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THE RAPID RESPONSE OF *MYXICOLA INFUNDIBULUM* (GRÜBE)

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(Text-figs. 1–9)

The rapid escape response of the sabellid polychaete *Myxicola* is mediated through a giant nerve fibre, which Nicol (1948) has shown to be in protoplasmic continuity with branches which enter the segmental nerves and directly innervate the longitudinal muscle. The giant fibre occupies most of the interior of the ventral nerve cord and is one of the largest known, possessing a diameter of up to 1·7 mm. The motor branches are large too, having a diameter up to 85 μ.

Nicol & Whitteridge (1955) have investigated the transmission properties of the giant fibre. A single shock of sufficient strength applied to the nerve cord evokes an impulse which is conducted in both directions at a velocity of between 3 and 20 m/sec depending on the diameter of the fibre. This latter varies in different regions of the body, being greatest in the thorax where conduction velocity reaches its maximum value.

Histological evidence thus indicates that the giant fibre system represents a final common pathway innervating the longitudinal muscle fibres directly and without synapses. Physiological evidence confirms that here, as in other annelids, the giant fibre is a rapidly conducting, non-polarized axon adapted to ensure synchronous excitation of all the muscle fibres which it innervates. In the past little attention has been given to the properties of the muscular response so produced: in the present paper this aspect of the giant fibre reflex of *Myxicola* is discussed.

A recent study of the giant fibre reflex of the earthworm (Roberts, 1962*a*) has shown that in that animal the response is greatly affected by rapid accommodation at junctions situated between the giant fibres and the motor neurones supplying the longitudinal muscle. The giant fibres of the earthworm are thus internuncial neurones and it is of interest to compare its rapid response with *Myxicola* in which the giant fibre and its branches represent the final motor pathway.

Its ability to withstand manipulation, the absence of autotomy and the morphological simplicity of the giant fibre system make *Myxicola* an ideal experimental animal for this type of investigation.

MATERIAL AND METHODS

Myxicola infundibulum was obtained from the Salstone at Salcombe, Devon. The experimental procedure for kymograph recording is shown in Figs. 1 and 2. Thread from the posterior region of the worm was attached to a semi-isometric lever. For the majority of preparations a reasonably stiff lever was used, 1 g tension being represented by a 1 mm excursion of the writing point of the lever. It was arranged that the muscle was always under slight tension before each recording. For experiments involving electrical recording the pre-amplifier and oscilloscope were of standard design. Action potentials recorded from the giant fibre are large, thus obviating many of the difficulties usually encountered in electrical recording. For stimulating with electrical shocks of controlled intensity a signal-marker contact-maker (Hall & Pantin, 1937) was used. The turntable apparatus for providing controlled volleys of shocks has been described elsewhere (Roberts, 1962*a*) and further description is unnecessary here.

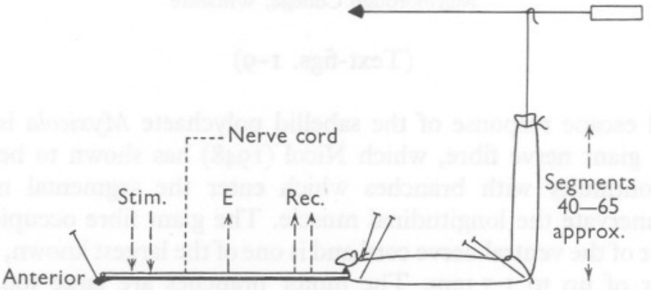

Fig. 1. *Myxicola infundibulum.* Nerve-muscle preparation. Nerve cord earthed (*E*) between the stimulating (*Stim*) and recording electrodes (*Rec*). Further explanation in text.

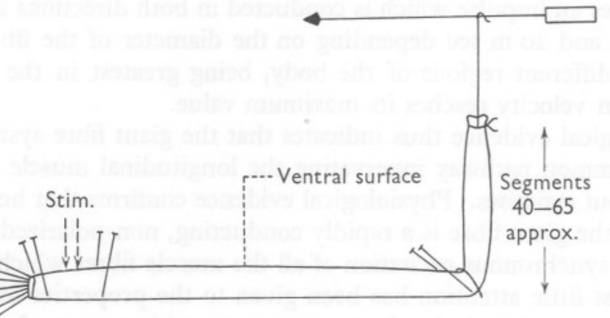

Fig. 2. *M. infundibulum.* Preparation for recording longitudinal muscle contractions in response to stimulation of tentacles or anterior mid-dorsal body wall.

EXPERIMENTS AND RESULTS

Direct observation of responses

Myxicola is found in sand at the low-tide mark. It lives in a mucus tube from which, when it is undisturbed, the crown of tentacles protrudes. Inside the tube it undergoes little apparent movement though periodically one or more weak waves of contracture are seen to pass slowly up or down the body. Slight stimulation, however, causes a rapid shortening, and the whole animal, including the branchial crown, is withdrawn inside the tube. The relaxation which follows is slow, and as it occurs the crown of tentacles slowly opens and the creature resumes its original appearance. Sometimes the twitch is followed by several slow 'antiperistaltic' waves which pass forward along the body resulting in the animal moving backwards further down its tube.

Very gentle tactile stimulation of the body surface at the anterior end of an unfatigued animal, applied for example by stroking with a camel hair brush, produces slow contractions of the longitudinal musculature. A single mechanical stimulus rarely produces more than one and at the most two such contractions. Only a very slight increase in the intensity of stimulation is necessary to evoke the rapid response which can be superimposed upon a pre-existing slow contraction. Slow contractions are thus elicited at a lower threshold than the fast contraction.

The nerve-muscle preparation

The worm was pinned to the wax floor of a dish about 40 segments from the anterior end, a ligature being tied at segment 60–65 and the thread attached to the recording lever. The nerve cord was exposed at the anterior end by dissection from the dorsal side and freed from surrounding muscle. The gut was deflected to one side and the anterior end of the nerve fixed in position by placing a pin through a piece of muscle to which the nerve was left attached (Fig. 1). The preparation was stimulated through a pair of platinum electrodes whose blunt tips were placed in contact with the surface of the nerve cord. A pair of recording electrodes were placed in contact with a more posterior part of the cord (Fig. 1).

The rapid response and latent period

Fig. 3 shows the rapid longitudinal contraction obtained by direct stimulation of the nerve cord with a single shock of sufficient strength to excite the giant fibre. The initial response, caused by a single giant fibre impulse, was followed by a relatively slow relaxation and no further contractions.

The responses of a large number of different preparations were recorded and it was found that although the speed of contraction (i.e. the rate of development of tension) is within narrow limits constant, the contraction height (i.e. tension achieved) varied considerably from one preparation to another despite the fact that the same number of segments and thickness of muscle was recorded in each case; the preparations were always in the same state of longitudinal relaxation before stimulation, and the response was always evoked by a single giant fibre impulse. The average preparation of those recorded is one which takes 53 msec. to produce a total tension of 7 g. The contraction shown in Fig. 2 may thus be regarded as typical.

Latent period measurements were made from preparations which were fixed to the floor of the dish at segment 45 with the stimulating cathode placed in contact with the nerve cord at segment 6. Rapid contractions of segments 40–70 were recorded on a fast drum in response to single condenser shocks, well above threshold for the giant fibre response.

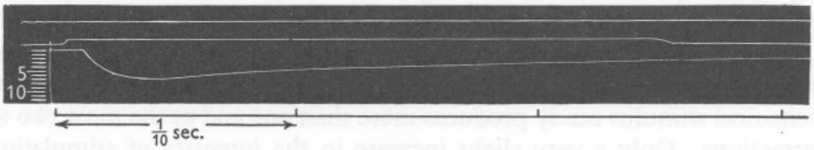

Fig. 3. *M. infundibulum*: nerve-muscle preparation. Rapid longitudinal contraction recorded in response to stimulation of nerve cord with a single condenser shock. Upper trace: time signal; middle trace: stimulus mark; lower trace: muscle record.

The latent period thus measured was found to range between different preparations from 8 to 15 msec. The shortest latent period recorded is shown in Fig. 3. The average, estimated from seven preparations, was found to be 11 msec. This latency represents the interval between the application of the stimulus to the nerve cord and the start of the muscular contraction, but it does not take into account the inertia of the recording system. The significance of this latent period is discussed below.

That each rapid contraction is the result of a single impulse in the giant fibre was ascertained by recording giant fibre activity and the mechanical response of the longitudinal muscle simultaneously. For each twitch recorded on the drum a single giant fibre impulse appeared on the oscilloscope screen. A twitch was always associated with a giant fibre impulse and the latter never failed to evoke a rapid contraction.

The all-or-nothing law

The nerve cord of a nerve-muscle preparation was stimulated with single shocks of gradually increasing intensity and the rapid contractions of the longitudinal muscle were recorded. The results (Fig. 4) indicate that there is a threshold intensity below which a single stimulus evokes no response, fast or slow, and above which a rapid contraction is recorded which is not increased either in size or speed by further increasing the intensity of stimulation.

Simultaneously recording giant fibre activity from the nerve cord indicates that the muscular responses are produced by single impulses in the giant fibre.

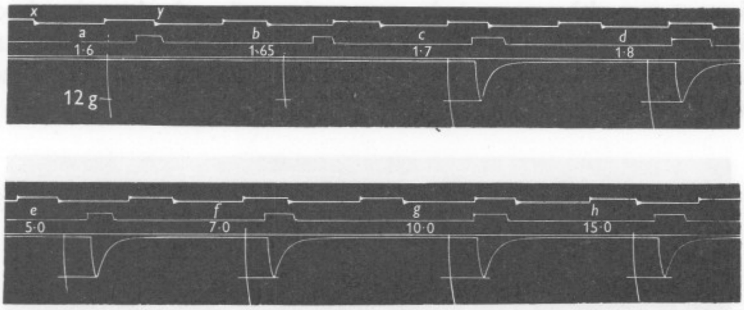

Fig. 4. *M. infundibulum*: nerve-muscle preparation. Rapid longitudinal contractions to direct stimulation of nerve cord with a series of single shocks of increasing intensity. Upper trace: time signals ($x-y$, 1 sec). Middle trace: stimulus marks. Lower trace: muscle records, each preceded by tracing of excursion of the lever recorded on stationary drum. Potentiometer readings (intensity scale): *a*, 1·6; *b*, 1·65; *c*, 1·7; *d*, 1·8; *e*, 5·0; *f*, 7·0; *g*, 10·0; *h*, 15·0.

Clonus and tetanus

The turntable apparatus was used to stimulate the nerve cord of a nerve-muscle preparation with groups of four shocks at various frequencies. The interval between successive shocks was varied by altering the position of the arms on the turntable. As Nicol (1951) found in *Branchiomma*, three types of response can be distinguished depending on the interval between the stimuli. When the interval is sufficiently long (exceeding 0·3 sec) each shock produces a twitch whose relaxation is complete, or about complete, before the next shock is delivered (Fig. 5, record *a*). With shorter intervals (0·3 sec to 30 msec) the four twitches are clearly distinguishable but the relaxation which follows each one is incomplete before the next shock is applied. Such clonic responses are seen in Fig. 5, records *b–e*. With very short intervals (less than 15 msec) the four twitches are fused to give smoothly summated tetanic contractions (fig. 5, records *f* and *g*).

Summation

In the previous section it was shown that successive contractions produced by repetitive stimulation of the giant fibre can summate to give larger responses (Fig. 5, records *f*, *g*). It is shown below that this is not a common occurrence in the life of the animal though it is an important property of the nerve-muscle machinery. Some details of the process were investigated by stimulating the nerve cord of nerve-muscle preparations and progressively decreasing the interval between the shocks. The turntable apparatus, equipped with the first and fourth arms only, was used to provide two shocks, the interval between them being varied by altering the distance between the arms and the speed of the turntable.

It is evident from the recordings obtained that with this particular recording technique a smoothly summated response is produced when the shocks are separated by not more than 12–15 msec. If the interval is greater than this the two component twitches of the double contraction can be discerned (Fig. 6).

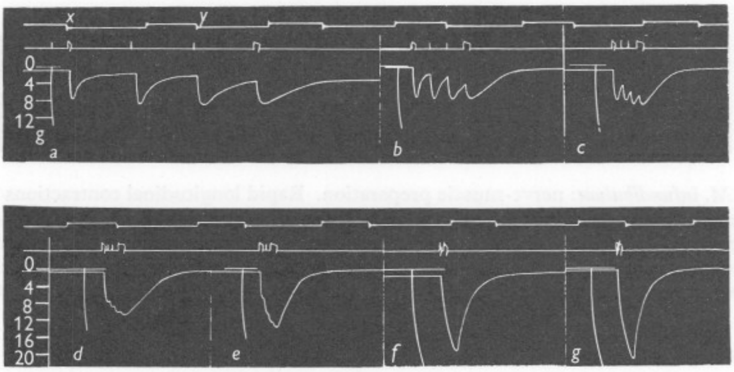

Fig. 5. *M. infundibulum*: nerve-muscle preparation. Rapid longitudinal contractions to direct stimulation of nerve cord with groups of 4 shocks at increasing frequencies. Upper trace: time signals ($x-y$, 1 sec). Middle trace: stimulus marks, the first and fourth recorded in the experiment, the second and third interpolated afterwards. Lower trace: muscle records. Approximate intervals between successive shocks: *a*, 0·5 sec; *b*, 140 msec; *c*, 70 msec; *d*, 50 msec; *e*, 30 msec; *f*, 14 msec; *g*, 12 msec.

Fig. 6 also shows what happens to the second response as the interval between the two shocks is gradually decreased. Records *a* to *c* indicate that the second response is as large as the first when it occurs *after* the relaxation phase of the latter; indeed with many preparations it was slightly larger (see Fig. 7). Records *d* to *g* indicate that the second contraction is diminished when it occurs *during* the relaxation phase of the first response. Records *g* to *l* show the summated response gradually increasing in size as the interval between the two shocks is further decreased to such an extent that the second response commences within the contraction phase of the first. Interestingly, the summated responses in records *i* to *l* are more than twice the size of the contraction produced by a single shock.

The results presented in the last two sections demonstrate that the magnitude of the rapid contraction, experimentally induced, depends on the number and frequency of shocks delivered to the nerve cord, that is, on the number and frequency of giant fibre impulses reaching the muscle. *Myxicola* thus has two simple mechanisms by which theoretically it could grade its escape response.

The extent to which it in fact uses these mechanisms in natural circumstances is discussed below.

Fatigue

The pattern of fatigue was investigated by repetitively stimulating the nerve cord at frequencies of up to 3 shocks/sec and examining the rate at which the muscular contractions declined in size and the time required for

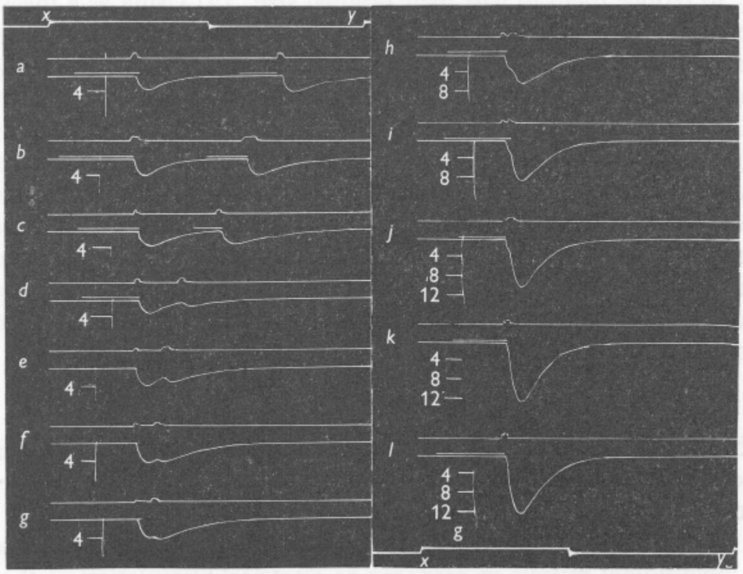

Fig. 6. *M. infundibulum*: nerve-muscle preparation. Rapid longitudinal contractions to direct stimulation of nerve cord with 2 shocks in succession. Time signal: $x-y$, 1 sec. Stimulus marks appear above each muscle record. Approximate intervals (msec) between the two shocks: *a*, 460; *b*, 360; *c*, 260; *d*, 140; *e*, 105; *f*, 65; *g*, 55; *h*, 30; *i*, 24; *j*, 18; *k*, 15; *l*, 10.

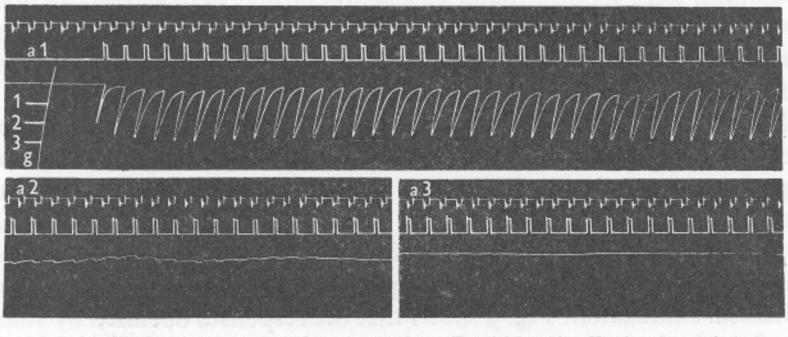

Fig. 7. *M. infundibulum*: nerve-muscle preparation. Rapid longitudinal contractions to direct repetitive stimulation of nerve cord. Upper trace: 1 sec time signals. Middle trace: stimulus marks; Lower trace: muscle record. *a*1, shocks 1–25; *a*2, shocks 150–168; *a*3, shocks 290–309.

recovery. The results can be summarized as follows: (1) On repetition the rapid contractions are maintained at a steady level for a considerable period of time (Fig. 7). They then undergo a gradual decline until after a very large number of shocks no further twitches can be recorded. The number of shocks required to fatigue the muscle depends on their frequency. At one per second the contractions do not start to decrease in size until approximately 30 shocks have been delivered, and it requires approximately 100 shocks at this frequency to reduce them to half their original size. (2) Using as a measure of fatigue a decrease in contraction size of 75% it was found that it requires a greater number of shocks to fatigue the muscle at low frequencies of stimulation that at higher frequencies. (3) Fatigue involves a decrease in the speed as well as in the magnitude of contraction and, in the majority of preparations investigated, a marked increase in the relaxation time. (4) Experiments to ascertain the recovery time of the muscle indicate that after contractions have been reduced to $\frac{1}{8}$ their original size by repetitive stimulation at 1 shock/sec it requires a minimum rest period of between 2 and 3 min for the original contraction size to be restored. However, the rate of decline on repetition is now more rapid and a much longer rest period must be given if the original pattern of fatigue is to re-established.

Rapid responses produced by peripheral stimulation

In the experiments described above the nerve cord was stimulated directly and the information thus obtained bears only on the motor side of the giant fibre reflex.

The sensory system was investigated by recording the rapid contractions of the longitudinal muscle in response to electrical stimulation of the mid-dorsal body wall and of the tentacles (Fig. 2). In order to avoid the possibility of the sensory endings adapting during manipulation some preparations were lightly anaesthetized with magnesium chloride before being set up. Other preparations were set up without an anaesthetic and were allowed an hour to recover before experiments were begun. No differences were observed between the results obtained from previously anaesthetized and unanaesthetized worms.

The relation between the intensity of peripheral stimulation and the magnitude of the rapid contraction was investigated by stimulating the body wall of the preparation shown in Fig. 2 with a series of single shocks of increasing intensity. The results demonstrate that although the threshold is slightly lower than with direct stimulation of the cord the same 'all-or-nothing' relationship exists between the intensity and response (Fig. 8). The same applies to mechanical stimulation: Fig. 9 shows that the responses obtained by stimulation of the body wall with single condenser shocks are identical with those obtained by prodding the tentacles or body surface.

By exposing the nerve cord a short way down the body (approximately segments 25–35) and recording the action potentials it was established that these contractions, like those produced by direct stimulation of the cord, result from single impulses in the giant fibre. Very rarely, and only with severe and prolonged mechanical stimulation of the body surface, is more than one impulse recorded and in these cases the muscular contractions are correspondingly enlarged as a result of mechanical summation of successive responses.

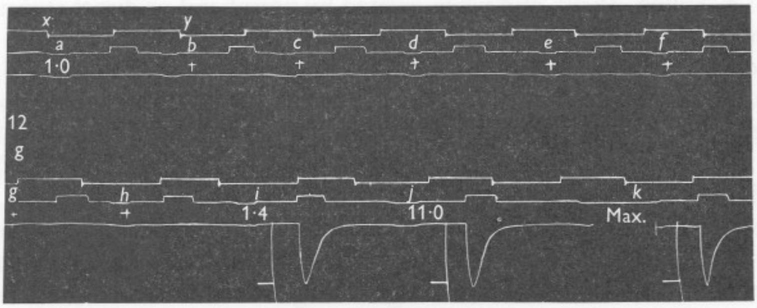

Fig. 8. *M. infundibulum*. All-or-nothing relation between intensity of peripheral stimulation and rapid response. Mid-dorsal body wall at anterior end stimulated with single shocks of increasing intensity. Upper trace: time signals ($x-y$, 1 sec). Middle trace: stimulus marks. Lower trace: muscle records. The preparation (see Fig. 2) was given 15 min rest interval between each recording. Potentiometer readings (intensity scale): *a*, 1·0; *i*, 1·4; *j*, 11·0; *k*, maximum.

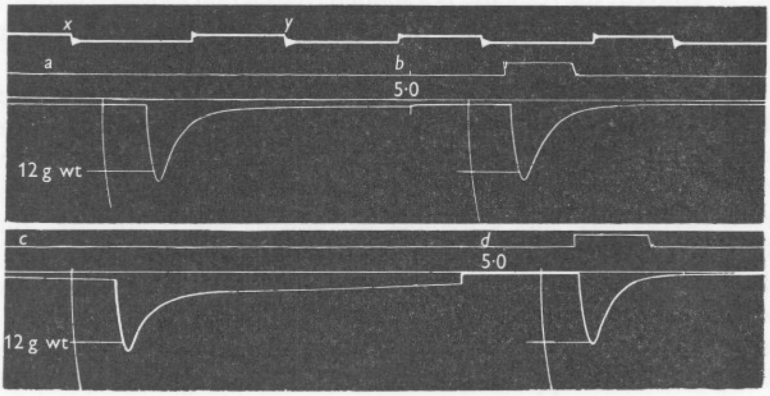

Fig. 9. *M. infundibulum*. All-or-nothing relation between intensity of peripheral stimulation and rapid response. Responses produced: *a*, by strong mechanical stimulation of branchial crown; *b* and *d*, by single condenser shocks applied to mid-dorsal body wall at anterior end; *c*, by strong mechanical stimulation of anterior mid-dorsal body wall. Other details as in Fig. 8.

DISCUSSION

The rapid escape response of *Myxicola infundibulum*, mediated through the single giant fibre, is a simple 'all-or-nothing' contraction which on repetition is slow to fatigue. These properties of the response are in accordance with both the physiological and morphological characteristics of the giant fibre itself. This fibre, sending motor branches without synapses to the longitudinal muscle fibres, represents the final common pathway in the escape reflex (Nicol & Young, 1946), and when excited by peripheral or direct stimulation it normally transmits only one impulse (Nicol & Whitteridge, 1955).

The features of the response are also in accordance with the animal's mode of life. *Myxicola* lives buried in the sand in a mucus tube from whose opening the branchial crown expands. The rapid contraction produced by a single giant fibre impulse is sufficient to withdraw the worm inside its tube. There would be no obvious advantage in undergoing a larger contraction for, once inside the tube, the animal is afforded as adequate protection as it reasonably could be. Neither would there seem to be any point in undergoing further contractions, fast or slow, for although it might remove the creature further from potential danger it would also increase the time required for emergence and the resumption of feeding and respiration. Nicol (1950), in discussing sensory adaptation in *Branchiomma vesiculosum*, has emphasized the compromise that exists between two conflicting needs of the organism, withdrawal to escape from adverse stimulation, and maintained expansion for respiration and feeding. The escape response of *Myxicola* shows one way in which this conflict is resolved: the response is a sudden contraction followed immediately by relaxation and reopening of the branchial crown. Sustained or abnormally large contractions are rare.

In Myxicola the response produced by a single impulse is large, and repetitive discharge of impulses in the giant fibre is unusual. Preliminary information suggests that a similar situation prevails in a number of other tubiculous polychaetes such as *Branchiomma* (Sabellidae), and *Hyalinoecia* (Onuphidae), *Filograna* (Serpulidae) and a number of eunicids and terebellids. Bullock (1948) implies that with tactile stimulation of the body wall single giant fibre impulses are transmitted in *Diopatra* (Onuphidae), *Lepidametria* (Polynoidae) and several other forms and these produce extensive escape responses. Nor is this situation confined to annelids. Young (1938) has shown that a single shock above threshold applied to the stellar nerve of *Loligo* evokes a very large twitch of the circular muscle fibres of the mantle, further increase in the intensity of stimulation not leading to larger responses. Since each stellar nerve contains one giant axon it seems likely that the large contractions are the result of single impulses transmitted in these.

The position in the earthworm contrasts sharply with this. Here a single giant fibre impulse evokes a very small twitch of the longitudinal muscle and repetitive impulse discharge as normally produced by peripheral stimulation is necessary for the production of larger responses (Roberts, 1962*a*). A similar situation appears to exist in *Nereis* in which graded escape responses can be observed and repetitive discharge of giant fibre impulses frequently occurs when the animal is stimulated peripherally. Bullock (1948) has recorded repetitive impulses in the bamboo worm, *Clymenella torquata* (Maldanidae), and in the errant burrower *Haploscoloplos bustorus* (Orbinidae) in which a weak stimulus is sufficient to evoke a long-lasting, high-frequency discharge in the faster conducting giant fibre. Preliminary evidence suggests that the absence of repetitive discharge in *Myxicola* may be due to a sudden lowering of the excitability of the giant fibre after it has transmitted an impulse thus preventing further afferent impulses from exciting it. Volleys of impulses characteristic of *Lumbricus* and *Nereis* may be due either to the absence of this phenomenon or to its developing less rapidly.

Another point of contrast concerns the full sequence of reactions which follows peripheral stimulation. In *Lumbricus* and *Nereis* the initial rapid contraction is followed by backward locomotion, antiperistaltic crawling in the case of *Lumbricus*, swimming in *Nereis*. In the former these reactions start as a posterior elongation caused by contraction of the circular muscles and it can be elicited at a lower threshold than that required to evoke a giant fibre response. *Myxicola* and other tubiculous polychaetes on the other hand display very little observable muscular activity apart from the rapid response.

The development of clonus and tetanus follows much the same pattern as that seen in *Branchiomma* (Nicol, 1951), but the frequencies required to induce them are different. Thus a tetanus is obtained with a frequency of only 13 shocks/sec in *Branchiomma*, whereas between 70 and 90 shocks/sec are required in *Myxicola*. This may of course be partly due to differences in recording conditions as well as to the speed of contraction evoked by a single shock. Nicol reports that in *Branchiomma* maximal tension is produced after 250 msec, a considerably longer period than is required in *Myxicola* in which it can take as little as 50 msec to reach maximal tension. It therefore requires a greater frequency of stimulation to fuse the faster contractions characteristic of *Myxicola*.

The speed of the muscular response produced by a single impulse depends on the rate at which the fibres comprising the longitudinal musculature are excited and this depends on the speed at which the impulse is conducted along the giant fibre. The giant fibre of *Myxicola* has a maximum conduction velocity of 20 m/sec (Nicol & Whitteridge, 1955), a speed which exceeds that so far found in any other polychaete. It is therefore not surprising that the contraction is correspondingly rapid. There is no information on conduction velocity in the giant fibres of *Branchiomma*, but their comparatively small size suggests that it is considerably slower than in *Myxicola* and this probably accounts for the slower speed of contraction of the muscle.

In *Myxicola* the gradual and slow decline in the rapid contractions evoked by repetitive stimulation of the nerve cord contrasts strikingly with the earthworm where accommodation at junctions situated between the giant fibres and the motor neurones supplying the longitudinal muscle causes the responses to fatigue extremely quickly (Roberts, 1962*b*). Though the muscular contractions have not been studied, rapid accommodation in the giant fibre reflex has also been demonstrated in *Nereis* and *Harmothöe* (Horridge, 1959).

Although maximum transmission velocity in the giant fibre of *Myxicola* is less than in the median giant fibre of *Lumbricus* the latent period is considerably shorter in the former (an average value of 11 msec in *Myxicola* as recorded from nerve-muscle preparations, compared with 40 msec in *Lumbricus* estimated in the same way). The explanation of this would seem to be that in the earthworm the motor axons supplying the longitudinal muscle are not continuous with the giant fibre, are not abnormally large, and transmit at speeds usually associated with normal-sized nerve fibres (Roberts, 1960).

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SUMMARY

In Myxicola the rapid muscular response produced by direct stimulation of the nerve cord with a single shock is usually large and obeys a simple 'all-or-nothing' relationship to the intensity of stimulation. A single shock of sufficient strength evokes a single giant fibre impulse which produces an extensive contraction of the longitudinal muscle.

The magnitude of the summated contraction obtained by repetitive stimulation of the nerve cord is found to depend on the number and frequency of the shocks, thus providing the animal with a mechanism by which, theoretically, it could grade its escape response.

The effect on the second contraction of sending in two shocks in succession is demonstrated. The second response is diminished when it occurs during the relaxation phase of the first, but enhanced when it commences during the contraction phase of the first.

The rapid responses fatigue slowly on repetition. When the frequency of stimulation is approximately one per second the contractions are maintained at first and then show a gradual decline in magnitude but do not cease to be recorded altogether until several hundred shocks have been delivered.

The responses obtained by peripheral stimulation also bear an 'all-or-nothing' relationship to the intensity of stimulation and there is no tendency

for graded responses to be produced by stimulating the body wall with shocks of increasing intensity. A single peripheral stimulus, electrical or mechanical, evokes a single giant fibre impulse irrespective of its intensity.

The results obtained with *Myxicola* are discussed in relation to the known morphology of its giant fibre reflex, the animal's mode of life, and the rapid responses of other annelids.

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