CONSIDERABLE uncertainty still exists concerning the nature of the mechanism which maintains the normal locomotory rhythm of terrestrial animals. Two types of theory have been advanced: (i) That the rhythm is determined by the existence of a closed chain of peripheral reflexes, each phase of a complete locomotory cycle setting up automatically the particular pattern of peripheral stimulation requisite for the elicitation of the succeeding phase in the cycle. (ii) That the rhythm is, fundamentally, a property of the central nervous system which is, however, susceptible to modification or extinction by peripheral stimulation.

Similar theories have been applied to the locomotory rhythm of aquatic animals but in such cases the balance of opinion is in favour of the view that the rhythm is of central and not peripheral origin.

The common leech (Hirudo medicinalis Ray) is of interest for such investigations for two reasons: (i) It exhibits two clearly defined and distinct types of locomotory rhythm. (ii) During normal terrestrial locomotion, the two phases of each step are very clearly related to the two very simple and clearly defined patterns of peripheral stimulation emerging from the suckers.

The leech possesses three main groups of muscles (circulars, longitudinals and dorso-ventrals); during terrestrial movements the dorso-ventrals remain inactive, whilst the circulars and longitudinals exhibit a characteristic rhythm of activity; during aquatic locomotion, the dorso-ventral muscles are held in a state of sustained contraction, the circular muscles are relaxed, whilst waves of contraction pass alternately down the ventral and dorsal bands of longitudinal muscles. The present paper deals with the neuro-muscular mechanism of both types of progression.

TERRESTRIAL LOCOMOTION

The kinematics of terrestrial locomotion in the leech (Hirudo medicinalis Ray) are essentially the same as those of the earthworm, and consist of alternating changes in length of the animal. Movement begins, in both forms, by the passage of a wave of contraction over the circular muscles, and these muscles, acting against a
The Mechanism of Locomotion in the Leech

posteriorly situated point d'apppui, extend the body forwards over the substratum; the wave of circular contraction is succeeded by a wave of contraction in the longitudinal muscles which, acting against an anteriorly situated point d'apppui, draw the body forwards over the ground. In the earthworm, each segment in turn acts as a point d'appui for neighbouring segments, but in the leech the fixed points are provided by the suckers. The posterior sucker acts as a point d'appui for the circular muscles and performs the function of the ventral setae of a segment lying at the anterior end of the “contraction wave”, or foot, of an earthworm; the anterior sucker of the leech is comparable to the setae of a segment lying at the posterior end of a contraction wave of the worm. As in the earthworm, both longitudinal and circular muscles contribute towards the forward progression of the animal and develop tensions, against the external resistance of a reasonably smooth surface, of 1.0-1.5 g. (see p. 419).

During each complete step the animal is exposed to well-defined and characteristic patterns of exteroceptive stimulation, each phase of muscular activity being ushered in by fixation of the appropriate sucker, and during the passage of the muscular waves the ventral surface of the body is moved over the surface of the substratum. The immediate problem is to determine how far such exteroceptive stimulation constitutes an essential part of the rhythmical mechanism of progression.

(A) The role of exteroceptive stimuli as pace-makers in terrestrial locomotion

When a leech is moving steadily over a level surface it is obvious that the onset of the locomotory waves is associated with the fixation of the suckers; fixation of the anterior sucker is the invariable prelude to a wave of activity over the longitudinal muscles; fixation of the posterior sucker immediately precedes a similar wave over the circular muscles. The dependence of the muscular rhythm on the fixation of the suckers can be studied in some detail by suspending an intact leech (by threads passing through the dorsal skin) to an isotonic lever. If such a preparation be left undisturbed, its behaviour is largely unpredictable and is characterized by alternating periods of typical swimming movements and periods of “searching” movements. These movements are almost certainly conditioned by the slight tension exerted by the lever: when entirely deprived of exteroceptive stimulation the intact animal invariably swims (see p. 421). Searching movements are of two types: (i) With the circular muscles partially or wholly contracted and with the anterior sucker protruded. (ii) With the longitudinal muscles contracted and with the posterior sucker protruded. During the first of these types of movement the anterior end of the animal moves from side to side and fairly frequent but irregular changes occur in the length of the animal (see Fig. 1 a); during the second type of movement, the posterior sucker moves in a somewhat similar manner but little or no change occurs in the length of the animal. In both cases the protruded sucker appears to seek a suitable point for attachment. If no such attachment is available for the anterior sucker, one of two changes in behaviour may occur: (i) The circular muscles relax, the dorso-ventral muscles contract and typical swimming movements occur in the
longitudinal muscles. (ii) The circular muscles relax and the longitudinal muscles contract, thereby giving rise to the alternative pattern of searching movements with the posterior sucker protruded. If no suitable attachment is available when the posterior sucker is protruded, the contraction of the longitudinal muscles is eventually replaced by a contraction of the circular muscles with consequent elongation of the body and protrusion of the anterior sucker. *No trace of a regular ambulatory rhythm has ever been observed in a freely suspended preparation.* If, however, a suitable point of attachment is provided for a protruded sucker (e.g. a small piece of coverslip) an immediate and predictable muscular response occurs; when the posterior sucker attaches itself, a wave of activity at once passes down the circular muscles whilst the longitudinal muscles simultaneously relax (see v. Uexküll, 1905). Similarly, if the anterior sucker is allowed to attach itself, as soon as a wave of circular contraction has extended over the whole body, a wave of contraction passes down the longitudinal muscles of the whole body (Fig. 1 a).

Since complete isotonic contraction of the longitudinal muscles at the hind end of the animal leads invariably to the protrusion of the posterior sucker, while contraction of the circular muscles at the anterior end of the animal leads to protrusion of the anterior sucker, it is possible to elicit a typical walking rhythm in the suspended leech by the provision of suitable attachments for each sucker in turn (Fig. 1 b).

Since no true rhythm of circular and longitudinal activity has ever been observed in a leech deprived of all exteroceptive stimulation, it seems legitimate to conclude that the normal ambulatory rhythm is either the direct expression of rhythmically applied tactile stimuli or is a centrally determined rhythm which can only express itself against a peripheral background of a clearly defined nature.

At first sight the patterns of peripheral stimulation, essential for normal ambulation, appear to depend, specifically, upon the attachment of the suckers to the substratum; in fact this is not the case. Removal or denervation of the suckers does not abolish the locomotory rhythm. The posterior sucker can readily be amputated and the anterior sucker can be entirely immobilized by cutting the nerves supplying it from the oesophageal ganglia. After both these operations, a leech may exhibit normal ambulatory movements so long as the animal is in contact with the ground; some slip may occur, but the characteristic regular rhythm of circular and longitudinal contractions occurs essentially as in the intact animal. These facts show clearly that although the fixations of the suckers may normally act as time signals for each main phase of normal progression in the intact animal, they are not playing an essentially specific role.

So long as the two suckers are present and are able to attach themselves to the substratum, the absence of other tactile stimuli does not appear to influence the locomotion of the leech to any marked degree, for normal walking movements occur when the general surface of the body is in contact with air. On the other

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1 Protrusion of the suckers has never been observed under any other conditions. It is significant to note that protrusion of the posterior sucker only occurs if the longitudinal muscles are allowed to shorten to their normal extent during their contraction; protrusion does not occur if the muscles contract isometrically.
Fig. 1a and b. Records (reading from left to right) of an intact leech suspended in air to an isotonic lever. At A the anterior sucker was allowed to attach itself to a small piece of coverslip, shortly after which the posterior sucker—if attached—detached itself spontaneously. At P the posterior sucker was allowed to attach itself to a small piece of coverslip, whereupon the anterior sucker—if attached—detached itself spontaneously.

**Note (i)** The contraction of the longitudinal muscles which follows attachment of the anterior sucker. If attachment of the anterior sucker is effected when circular contraction is restricted to the more anterior segments of the body, the first effect of fixation is complete longitudinal relaxation throughout the body, and this is then followed by a complete wave of longitudinal contraction throughout the whole body (Fig. 1a, b, A).

(ii) The rapid and complete relaxation of the longitudinal muscles on attachment of the posterior sucker. In all cases relaxation of the longitudinal muscles is accompanied by contraction of the circular muscles and vice versa.
hand, tactile stimulation appears to play an essential role in the movements of an animal from which the suckers have been removed. If threads be attached to the anterior and posterior regions of the dorsal surface of such a preparation, it is possible to lift the animal off the ground during spontaneous ambulation: under such circumstances, all locomotory rhythm ceases and the animal either remains extended and quiet or exhibits obvious swimming movements (Fig. 2). If the hind end of such an animal be lifted from the ground at the moment of complete longitudinal relaxation—no subsequent wave of longitudinal contraction extends to the posterior region. Similarly, if the posterior end of the animal be lifted from the substratum during a phase of longitudinal contraction, the ensuing circular wave is either restricted to the anterior end of the animal or it may be inhibited altogether until the posterior end of the body is again allowed to come into contact with the ground.

The above data do not show how far the ambulatory rhythm is of central or of peripheral origin, but they show very clearly that the rhythm is dependent on a background of tactile stimulation either from the suckers or from the ventral surface of the body. So far as has been determined (see p. 427) the central nervous system of the leech, when isolated from all peripheral sense organs, possesses no inherent ambulatory rhythm of its own, and we may conclude, for the time being, that if any such rhythm exists, it only displays itself when the nerve cord is receiving suitable impulses from the periphery; such impulses can undoubtedly originate in the tactile sense organs situated on the suckers or on the ventral side of the body, and it may be that they can arise elsewhere. On the other hand, it is equally probable that the ambulatory rhythm is the expression of rhythmically applied

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Fig. 2. Record of a leech, after denervation of both suckers, walking on a horizontal glass plate. Note cessation of ambulation as soon as contact with the plate is removed; when freely suspended the preparation showed typical swimming movement until ventral contact with the plate was again established. The rapid swimming rhythm can just be detected from the waviness of the tracing. The record reads from right to left.
Fig. 3a and 3b. Records (reading from left to right) showing the effect of mechanical stimulation (with a camel's hair brush) of the dorsal and ventral surfaces of (3a) intact leech with denervated suckers (b), decapitated leech. $D=$ beginning of dorsal stimulation; $d=$ end of dorsal stimulation; $V=$ beginning of ventral stimulation; $v=$ end of ventral stimulation. Dotted arrows indicate cessation of stimulations. Note development of swimming movements on relaxation of longitudinal muscles.
peripheral stimulation—the asset of longitudinal contraction being initiated by impulses emerging from the anterior sucker or from tactile sense organs which are only active when the ventral surface of the body is fully extended over the surface of the ground; suitably the onset of circular contraction may be initiated either by impulses emerging from the posterior sucker or from tactile sense organs which are only active when the actual surface of the body is in contact with the ground and when longitudinal muscles are contracted.

![Image of a decapitated preparation showing reflex inhibition of longitudinal muscles by attachment of the posterior sucker.](image)

Fig. 4. Record of a decapitated preparation showing reflex inhibition of longitudinal muscles by attachment of the posterior sucker. The longitudinal muscles were held in a prolonged state of contraction by strong tactile stimulation of the dorsal surface. As soon as the longitudinal muscles relaxed, the posterior sucker detached itself and the longitudinal muscles again responded to the dorsal stimulation.

It is not easy to analyse the nature of the reflexes associated with tactile stimulation of the ventral surface of the body. It can, however, be shown that there is probably no qualitative difference between the responses to such stimulation when

1 It is difficult to apply stimuli comparable in strength and nature to the frictional stimuli which automatically occur during normal ambulation. As a general rule diffuse stroking of the ventral surface of the suspended body (of intact or decapitated animals) leads, when applied during a phase of longitudinal contraction, to rapid and extensive relaxation of the longitudinal muscles (Fig. 3); this response is strikingly similar to that given by the attachment of the posterior sucker. Similar stimulation to the dorsal surface does not effect longitudinal relaxation, and, if applied during a phase of longitudinal relaxation, leads to the contraction of these muscles. It is, however, unwise to lay too much stress on the significance of these reactions during normal ambulation.
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The latter is applied to the posterior and anterior ends of the body. If tactile stimulation applied at the posterior end of the body were responsible, in the absence of the posterior sucker, for the onset of a circular wave at the anterior end of the body, one would expect to find that transection of the nerve cord would abolish the ambulatory rhythm of that part of the body lying anteriorly to the transection. This is not the case, for comparatively short lengths of the body, if connected to the suboesophageal ganglion, exhibit active ambulation.

It is of interest to note that exteroceptive stimulation not only ushers in contraction of one set of muscles but also induces relaxation in the antagonistic musculature. If the suboesophageal ganglion be removed, the circular muscles of the leech fail to respond to moderate reflex stimulation—but the power to affix the posterior sucker (after reflex contraction of the longitudinal muscles) persists. A decapitated leech, therefore, provides the possibility of testing any inhibitory influence exerted on the longitudinal muscles by the fixation of the posterior sucker. For this purpose, the preparation is subjected to slight tension from an isotonic lever and the longitudinal muscles are reflexly contracted by tactile stimulation of the dorsal surface of the animal. As soon as the posterior sucker is protruded, it is allowed to attach itself to a small piece of coverslip. Immediate relaxation of the longitudinal muscles occurs even if the dorsal stimulation be continued during the process of attachment of the sucker (Fig. 4). Preparations vary somewhat in their sensitivity to dorsal stimulation, and the effect of fixation of the sucker on the longitudinal muscles is best observed when these muscles normally remain contracted for some
time after the dorsal stimulation has been discontinued. The inhibitory influence, produced by fixation of the posterior sucker, upon the motor neurones of the longitudinal muscles, is also illustrated by Fig. 5 which is an oscillograph record taken from the proximal end of a posterior segmental nerve before, during, and after normal fixation of the sucker. It will be noticed that fixation of the sucker completely abolishes the large impulses which are characteristic of the posterior segmental nerves during contraction of the longitudinal muscles. It is clear that fixation of the posterior sucker induces an active inhibition of the longitudinal muscles and that this action is not dependent on the presence of the suboesophageal ganglion. How far a corresponding effect is exercised by the anterior sucker on the circular muscles cannot, at present, be determined.

Fig. 6. Records showing sensory discharge in a segmental nerve in response to a short passive stretch of the skin and longitudinal muscles. Time signals in 0.01 and 0.1 sec.

(B) The role of proprioceptive stimuli in terrestrial locomotion

During a normal locomotory cycle, extensive changes occur in the form of the whole body and it has long been suspected that proprioceptor reflexes might play a significant role in the co-ordination of the whole cycle. Hitherto, there has been no direct evidence to support the view that stretch receptors are present in the muscles or other tissues of the leech, and the following preliminary observations are therefore of some interest. An anterior segmental nerve was dissected out for a distance of about 2 mm. and after severance from the spinal cord its distal end was placed on two fine platinum electrodes leading to an amplifier and oscillograph. Fig. 6 shows the activity of the sensory fibres in this nerve when the body wall of the segment was subjected to very gentle passive stretch. So far as could be deter-
mined, the sensory elements are located both in the skin and in the segmental muscles, but it is difficult to remove the skin without damage to the underlying muscles. It seems clear that stretch receptors are present in the leech; the following

![Image of efferent discharges in response to passive stretch.](image)

**Fig. 7.** Efferent discharges in response to passive stretch. The lower record is a continuation of the upper and shows the response to a more prolonged stimulus than was applied in the upper record. Time marked in $\frac{1}{10}$ and $\frac{1}{100}$ sec.

![Image of tracings showing forces exerted against the substratum by a normal intact leech walking over a glass surface.](image)

**Fig. 8.** Tracings showing direction and magnitude of the forces exerted against the substratum by a normal intact leech walking over a glass surface. $+$ = pull due to longitudinal muscles; $-$ = thrust due to circular muscles.

experiment shows that their activity sets up efferent motor discharges in neighbouring parts of the body. The anterior half of a leech was opened from the dorsal surface and the central nervous system exposed. One anterior nerve was then dissected out for about 2 mm. and severed, distally to a fine ligature, which was
subsequently used for placing the nerve on the electrodes. The preparation was firmly pinned to a cork and all other segmental nerves in the anterior half of the body were cut. The anterior end of the posterior half of the body was secured by pins, all segments in the neighbourhood of the pins were denervated, and the muscles and skin removed from a short region of the nerve cord. In this way the

Fig. 9(a). Isometric contraction of the longitudinal muscles of an intact leech walking normally but with posterior end attached to an isometric lever. Note long and powerful contraction. (b) Isometric contractions of longitudinal muscles of a freely suspended intact leech.

anterior end of the preparation was only connected to the posterior region of the body by the nerve cord itself and tension could be applied to the posterior end of the body without causing any mechanical disturbance in the anterior half of the body. Electrodes were then placed on the proximal end of the exposed segmental nerve and the posterior (intact) part of the body was subjected to gentle localized stretch. Fig. 7 shows the efferent impulses set up in the nerve under observation.
The Mechanism of Locomotion in the Leech

It thus seems clear that passive changes in the form of the body of a leech can, under suitable circumstances, set up efferent discharges in the segmental nerves.

It is impossible at the moment to assess the precise role of proprioceptor reflexes in the co-ordination of normal locomotion but there can be little doubt that stretch receptors play a dominating role when the locomotory movements of a leech are impeded by an external resistance greater than that provided by ordinary friction with the substratum. By means of the apparatus described elsewhere (Gray & Lissmann, 1938), it is possible to show that the maximum external frictional resistance overcome by the longitudinal muscles during a normal cycle is of the order of 1.5 g. and that the duration of the contraction is approximately 2.0 sec. (Fig. 8). When, however, the isotonic contraction of the longitudinal muscles is prevented by attaching the posterior end of a normally walking leech to an isometric lever, the force developed may rise to as much as 80 g. and the contraction may last for relatively very long periods, e.g. 60 sec. (see Fig. 9). These sustained contractions appear to be largely independent of the suboesophageal ganglion and it seems reasonable to associate them with the efferent impulses set up by passive stretch. The leech thus appears to possess a stretch reflex essentially similar to that found in higher vertebrates and to the resistance reflexes of such a fish as the eel (Gray, 1936 b).

It is significant to note that the frequency of the ambulatory rhythm depends upon the rate at which the longitudinal muscles undergo complete isotonic contraction. If the rate of isotonic contraction be altered by the attachment of a constant load to the hind end of the animal, the frequency of the rhythm is decreased (see Fig. 10). If the muscles are compelled to contract isometrically the ambulatory rhythm is abolished, but reappears as soon as the longitudinal muscles are allowed to shorten freely to their normal extent.
One inherent property of the nerve cord seems clear, viz. its ability to transmit waves of longitudinal or circular contraction over one or more completely denervated segments (see Fig. 11). In this respect the nerve cord of the leech resembles that of the earthworm and many other types of animal. A further analysis of the properties of the cord is less easy, but the following observations have been made:

(i) Removal of the suboesophageal ganglion entails marked loss of tone and no ambulatory movements have been seen except in response to relatively strong stimulation.¹

(ii) When the whole central nervous system is isolated from the periphery by section of all segmental nerves, considerable electrical activity, in the form of irregularly spaced impulses, can be detected in the segmental nerves. The number and size of these impulses are greatly reduced by removal of the supra- and suboesophageal ganglia.

(iii) The isolated nerve cord with or without the oesophageal ganglia has so far failed to reveal a type of electrical rhythm reminiscent of the typical mechanical rhythm of ambulation.

¹ A fairly well-defined ambulatory rhythm can sometimes be maintained in a decapitated leech by drawing the body passively over a relatively rough surface; the first response to tension is a wave of circular contraction starting at the anterior end of the preparation, and this is followed by a wave of longitudinal contraction. The whole response is clearly the same as that observed in the earthworm, but is much less powerful. It is difficult to see how this reflex can, in the case of the leech, play a role in normal locomotion since in this animal no longitudinal muscles are active until the whole of the circular muscles are in a state of isotonic contraction.
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(D) Summary of the mechanism of the ambulatory rhythm

The following conclusions may form a basis for further analysis of normal ambulation:

(i) Fixation of the posterior sucker initiates simultaneously (a) a wave of excitation over the circular muscles, (b) inhibition of the longitudinal muscles.

(ii) Fixation of the anterior sucker initiates a wave of excitation over the longitudinal muscles.

(iii) The passage of waves of muscular contraction is independent of segmental reflexes.

(iv) In the absence of suckers, ambulation only occurs when the ventral surface of the body is in contact with the substratum.

(v) The frequency of the ambulatory rhythm depends upon the rate at which the longitudinal muscles are allowed to shorten isotonically. During isometric contraction the rhythm is abolished—and local stretch reflexes are active.

(vi) Ambulation has never been observed in the absence of all recurrent peripheral stimulation and there is, at present, no direct evidence to indicate the existence of an ambulatory rhythm inherent in the central nervous system.

For the time being the balance of the evidence is in favour of the view that the ambulatory rhythm is determined by recurrent peripheral reflexes—usually those associated with the suckers.

MECHANISM OF SWIMMING IN THE LEECH

If a leech is placed in a bowl of water and is prevented (e.g. by circulation of the water) from attaching either sucker to a solid object—the animal responds by swimming actively through the water until the anterior end is allowed to come into contact with the surface of the bowl; as soon as the anterior sucker attaches itself, the animal ceases to swim. Swimming is effected by the propagation of bilateral waves of contraction along the relaxed longitudinal muscles; the dorso-ventral muscles being maintained in a state of tonic contraction. The body is, thus, flattened dorso-ventrally and exhibits sinusoidal flexions comparable to those of eel-like fishes.

The ease with which a leech can be excited to swim (unlike the degree of stimulation required to elicit terrestrial locomotion), does not depend upon the integrity of the suboesophageal ganglion, for decapitated leeches swim actively. This phenomenon is in no way due to the effect of injury associated with decapitation for it persists for many days. If decapitated and intact leeches are induced to swim and then left undisturbed, the decapitated animals nearly always swim for longer periods than do the intact individuals. This phenomenon was interpreted by Bethe (1898), as evidence that the higher centres of the nervous system (supra and suboesophageal ganglia) exercised an inhibitory influence on the activity of the nerve cord. This interpretation seems doubtful. Throughout the whole course of these experiments, it became abundantly evident that when an intact, or decapitated leech was isolated from all external tactile stimulation it almost invariably
exhibited long sustained swimming movements if subjected to transient stimulation. A normal leech, freely suspended in water, only ceases to swim when its anterior sucker comes into effective contact with a solid object, and since removal of the suboesophageal ganglion liberates the nerve cord from all exteroceptive stimuli arising in or near the anterior sucker it is not surprising that the decapitated preparation should exhibit prolonged periods of spontaneous swimming. This conclusion is strongly supported by the fact that persistent swimming is also characteristic of preparations in which the sub- and supra-oesophageal ganglia remain intact but in which the anterior sucker has been denervated.

We may conclude that two distinct patterns of neuromuscular rhythm exist in a leech: (i) the rapid swimming rhythm which can only express itself in the absence
of tactile stimulation from the ventral surface of the body or from the suckers, (ii) the slow ambulatory rhythm which can only express itself if these patterns of tactile stimulation are present.

The persistent swimming of a decapitated-preparation can be rapidly abolished by gentle diffuse touch applied to the ventral surface of the animal (see Fig. 12), the rhythm sometimes emerging again spontaneously as soon as ventral contact is removed, and always in response to gentle mechanical stimuli applied to the dorsal surface. Touching the dorsal side of the preparation not only fails to inhibit the rhythm but may lead to an increase in the amplitude of the movements (Fig. 12) or, occasionally, to an accelerated rhythm. These responses are probably of functional significance; persistent and gentle stimulation of the ventral surface of a normal swimming leech will only occur where the animal comes into natural contact with the ground; whereas, dorsal stimulation may not infrequently be produced by contact with surfaces unsuitable for attachment.
Gentle dorsal stimulation accentuates the swimming rhythm, strong dorsal stimulation (e.g. by pinching) completely abolishes the rhythm and results in contraction of the longitudinal muscles. Such contraction may persist for some-time after the mechanical stimulus has ceased, but it can readily be brought to an end by gently stroking the ventral surface of the body with a fine brush (Fig. 13).

The reflexes displayed by a decapitated leech in water form a remarkable analogy to those exhibited by the spinal dogfish (Gray & Sand, 1936) although the effect of ventral and dorsal stimulation are reversed. In the dogfish, gentle pressure applied to the body accelerates the spinal swimming rhythm, stronger pressure inhibits the rhythm.

The propagation of the waves of contraction which pass over the longitudinal muscles of a swimming leech, like that of fishes (Gray, 1936 a; Gray & Sand, 1936), does not depend on the complete integrity of the muscles themselves. It is possible to remove the whole of the skin and musculature from at least three segments of a leech (leaving the anterior and posterior ends of the body united by the exposed nerve cord only) and to pin the preparation firmly to a cork. Such a preparation exhibits complete co-ordination of swimming movements (see Fig. 14). Further, it is possible to sever all the muscles of the body by a circular cut (keeping the nerve cord intact) and, having rotated one half of the body through 180°, to secure the two halves of the musculature by ligatures. After such treatment, co-ordination still occurs and the wave of contraction continues to pass along its original morphological course. These facts show that the propagation of the swimming waves is not determined by the propagation of mechanical stimuli but by the nerve cord itself. On the other hand, the rhythm is not entirely independent of extraneous mechanical conditions for it is definitely slowed by increase in the
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viscosity of the medium (Table I) and by slight tension applied longitudinally to the body (Table II).

The precise nature of the swimming rhythm is obscure, but it seems significant that all attempts to detect a rhythm of electrical activity in the nerve cord of a leech

Table I

<table>
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<tr>
<th>Preparation</th>
<th>Medium</th>
<th>Temperature °C</th>
<th>Relative viscosity</th>
<th>No. of cycles per min.</th>
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Table II

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<th>Average no. of swimming cycles per min.</th>
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<tr>
<td>+ 0.5 cm.</td>
<td>78</td>
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<tr>
<td>+ 1.0 cm.</td>
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<tr>
<td>+ 1.5 cm.</td>
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<td>+ 2.0 cm.</td>
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</table>

after removal of the suboesophageal ganglion and severance of all the peripheral nerves have failed. The following experiment suggests that the integrity of a certain amount of the musculature is required for the maintenance of the rhythm. The suboesophageal ganglion of a leech was removed—and the nerve cord exposed for about 8–10 segmental ganglia; one segmental nerve from the 4th or 5th ganglion was prepared for electrical recording—the remainder all being severed. The preparation was pinned to a cork and the posterior end allowed to hang freely in Ringer’s solution. When the hind end of the preparation exhibited swimming movements, a well-defined rhythm of nervous impulses was detectable in the segmental nerve (Fig. 15). As soon as the nerve cord was cut at the anterior end of the intact half of the preparation, all rhythm in the segmental nerve ceased, although active swimming movements in the hind end continued uninterruptedly. In this condition, the nerve cord of the preparation consists of two regions: (i) an anterior half which is isolated from all peripheral sensory fields, (ii) a posterior
half which retains its normal sensory connexion. In some preparations of this type it was found that when one of the ganglia of the anterior half was touched or gently pressed with a fine brush, outbursts of electrical activity could be detected in the segmental nerves, but these outbursts showed no evidence of a true rhythm. On the other hand, when one of the ganglia of the posterior half of the preparation was subjected to similar stimulation, the swimming movements were markedly accelerated and their amplitude increased for some time after the cessation of the stimulus. It is, therefore, difficult to avoid the conclusion that the rhythmical

activity of the segmental nerves depends on the general level of excitation of the nerve cord, and this, in the absence of any extrinsic source of stimulation can only be maintained by the proprioceptive activity of a definite amount of the longitudinal musculature; so long as this musculature is active, the whole cord displays its characteristic rhythmicity. This shows clearly that the result of local proprioceptive activity is not restricted to the segment in which it occurs.

The nature of the electrical rhythm in the segmental nerves of a swimming leech exhibits features of some interest. It will be seen from Fig. 15 that bursts of
large nerve impulses occur in the posterior nerves at a frequency identical with that of the mechanical rhythm of posteriorly situated segments. In Fig. 15 each burst consists of 12–18 impulses and between successive bursts the nerve is inactive. In different records, considerable variation was found in the number of large impulses constituting each burst, and in a number of instances (e.g. Fig. 16) bursts of smaller impulses occurred between successive groups of the larger impulses; presumably the large and small impulses were recorded from separate groups of fibres supplying antagonistic (ventral and dorsal) groups of longitudinal muscle fibres.

Fig. 16. Continuous record of the activity of an anterior segmental nerve of a decapitated leech whose intact posterior region was exhibiting a mechanical rhythm at an approximate frequency of one cycle in 0.7 sec. Note the groups of smaller impulses alternating with those of the larger impulses. The time is shown in \( \frac{1}{10} \) sec.

Regularly spaced bursts of impulses of the above type have never been observed in a nerve which emerges from a region of the nerve cord which is completely isolated from rhythmically active muscles. If, however, such an isolated cord be allowed to become moribund, marked rhythmicity frequently emerges. Such rhythms have, however, no resemblance to that characteristic of the swimming preparation; they are of a variable and usually prolonged nature—sometimes lasting for 20 sec.; their frequency is very much less than that of the swimming rhythm.
DISCUSSION

It is clear that the nervous system of the leech can exhibit two distinct types of locomotory rhythm one of which emerges whenever the body is deprived of all extrinsic tactile stimulation to its ventral surface or suckers—the other when such tactile stimulation is present. In the first case the animal swims, in the second case it walks.

So far as is known, the nature of a swimming rhythm has only been investigated in one other type of animal, viz. fish. v. Hoist (1935) has shown that the whole of the dorsal nerve roots can be severed from the nerve cord of a tench without destroying the ability to swim, thereby showing that the rhythm must be of central origin comparable to the respiratory rhythm described by Adrian & Buytendijk (1931) in the medulla of the goldfish. In this respect there appears to be a difference between the central nervous system of the fish and that of the leech since all attempts to detect a rhythm in the isolated nervous system of the leech have failed. On the other hand, the swimming rhythm of the leech has certain features which recall that of the dogfish (Gray & Sand, 1936): (i) it is maintained for prolonged periods by a preparation which is isolated from the influence of the higher centres of the nervous system; (ii) it is independent of the removal of a substantial amount of the active musculature; (iii) it is readily susceptible to inhibition and acceleration by suitable tactile stimulation of relatively low intensity; (iv) it is inhibited by strong tactile stimulation. In contrast to the leech and the dogfish, it must be remembered that other types of spinal preparations (e.g. the eel) usually only exhibit rhythmic movements so long as an extrinsic source of stimulation is available (Gray, 1936 a). Only one hypothesis appears to cover all these observations, viz. a swimming rhythm emerges if the general level of excitability of the nerve cord is maintained at an adequate level. In the leech this level appears to be maintainable by the proprioceptor sense organs in the skin and muscles; in the eel the level of activity from such sources is inadequate and must be supplemented by tactile stimuli or by electrical stimuli applied to the nerve cord. In the dogfish neither tactile nor artificial stimulation is necessary. If this be correct, the roles of the proprioceptors in the leech are not necessarily those of pace-makers or time-markers for each phase of the muscular movement but to maintain the level of excitability of the cord as a whole; at the same time, it is possible that the proprioceptors of the leech also act as pace makers.

This conception of the nature of the swimming rhythm suggests that it is somewhat similar to the stepping rhythm of the mammal. Sherrington (1931) and Graham-Brown (1912) showed that stepping can be produced in completely deafferented muscles, so long as an adequate source of stimulation is available to the nerve cord. On the other hand, the ambulatory rhythm of the leech, unlike that of the mammal, only emerges against a background of well-defined exteroceptive stimulation. The absence of any inherent electrical rhythm in the isolated nerve cord of the leech and the conclusions to be drawn from a study of the effects of exteroceptive stimulation upon the mechanical ambulatory rhythm leave little doubt that
The Mechanism of Locomotion in the Leech

The concept of a closed chain of peripheral reflexes provides the simplest hypothesis which will cover the facts. Before concluding that the nervous mechanism of ambulation in the leech is fundamentally different from that of the mammal it must be remembered that when the limbs of a spinal dog are hanging freely in air the conditions are more comparable to those which elicit a swimming response in the intact animal than to those which exist during terrestrial locomotion. If it is legitimate to regard the "stepping" reflex of mammals as a "swimming" reflex, it is conceivable that a true ambulatory rhythm in the limbs of such animals may depend upon peripheral reflexes to a greater extent than is commonly believed to be the case.

SUMMARY

1. The type of locomotory activity which can be displayed by an intact leech depends upon the presence or absence of particular patterns of exteroceptive stimulation reaching the nerve cord via the suckers or ventral surface of the body. If such peripheral patterns be present, the animal can walk but cannot swim, if such patterns be absent the animal can swim but cannot walk.

2. The frequency of the ambulatory rhythm is normally determined by the rhythmical adhesion of the suckers. Adhesion can only occur when a sucker is in the protruded position.

3. The protrusion of the suckers is dependent upon the isotonic contraction of the body muscles. The posterior sucker is not protruded during isometric contraction of the longitudinal muscles. It invariably occurs when these muscles contract isotonically. Fixation of the posterior sucker induces active relaxation of the longitudinal muscles. Protrusion of the anterior sucker is dependent upon contraction of the circular muscles.

4. If the isotonic contraction of the longitudinal muscles is impeded by an external resistance the ambulatory rhythm is reduced in frequency; in extreme cases, the rhythm ceases and is replaced by a very powerful and prolonged contraction of the longitudinal muscles. These phenomena are attributed to the activity of stretch receptors whose presence is inferred from the electrical activity set up in the sensory and motor fibres of the segmental nerves. It is suggested that the normal ambulatory rhythm is best regarded as a closed chain of peripheral reflexes.

5. The transmission of the waves of longitudinal and circular contraction along the body, during ambulation, is shown to be independent of the integrity of considerable regions of the somatic musculature.

6. Decapitated leeches only exhibit an ambulatory rhythm in response to strong stimulation. The loss of muscular tone characteristic of an animal deprived of the suboesophageal ganglion is associated with a marked reduction in the arhythmical electrical discharges detectable in the segmental nerves of an isolated nervous system subsequent to removal of the suboesophageal ganglion.

7. Both intact and decapitated preparations swim readily when released from all tactile stimuli. The frequency of the swimming rhythm is affected by changes in
the viscosity of the medium and by tension applied longitudinally to the body. The rhythm can be accelerated or suppressed by appropriate exteroceptive stimulation.

8. The whole nerve cord exhibits a marked electrical rhythm so long as it is in organic connexion with a limited region of the body displaying mechanical swimming movements; the frequencies of the mechanical and electrical rhythms are identical.

9. No electrical rhythm, comparable to that which might be expected to be characteristic of ambulation or swimming, has been detected in the isolated central nervous system.

REFERENCES