The kinetics of locomotion in the earthworm and the nature of the factors which control the various phases of the ambulatory cycle have been subjects of extensive investigation. Numerous theories have been advanced, but a general survey of the literature suggests that the time has not yet been reached at which the more outstanding observations can be fitted into a relatively precise picture. The observations recorded in this paper are, however, relevant for this purpose.

THE KINETICS OF NORMAL LOCOMOTION

Before it is profitable to consider the nature of the neuro-muscular control of ambulation it is essential to have an adequate picture of the kinetics of a normal cycle. Many accounts of the locomotion of the earthworm are inadequate in this respect, and it is therefore desirable to give a summarized account of such a cycle as derived from cinematograph records.

So long as the worm is at rest and in contact with the ground, both the longitudinal and circular muscles of all segments are partially relaxed; forward progression begins by the contraction of the circular muscles of the anterior segments, and a wave of circular contraction passes backwards over the body of the worm. When this wave has passed over the front half of the body (60–70 segments), the circular muscles at the extreme anterior end of the body relax and contraction of the longitudinal muscles sets in. A wave of longitudinal contraction then passes backwards and, having also passed over the front half of the body, is replaced in turn by a second wave of circular contraction which, like the first, starts from the anterior end of the animal. So long as its longitudinal muscles are contracted to their maximal extent, a segment remains at rest relative to the ground (Fig. 1). When relaxation of the longitudinal muscles sets in, the segment begins to move forward over the ground with increasing velocity until its longitudinal relaxation is complete; while its longitudinal muscles are undergoing contraction, the forward velocity of the segment over the ground decreases until the segment comes to rest again in a state of maximum longitudinal contraction. Each segment therefore moves forward, over the ground, in a series of steps each of 2–3 cm. in length,
and during steady progression the whole worm moves forward at a speed equal to the length of one step multiplied by the frequency at which the locomotory waves pass over the body. During each of its phases of maximum longitudinal contraction a segment is attached to the substratum by the protrusion of the posteriorly directed setae. Several adjacent segments exhibit, simultaneously, a maximum state of longitudinal contraction and thereby co-operate to form a "foot" or point d'appui against which the active muscles of adjacent segments can exert a tension. Those segments which lie immediately anterior to the "foot" are undergoing circular contraction, and are extending forwards, relative to the ground, by exerting (owing to circular contraction) a backward thrust against the foot equal to the frictional resistance generated by the movement of the extending segments over the substratum. On the other hand, those segments of the worm which lie immediately posterior to the foot are undergoing longitudinal contraction and are exerting a backward pull on the foot equal to the frictional resistance of the posterior segments moving over the ground. It will be observed that both circular and longitudinal muscles, although in one sense mutually antagonistic, both contribute to the forward propulsion of the body over the ground (see also Gray & Lissmann, 1938).
The time relationships between the different phases of each “step” depend, somewhat, upon the activity of the worm, but the frequency of the movements during the present observations was of the order of 7–10 per min.: the time occupied by one complete ambulatory cycle varied from 4 to 11 sec., each segment remaining contracted for approximately half this period. The significance of these periods will be apparent later.

THE ROLE OF PERIPHERAL TACTILE REFLEXES DURING AMBULATION

When an intact earthworm is suspended vertically in air, it may exhibit, for considerable periods of time, a normal and well-defined ambulatory rhythm. In this respect the worm differs from the leech (Gray, Lissmann and Pumphrey, 1938), where a regular ambulatory rhythm is dependent upon a well-defined pattern of tactile stimulation emerging from the suckers or the ventral surface of the body. It is, however, almost certain that the rhythm displayed by a vertically suspended earthworm is dependent upon the stretch stimulus which is automatically applied by the weight of the animal’s body. If an actively moving earthworm, suitably suspended by cotton threads, be deprived of contact with a horizontal substratum, the rhythm of ambulation ceases and the animal remains in the extended state with the circular muscles contracted; if longitudinal tension be then applied, a well-defined rhythm emerges (Fig. 2). Similarly, if an intact or decapitated preparation be suspended vertically, in air, the resultant rhythm can be stopped by immersing the body in water; the rhythm emerging again when the preparation is again transferred to air. It seems clear that under normal conditions a background of tactile stimulation from the ventral surface is essential for the display of a locomotory rhythm; in this respect, the earthworm resembles a leech from which the suckers have been removed (Gray et al. 1938).
THE ROLE OF PROPRIOCEPTOR REFLEXES DURING AMBULATION

The elicitation of an ambulatory rhythm in response to stretch was first demonstrated by Friedländer (1888) who showed that if the posterior half of a worm be severed from the anterior half, and the two portions united by a thread, the posterior half may exhibit locomotory movements co-ordinated with those of the anterior half, so long as the whole preparation is free to move horizontally over a relatively rough surface. On a smooth surface no movements of this type occur. Biedermann (1904) and, later, Moore (1922a) showed that if tension be applied to a recently decapitated worm the initial response is contraction of the circular muscles at the anterior end of the preparation and that this is followed by a typical and complete wave of peristalsis.

Before assuming that stretch reflexes are of functional significance it is necessary to show that the tension required to initiate circular contraction is of the same

![Fig. 3. Response of an inactive preparation to longitudinal tension. The record reads from right to left. At A the preparation was exposed to a tension of 5 g. Note the initial contraction of the circular muscles, followed by a typical ambulatory rhythm.](image)

order of magnitude as that which is set up by the contraction of the longitudinal muscles in a normal intact animal. To obtain an estimate of this force, an earthworm was allowed to crawl on to a horizontally suspended bridge provided with counterweights (see Gray & Lissmann, 1938). Under appropriate conditions, the anterior segments of the worm attach themselves to the bridge by the protruded setae, whilst the hinder part of the body is in contact with the fixed platform; during such conditions the tension exerted by the longitudinally contracting segments (situated on the bridge) on the hinder segments (lying on the platform) could be determined by measuring the degree of displacement of the counterpoise weights of the bridge. In this way the tension exerted by the longitudinal muscles was found to vary from 2 to 8 g, according to the size and rate of movement of the worm. Fig. 3 shows that when this amount of tension is applied to an inactive decapitated preparation, the circular muscles at once undergo contraction. This reflex, almost certainly, plays a part in the normal ambulation of the posterior half of the body of an intact worm moving over a rough surface, but it cannot occur in the case of
segments situated at the anterior end of the body, for in this region the uncontracted circular muscles are not subjected to tension immediately prior to their contraction. The stretch reflex of the circular muscles cannot therefore initiate the normal ambulatory cycle of the intact worm, although it can facilitate the spread of circular contraction over the posterior region of the body.

Passive stretch only elicits a contraction of the circular muscles if it be applied to a preparation in which both circular and longitudinal muscles are initially inactive. If tension be applied during any other conditions the response is different. For example, if tension be applied to a preparation whose longitudinal muscles are actively contracting, a marked reinforcement occurs and the tension of these muscles may rise to as much as 70 g. as a reflex result of the applied tension (Fig. 4). It can also be shown that passive tension applied to inactive longitudinal muscles elicits their contraction. This can be demonstrated in the following way. A decapitated worm is suspended vertically from an isotonic lever and the preparation is left until the ambulatory rhythm has become relatively slow. In the early stages of such a preparation, the relaxation of the longitudinal and the contraction of the circular muscles pass smoothly into each other without any break in the tracings on a kymograph drum. As such a preparation ages, the rhythm slows down and the tracings show very clearly the moment at which the circular muscles begin to contract. Fig. 5 represents such a tracing and shows three phases of activity:
(i) a rapid contraction of the longitudinals, (ii) a slow period of relaxation of the longitudinals, (iii) a relatively quick contraction of the circulars. In preparations of this type, passive tension reflexly excites the longitudinal muscles if applied at the right moment. If transitory tension be applied during the early stages of longitudinal relaxation, the rate of elongation of these muscles is accelerated (Fig. 5), and the onset of circular contraction is also accelerated. With lapse of time, however, the response of the circular muscles to tension becomes less and less apparent and finally disappears; under such circumstances, tension applied to fully relaxed longitudinal muscles causes the latter to respond by active contraction (Fig. 6). Definite responses of this type can only be obtained in preparations wherein the circular muscles are no longer excitable, but it seems legitimate to assume that if tension be applied to fully relaxed longitudinal muscles in an intact worm these muscles will contract. Such responses almost certainly occur at times during normal ambulation for, not infrequently, a wave of longitudinal contraction fails to pass to the posterior extremity of the animal; in such cases the succeeding wave invariably passes through and the segments concerned exhibit an abnormally large step.

Since contraction of longitudinal muscles can be elicited by transitory tension, and since the relaxation of these muscles can also be accelerated by similar stimuli, it is possible to initiate a rhythm in these muscles by applying a regular series of short passive twitches, the frequency of the rhythm increasing with the frequency of the twitches (Fig. 7).

The above data show fairly clearly that, once an ambulatory rhythm has been established in the anterior segments of a worm, all posteriorly situated segments are liable to be automatically exposed to a pattern of mechanical stimulation (due to movements of the muscles of the anterior segments) of such a nature as to maintain a rhythm which is co-ordinated with that of the anterior segments. For example, if we consider a complete ambulatory wave as is shown diagrammatically in Fig. 8 and imagine that central conduction along the nerve cord is suddenly blocked at a point $p$, the following conditions will arise owing to the tension set up by the longitudinal contraction occurring in segments 1–3: (i) Segments 4–6 will...

Fig. 6. Preparation with inactive circular muscles. Note the contraction of the longitudinal muscles in response to passive stretch. The preparation showed no spontaneous rhythm. The longitudinals did not respond to the first stimulus; at the third and fourth stimulus slight traces of circular contraction are seen. Note the effect of stretch (6 seq.) applied during relaxation of longitudinal muscles, the rate of elongation of the muscles being greatly accelerated.
contract against the elastic resistance of segments 8–13 as well as against the frictional resistance of the substratum. The tension developed by segments 4–6 will thereby automatically increase as in Fig. 4. (ii) Segment 7, with fully relaxed longitudinal muscles, will undergo longitudinal contraction as in Fig. 6. (iii) Segments 8–13, with partially relaxed longitudinal muscles, will undergo (a) accelerated longitudinal relaxation as in Figs. 5, 6, and (b) active circular contraction as in Fig. 3. The combined effect of all these reflexes gives a pattern which is identical with that of normal ambulation.

![Graph showing effects of stretch stimuli on rhythm frequency.]

Fig. 7. Effect of stretch stimuli of short duration on the frequency of the rhythm of two (a and b) decapitated preparations. Note the increase in frequency caused by increase in frequency of the applied stimulus or by an increase in the intensity of the stimulus.

![Diagram of segments showing relax and contract areas.]

Fig. 8. ← direction of wave; → direction of progression.

On the other hand, it is important to remember two fundamental facts: (i) Complete co-ordination of movement can be displayed between two regions of the body which are connected by the nerve cord only, and under circumstances in which there is no possibility of transmission of mechanical stimuli (Biedermann, 1904). (ii) Stretch reflexes are not likely to be operative when movement is occurring on a very smooth surface; nor can they, under any circumstances, initiate an ambulatory rhythm in the anterior segments of a preparation lying freely on a horizontal surface. At this stage it is convenient to consider the inherent properties of the central nervous system when this is deprived of all peripheral influences.
An attempt to elucidate the inherent properties of the nerve cord has been made by recording its electrical activity under various conditions. In a number of preparations oscillograph records were taken from electrodes placed on an exposed region of the cord during two successive ambulatory waves. For such records the preparation was arranged as follows: An incision, about 2 cm. long, was made in the dorsal surface just behind the clitellum, the nerve cord was exposed, and the segmental nerves cut. The preparation was then firmly pinned to cork through the denervated region, the intact regions being freely suspended in air or placed on glass plates. So long as the preparation was at rest, no electrical rhythm was detectible, but as soon as peristaltic movements set in, a well-defined electrical rhythm emerged whose frequency was identical with that of the mechanical rhythm. So far as could be determined, the phase of increased electrical activity coincided with the phase of longitudinal contraction, but further data are desirable. The point of immediate significance is the fact that the frequency of the electrical rhythm is identical with the frequency of the mechanical rhythm of ambulation,

1 We owe our thanks to Dr R. J. Pumphrey for considerable assistance with this section of the work.
and that the duration of the active periods is of the same order of time as the period of activity of the longitudinal muscles, viz. about 2 sec.

An investigation of the totally isolated nerve cord has given results which are not easy to interpret. For such observations, the worm was narcotized with 5% ethyl alcohol, the nerve cord was isolated for a length of 2 or 3 cm., placed horizontally on a fine wire grid in a damp chamber and the electrical activity recorded in the usual way. After the effect of the anaesthetic had worn off, nearly every preparation gave evidence of rhythmical activity for prolonged periods of time. Occasionally, as in Fig. 9, the frequency and duration of these rhythms were comparable to those

Fig. 10. Oscillograph record from the isolated nerve cord of an earthworm showing a very rapid and persistent rhythm. The frequency is about two per second. The figures at the base of each strip of the record show the time in seconds.
displayed by the nerve cord of a worm undergoing typical peristaltic movement, but more often the characteristics of the rhythms were totally unlike those of true peristalsis. In some instances, as in Fig. 10, the frequency was of the order of 2 per sec., in others the frequency was very low, and the periods of nervous activity lasted for as much as 20 sec. (Fig. 9). Although the rhythmic activity of the isolated nerve cord is perhaps comparable to that observed in Dytiscus (Adrian, 1931) or in the brain stem of the goldfish (Adrian & Buytendijk, 1931), it may be doubted how far this type of activity in the nerve cord of the earthworm has any ambulatory significance. It must be remembered that the nerve cord is surrounded by a sheath containing muscle fibres, and that it is capable of a certain amount of independent movement. We have frequently observed grouped discharges from the cord immediately after spontaneous movements of the preparation.

The electrical rhythms observed in the isolated cord are not improbably comparable to those mentioned by v. Holst (1937) and associated by him with normal ambulation. The present observations seem to give, however, very little positive support to the view that a true ambulatory rhythm can be displayed by a nerve cord after complete isolation from all peripheral connexions.

ELICITATION OF PERISTALSIS BY DIRECT CURRENT STIMULATION

According to Moore (1922b) the circular muscles of the earthworm can be excited to contract by passing a direct current through the preparation when the head is directed towards the cathode. Attempts to repeat these observations have failed, but we have observed a marked effect of direct current on the ambulatory
activity of decapitated preparations. If a preparation, showing no spontaneous
movements, is placed on a damp glass plate with the head end towards the positive
pole, it is nearly always possible to elicit active peristalsis when a suitable density
of current is passed through the preparation from electrodes placed on the surface
of the glass. If the direction of flow of the current be reversed, peristalsis ceases
and may be followed either by a prolonged contraction of the longitudinal muscles
or by anti-peristalsis. Fig. 11 shows a kymograph record of a typical preparation.
It will be noted that peristalsis often persists for some time after the current ceases
to flow, and that the latent period before peristalsis begins, on making the current,
is often very long—sometimes as much as 20 sec. We have also observed that the
passage of a direct current through a preparation, which is responding rhythmically
to passive stretch, exercises a considerable influence on the behaviour of the
preparation.

The significance of these results should not be exaggerated, but they suggest
that spontaneous ambulation may be associated with a change in the electrical
polarity of the central nervous system, whereby the anterior end becomes electro-
positive to the posterior end.

DISCUSSION

The above data suggest that, under normal conditions, ambulation in the
earthworm is determined by a rhythmical mechanism which normally only displays
activity when the animal is receiving tactile stimulation from the ventral surface
of the body; if such stimulation be withdrawn the transition from a state of circular
contraction to one of longitudinal contraction no longer occurs. Two explanations
appear to be available: (i) that longitudinal contraction is initiated by the activity
of the tactile sense organs on the ventral surface of the body, (ii) that the transition
from circular to longitudinal contraction is effected by a central mechanism which
is inactive in the absence of an adequate level of peripheral excitation. This is
normally provided by the ventral surface of the body, but can also be derived from
stretch receptors. It is impossible, at this stage, to decide between these two
possibilities, for a decision must rest on an interpretation of the electrical rhythms
displayed by the isolated nerve cord. If, under normal circumstances, the rhythm
of ambulation is determined by the recurrent incidence of a peripheral tactile
reflex, it is difficult to see why it should be equally well sustained by the activity of
stretch receptors which cannot possibly be active in the anterior segments of a
normal intact animal. On the other hand, positive evidence in support of an
inherent central ambulatory rhythm is, at present, not available.

Once a rhythm has been established in the anterior segments of the worm, it
is possible to see how it is conducted to the posterior segments. This is effected in
two ways: (i) by central conduction along the nerve cord, (ii) by a chain of peri-
pheral reflexes. When the musculature of a segment is responding to excitation
from the nerve cord it is simultaneously being exposed to mechanical stimulation
(due to movements of the muscles of anteriorly situated segments) of such a nature
as to cause a response identical in nature with that due to the excitation reaching it by conduction along the fibres in the nerve cord. Stretch reflexes would not be operative when the animal is moving on a very smooth surface, and since, under such conditions, peristaltic waves pass over the intact animal, it is improbable that the stretch reflexes are necessary in order to compensate for decremental conduction via the nerve cord. It seems more likely that the reflexes are operative when the worm is moving over an irregular surface along which the external resistance is variable. All the reflexes would then co-operate with the nerve cord to produce a muscular effort exactly adjusted to external conditions.

SUMMARY

1. In the absence of longitudinally applied tension, an intact or decapitated earthworm only exhibits peristalsis so long as its ventral surface is in contact with the substratum.

2. The reflex response of a decapitated earthworm to mechanical tension depends upon the precise conditions under which the stimulus is applied. When the muscles of a segment are responding to stimuli which reach them from the efferent tracts in the nerve cord, they are simultaneously being exposed to mechanical tension (due to movements of the muscles of anteriorly situated segments) of such a nature as to cause a reflex response identical in nature to that induced directly by the nerve cord. It is suggested that tension reflexes are chiefly of functional significance when the animal is moving over an irregular surface.

3. During normal peristalsis the nerve cord of an earthworm exhibits an electrical rhythm whose frequency is identical with that of the muscular rhythm. The isolated nerve cord may exhibit an electrical rhythm for prolonged periods, but it is uncertain how far this phenomenon bears any relationship to the muscular rhythm displayed by the intact animal.

4. Peristalsis can be elicited in an inactive decapitated preparation by making the anterior end electropositive to the posterior end. Peristalsis is inhibited by reversing the direction of flow of the current.

REFERENCES