3A–D show responses to sinusoidal stretch at four different frequencies. In each record the segment was stretched 0.6 mm from a resting length of 1.0 to 1.6 mm. The results show that as the frequency of stretch was increased there was a reduction in the number of spikes with each cycle of stretch. At the highest frequency of stretch tested

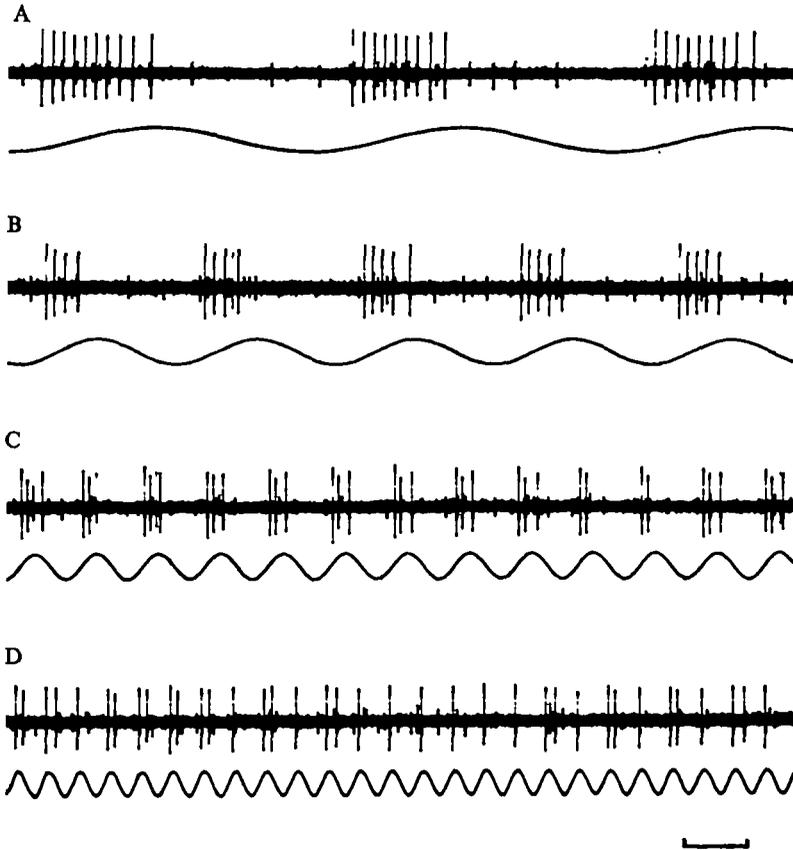


Fig. 3. Responses of a single unit in SN I to different frequencies of sinusoidal stretch. Upper traces show activity in the stretch-sensitive unit. Lower traces show frequency of sinusoidal stretching. The amplitude of stretch (0.6 mm) was constant at all frequencies. Frequency: 6/min (A); 12/min (B); 30/min (C); 60/min (D). Time: 2 s.

(60/min) the unit fired only once or twice with each cycle of stretch. At lower frequencies than those shown in Fig. 3 there was also a reduction in the number of spikes per cycle. In one preparation, for example, 0.6 mm stretch at 6/min produced a mean of 6.0 spikes (± 0.71 S.D.) per cycle of stretch. However, stretching at 3/min gave only 3.2 spikes (± 1.30 S.D.), and at 2/min only 2.2 spikes (± 0.45 S.D.). At even lower frequencies, which produced essentially a maintained stretch, spiking was rarely or never seen. Thus there was an optimum frequency of stretching in terms of the responsiveness of the stretch-sensitive unit; this optimum ranged from 4/min to 6/min.

Effects of changing stretch amplitude

The effects of varying the amplitude of stretch on the sensory response are seen in Fig. 4 A-C. Each record shows responses to the first five cycles of stretch following a 5 min rest period. Each record shows a reduction in the number of spikes with successive cycles. This reduction was probably the result of sensory adaptation.

Fig. 5 shows the quantitative nature of the adaptation at three levels of stretch. Each bar represents the mean number of spikes in each of five successive responses to

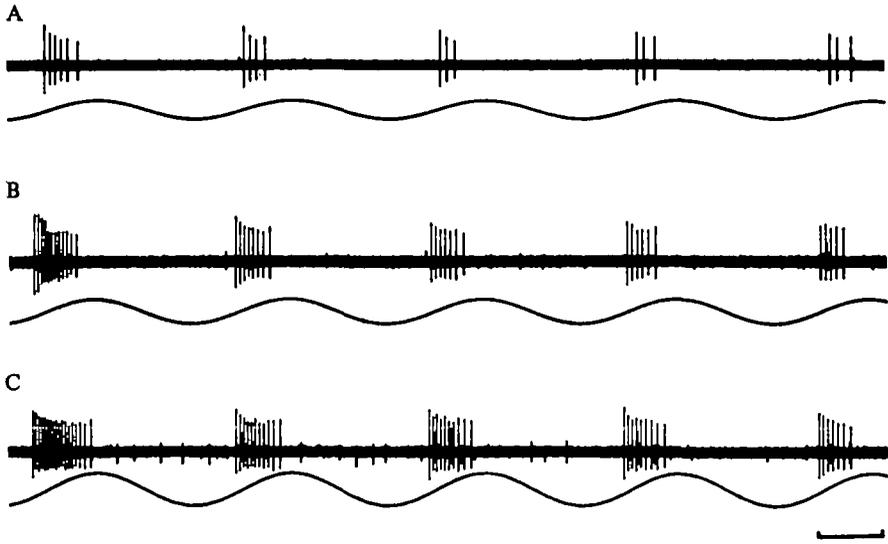


Fig. 4. Responses of a single unit in SN I to different amplitudes of sinusoidal stretch. Increased spiking activity in the nerve (upper traces) is seen as the amplitude of stretch of the segment is increased (lower traces). The frequency of stretch was held constant (4/min). Amplitude of stretch in the segment: 0.4 mm (A); 0.6 mm (B); 0.8 mm (C). Time: 5 s.

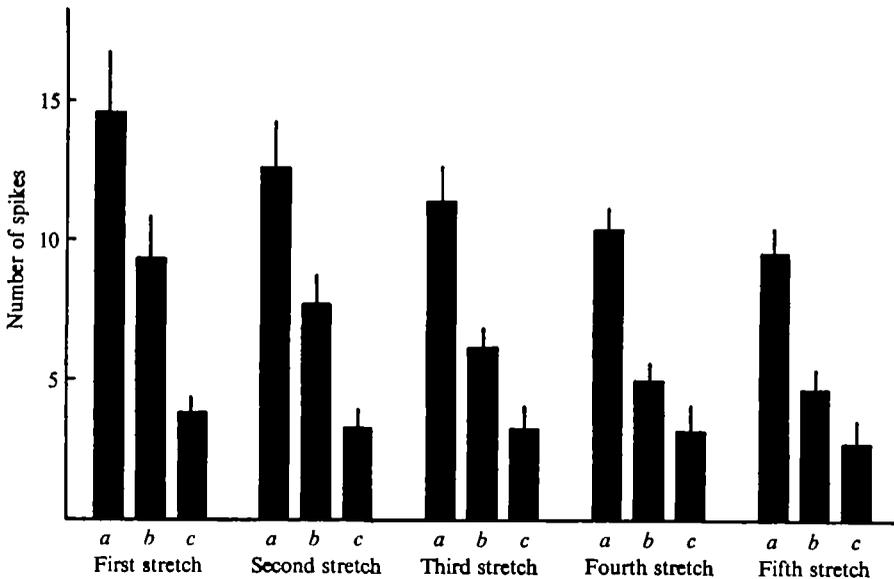


Fig. 5. Adaptation of stretch-sensitive unit in SN I. The bars indicate the mean number of spikes occurring in response to the first five cycles of longitudinal stretching at 4 cycles/min (sinusoidal). Results for three different amplitudes of stretch are given: 0.7 mm (a); 0.5 mm (b); 0.3 mm (c). Vertical lines indicate 1 S.E.

stretches of 0.3 mm (6 animals), 0.5 mm (6 animals) and 0.7 mm (5 animals). At each level of stretch there was a tendency for the number of spikes produced with each cycle to level off and reach some 'steady-state' level of responsiveness. In all preparations the steady-state level occurred after only a few cycles of stretch. At any

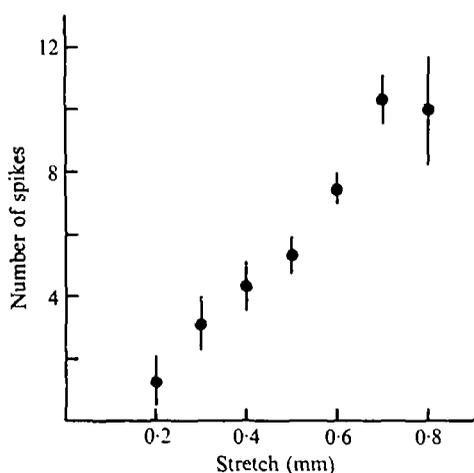


Fig. 6

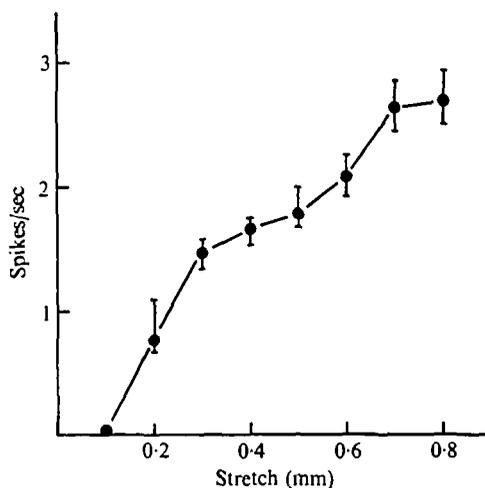


Fig. 7

Fig. 6. Relationship between the amount of longitudinal stretch and the number of spikes in SN I. Each point represents the mean number of spikes (± 1 s.e.) per sinusoidal cycle of stretch. These data are from six preparations.

Fig. 7. Relationship between the amount of longitudinal stretch and the frequency of spiking in SN I of one preparation. Each point represents the mean of three measurements of spike frequency during three consecutive cycles of sinusoidal stretching. Vertical lines indicate ranges.

particular amplitude of stretch the steady-state number of spikes per cycle was similar from one preparation to another and was clearly dependent on the amount of stretch.

Fig. 6 shows the relationship between the steady-state level of responsiveness and the stretch amplitude. Each point represents the mean number of spikes per cycle for the last three in a series of five cycles. A direct relationship was found within a range of 0.2 to 0.7 mm stretch. Below 0.2 mm stretch, spiking was rarely seen. With increases in stretch greater than 0.7 mm no increase in the number of spikes was seen. This upper portion of the graph may represent the upper physical limits of longitudinal stretch, as well as the maximal responsiveness of the stretch-sensitive unit. From this graph we can calculate the approximate sensitivity of the stretch-sensitive unit. Within a range of 0.2–0.5 mm stretch the sensitivity (slope) was approximately 1.3 spikes/0.1 mm stretch. In the range of 0.5–0.7 mm stretch, the sensitivity increased to approximately 2.5 spikes/0.1 mm stretch.

In addition to the relationship between the number of spikes and the amount of stretch, Fig. 4 also shows an increase in the frequency of spiking as the stretch was increased. For example, the minimum interspike interval with a stretch of 0.4 mm (Fig. 4A) was approximately 400 ms, or nearly twice that seen with 0.8 mm stretch (Fig. 4C). An estimate of the mean spike frequency during each stretch was obtained by taking the reciprocal of the mean interspike interval within a series of spikes. For example, in Fig. 4A the mean interspike interval throughout the first response is approximately 510 ms, corresponding to a spike frequency of 2/s. In Fig. 4C the mean interspike interval is approximately 260 ms, corresponding to a mean frequency of nearly 4/s.

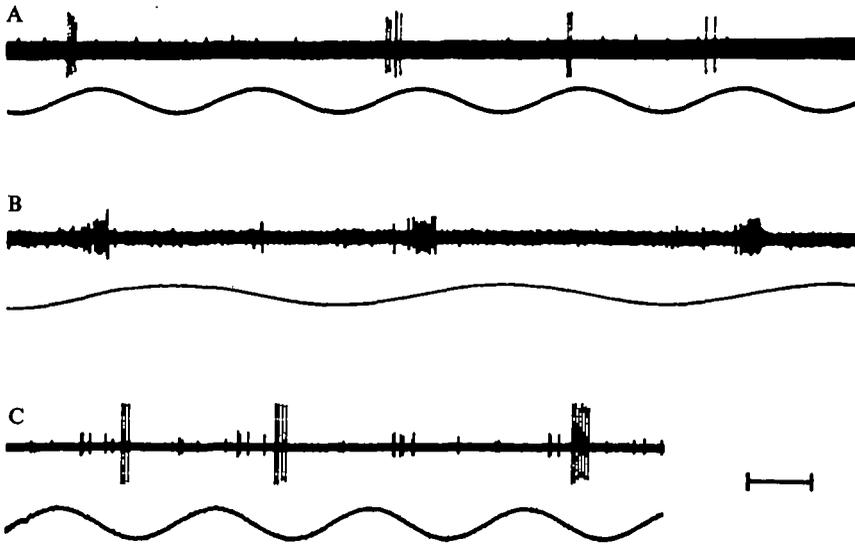


Fig. 8. Responses of SN II-III to longitudinal stretch. Upper traces show activity in the nerve. Lower traces show sinusoidal stretching. In A and B two different kinds of responses to increased stretch are seen. In C a unit responds to longitudinal relaxation. Time: 2 s (A, B); 4 s (C).

The relationship between the mean spike frequency and amount of stretch is given in Fig. 7. Each point represents the mean of three frequency measurements for each value of stretch. These values were obtained from the third, fourth and fifth cycles of stretch, during which the number of spikes and spike frequency had essentially reached steady-state values. Fig. 7 shows a direct relationship between spike frequency and the amount of stretch within a range of 0.1–0.7 mm stretch. No increase in spike frequency is seen at stretches greater than 0.7 mm. In summary, the results indicate that both the number of spikes and the spike frequency in the stretch-sensitive unit were directly related to the amount of longitudinal stretch in the segment.

Stretch-sensitive units in segmental nerve II-III

In five preparations stretch-sensitive units were examined in segmental nerve II-III (SN II-III). Responses of these units were much more variable than those of SN I. Fig. 8 shows three types of stretch-sensitive responses, each occurring in a different preparation; in some cases two types were seen in the same nerve.

The first response, shown in Fig. 8 A, slightly resembled the response of SN I. Activity consisted of a series of spikes occurring during increased longitudinal stretch. The amplitude sensitivity of the response was much lower than that for SN I; in some cases maximal stretch produced only one or two spikes. The sensitivity of the response to different frequencies of stretch was also different from that in SN I. Optimal responsiveness, in terms of number of spikes and frequency of spiking, was in the range of 20–60 stretches/min. However, even at these optimal frequencies some cycles of stretch failed to produce spiking.

A second type of spiking activity was also seen during increases in stretch (Fig. 8 B). The amplitude of this spiking was always small (less than 50 μ V), and it was therefore

difficult to determine if only one sensory unit was involved. The firing was initiated with stretches as low as 0.3 mm and consisted of a high frequency burst of spikes. Maximal frequency was 20–30 spikes/s. Unlike the activity in SN I this spiking ceased abruptly well before maximum stretch was reached. Thus the unit appeared to respond only within a small range of the total applied stretch.

A third type of response is seen in Fig. 8C. This activity apparently arose from a single neural unit, but activity was seen only as longitudinal relaxation was occurring. Visual observation of the preparation revealed that this unit fired just as resting length of the segment was reached. Although the interspike intervals in the series of spikes were uniform, the number of spikes seen during each cycle of relaxation was highly variable. Occasionally during some cycles of relaxation no firing was seen.

DISCUSSION

Characterization of stretch-sensitive units

Several stretch-sensitive units were identified in the segmental nerves of the earthworm. One unit, seen in SN I, showed consistent and quantifiable responses to longitudinal stretch in all preparations. On the basis of its responsiveness to sinusoidal stretching the unit appeared to be primarily phasic in nature. That is, the unit was sensitive to changes in segmental stretch rather than fixed position of the segment. The use of sinusoidal stretch, though convenient and presenting the fewest mechanical problems, did not allow determination of whether the stretch-sensitivity of the unit was specific for velocity or acceleration of stretch.

The amplitude and frequency of the stretching applied to isolated preparations approximate those of the stretching seen in intact animals during locomotory activities. In our preparations sensitivity to stretch was seen within a range of 0.2–0.8 mm stretch for one segment. These values are close to the actual changes in length observed during usual locomotion. Typically the length of a segment at rest varies from 0.6 to 1.0 mm and increases by at least 50–100% during segmental elongation (circular muscle contraction). The range of optimal sensitivity to various frequencies of stretch in the isolated preparations is comparable to the frequencies of locomotory activities in intact animals. We observed optimal responsiveness of the stretch-sensitive unit to frequencies of stretch ranging from 4–6/min at 17 °C. According to Gray & Lissmann (1938) the frequency of peristaltic waves in intact animals ranges from 7–10/min (presumably at room temperature, perhaps 22 °C). In summary, it appears that the ranges of sensitivity of the stretch unit to stretch amplitude and frequency closely match the ranges of amplitude and frequency during locomotion.

The responses to longitudinal stretch seen in SN II–III are more diverse than those seen in SN I. Results from SN II–III indicate that several types of stretch-sensitive units may exist in the earthworm body wall. Some units appeared to be phasic, signalling only rapid and large increases in longitudinal stretch; others fired only within a given range of stretch. Still others fired during longitudinal relaxation. The latter type could in fact be circular muscle stretch-sensitive units. Stretch-sensitive units in SN II–III showed some similarity to certain arthropod proprioceptors, namely joint movement and position receptors and chordotonal organs (Finlayson, 1968). In the chordotonal organs responses to relaxation as well as stretching of a particular joint may be seen (Bush, 1965).

A major problem encountered in studying any type of mechanoreceptor is the localization of the mechanosensitive neurones. Numerous investigators have identified nerve cell bodies in the peripheral nerves, muscle layers, and epidermis of the earthworm (Dawson, 1920; Ogawa, 1939; Knapp & Mill, 1971). Neurones in any of these locations would be well suited to monitoring stretch of the body wall.

Role of sensory input in locomotion

The importance of peripheral receptors in controlling locomotory activity in earthworms has long been suspected, as a result of numerous classical behavioural and physiological studies. The studies of Friedländer (1894) showed that rhythmic locomotory waves could successfully pass from the anterior to the posterior half of a completely transected earthworm if the two halves were mechanically coupled with threads. However, in the absence of peripheral sensory inputs and mechanical coupling between segments the ventral nerve cord can still successfully conduct locomotor excitation across several segmental ganglia (Biedermann, 1904; Bovard, 1918). In Bovard's experiments the peripheral nerves were severed and the body wall removed from several segments near the middle of the worm, thus leaving several segments of denervated ganglia connecting the intact anterior and posterior ends. In these preparations successful coordination between ends was dependent upon the length of the denervated nerve cord; when the length of free nerve cord was only four segments coordination between ends was easily demonstrated, but with lengths greater than eight segments coordination was rarely seen. Bovard theorized that during normal locomotion the wave of central excitation is reinforced in each segment by reflexes associated with muscular contraction.

This idea is further supported by the studies of Collier (1939*a, b*) who showed that rhythmic peristalsis could be reflexively induced by longitudinal tension or stretch applied to 20–40 segments of vertically suspended earthworm. The so-called 'tension reflex' resulting from the applied tension begins with an active lengthening of the preparation (circular muscle contraction). This is followed by an active shortening (longitudinal muscle contraction). After removal of the applied tension rhythmic peristaltic waves may continue, but seldom for more than 3 min. If continuous tension is applied, peristalsis may persist for up to 25 min. Tactile stimulation affects locomotion in several ways; it may evoke peristalsis in non-locomoting animals, or it may result in arrhythmic contractions accompanied by slowing or arrest of ongoing peristalsis.

Similar behavioural studies by Gray & Lissmann (1938) also emphasized the importance of sensory stimulation in initiating and maintaining rhythmic locomotion. In addition, these investigators recorded electrical activity from isolated ventral nerve cords but found no rhythmic electrical activity comparable to the locomotory rhythm in intact animals. In unpublished experiments we have recorded activity from individual segmental nerves in partially deafferented preparations. The preparations consisted of intact posterior or anterior halves of an earthworm along with approximately 20–30 segments of deafferented ventral nerve cord (body wall removed). Rhythmic peristaltic waves initiated in the intact end of such preparations progress successfully to the deafferented region, but corresponding rhythmic electrical outputs in segmental nerves do not progress more than a few segments into the deafferented

region of the nerve cord. Thus both behavioural and electrophysiological studies support the hypothesis that sensory input from stretch-sensitive units reinforces and maintains the central motor pattern of earthworm locomotion.

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