

STUDIES IN ANIMAL LOCOMOTION

IV. THE NEUROMUSCULAR MECHANISM OF SWIMMING IN THE EEL

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(With Three Plates and One Text-figure)

DURING the normal progression of a fish through water each segment of the body executes a series of transverse movements whose phase is slightly behind that of the segment lying anteriorly to itself, whilst the muscles on the two sides of each segment differ in phase from each other by one-half of a complete muscular cycle. So long as these conditions are fulfilled, regular waves of contraction pass alternately down each side of the body and tail of the fish. On the form, velocity and frequency of these waves depends the rate of progression of the animal through still water (Gray, 1933*a*). It is obvious that the form of the waves depends, in turn, on the degree of contraction taking place in each segment and on the phase difference which exists between successive segments. The present paper deals with the locomotory rhythm of the eel (*Anguilla vulgaris*), a form well suited to the purpose in view of its clearly defined muscular movements and of the remarkable viability of the fish. So far as is known, the mechanism controlling the co-ordination of fish movement has not been subjected to extensive experimental analysis, but, during the progress of the present work, important contributions have been made by von Holst (1934, 1935), to whose results reference is made in the text.

When an intact eel is swimming freely in water the rhythmical contraction of the segmental muscles might be determined by nervous impulses of either peripheral or central origin. Peripheral impulses might arise in the skin wherever it is mechanically stretched by contralateral muscular contraction or where it is subjected to pressure against the surrounding water. Similarly, proprioceptor impulses might arise in muscles or in connective tissue where these are subjected to tension by muscular contraction or passive stretch. Ten Cate and ten Cate-Kazejewa (1933) have recently reported that if the whole of the somatic musculature be removed in the neighbourhood of the pectoral fins of the dogfish and the spinal cord cut, the fish can still swim. Ten Cate and ten Cate-Kazejewa conclude that the source of the excitation of the musculature lying posteriorly to the operation lies in the mechanical stretch induced in these muscles by the skin which connects them to the muscles lying anterior to the operation. If this view be correct the rhythm of

swimming may be determined by a chain of mechanically excited reflexes comparable to Friedländer's (1894) conception of the locomotory mechanism of the earthworm, and to Philippon's (1905) conception of the stepping reflex in spinal mammals.

CONDUCTION OF RHYTHM BY SPINAL CORD

If the propagation of a wave of contraction along the body of an eel were determined by the propagation of a particular set of mechanical conditions capable of exciting successive neuromuscular units then the propagation of a wave of contraction should cease when it is no longer possible for the requisite mechanical stimulus to propagate itself. That the skin of the eel plays no mechanical or physiological role in the propagation of muscular contractions along the body of the fish can readily be shown by removing the whole of the skin under urethane. As soon as the effect of the anaesthetic has worn off, the fish swims normally and with undiminished vigour. It may be concluded that although nervous impulses arising in the skin may modify the activity of the segmental muscles they play no essential role in the act of swimming. If impulses arising in the muscles or associated connective tissue were a necessary part of the neuromuscular mechanism, the removal of a group of muscles from both sides of the animal should abolish the rhythmical response of all the muscles lying posteriorly to the demusculated region. Such an effect is not observed in the eel, since the removal of all the muscles over a region of 5 in. (the total length of the fish being 20 in.) failed to abolish or substantially to modify the activity of the posterior part of the body. In observing the behaviour of such a fish it is necessary to distinguish carefully between the transmission of an active muscular rhythm and the transmission of a mechanical wave over an otherwise inert region of the body. The following experiment appears to eliminate any confusion introduced by purely mechanical movements. A fish was anaesthetised and the whole of the muscles were removed for a length of 3 in. from both sides of the animal immediately behind the anus, leaving two regions of the body connected only by the vertebral column. Wooden splints were then attached by wire bands to each side of the vertebral column in such a way as to hold the latter quite rigid and to fill the space normally occupied by the segmental muscles. As soon as the effect of the anaesthetic had worn off the fish began to swim normally, and by fixing the splints in a rigid clamp or by pressing the splints firmly to the bottom of a tank, it was possible to observe the presence or absence of movements in the posterior region of the body. Whenever the anterior end of the body exhibited active swimming movements the latter were unmistakably propagated over the posterior region also (see Pl. I, fig. 1). Only feeble movements of the anterior end of the body failed to pass over the demusculated region. In view of these facts it is difficult to avoid the conclusion that the transmission of regular rhythmical waves of muscular contraction can occur in the entire absence of any peripheral impulses arising in the somatic muscles, and that the transmission is effected by the spinal cord only. These results agree with those recently obtained by von Holst (1935), who immobilised the muscles by section of the spinal nerves or by the insertion of a rigid rod beneath the skin. It is conceivable that

proprioceptor impulses entering the cord from active or stretched muscles may reinforce impulses of central origin, but for this there is no direct evidence.

ELICITATION OF SWIMMING BY STIMULATION OF SPINAL CORD

Numerous workers have shown that the removal of all parts of the brain of the dogfish lying in front of the medulla does not abolish normal locomotory rhythm. This conclusion has been verified in the case of the eel, so that the source of rhythmical activity must be sought in the medulla and spinal cord. For an investigation of the role of these two regions of the central nervous system two types of preparation have been used: (i) the freshly decapitated fish, (ii) the chronic spinal fish.

It has been known for many years that a decapitated eel may exhibit active movements. If the head be removed by a quick cut immediately behind the medulla, the trunk may do one of three things: (i) remain quite inert, (ii) swim forward gently but normally for a few seconds, or (iii) exhibit a rhythmical series of waves of large amplitude starting at the tail and moving anteriorly along the body, the preparation thus exhibiting a figure of eight movement which is equivalent to backward swimming with waves of abnormally large amplitude. Movements of any kind usually last for a brief period only, after which the preparation becomes inert although certain well-defined reflexes can be elicited for at least an hour after decapitation. These reflexes will be considered later, but for the moment it is of interest to note that the decapitated preparation can be induced to swim by the application of appropriate stimuli to the severed end of the spinal cord.

As soon as any initial spontaneous movements have subsided, the anterior end of the vertebral column can be freed from muscles for a length of about 1 in. This usually provokes some localised reflex contraction of short duration, after which the abdominal wall can be pierced by a wire hook and the preparation suspended in water. The negative electrode from a stimulator capable of yielding rhythmical condenser discharges (approximately 50 per second) of variable intensity is then placed in the tank containing the fish, whilst two positive needle electrodes are placed one on each side of the spinal cord. No response occurs until the intensity of the shocks reaches a critical value; when this point is reached, regular forward swimming movements begin and are continued in favourable preparations for a considerable time.¹ The muscular waves travel from the anterior to the posterior end of the preparation, and, as in normal swimming, alternate on the two sides of the body. If one or other electrode be removed these movements cease but are resumed as soon as the second electrode is replaced. It is not easy to locate the precise points of stimulation, and for many purposes it is convenient to work with a simpler preparation wherein the two needle electrodes are replaced by a band of copper wire tightly wound round the exposed portion of the vertebral column. The frequency of the rhythmical contractions evoked by stimulation of the cord is of the order of 1 per second, a much lower frequency than that of the applied stimuli. If the strength of the stimuli is increased slightly beyond that required to elicit the above

¹ It has recently been found that a well defined rhythm can also be elicited by stimulation of the posterior end of the spinal cord.

response, the preparation becomes inactive, and if the strength of the stimulus be still further increased a new rhythmical response occurs wherein waves of contraction start at the tip of the tail (or at the posterior end of the animal if the tip of the tail has been removed) and pass forward. This response is of essentially the same type as that seen when a normal eel is swimming backward and as the figure of eight motion sometimes exhibited by the newly decapitated fish; within limits, the higher the intensity of the stimulus the greater is the amplitude of the movements. If separate electrodes are used for the stimulation of the two sides of the cord and one of the electrodes be removed when the reversed swimming reaction is being elicited, the posterior end of the body remains contracted to one side, although it may show an incomplete rhythm of relaxation; replacement of the electrode reinitiates rhythmical movements of the normal type. By using one electrode only it can be seen that an increase in the strength of the stimulus causes a contraction to pass further towards the anterior end of the preparation.

ELICITATION OF SWIMMING BY PERIPHERAL STIMULATION

The above observations appear to suggest that the normal locomotory rhythm involves specific activity of the medulla although the stream of impulses being supplied by the medulla is not itself of a rhythmical nature. It is important to note, however, that it is possible to elicit rhythmical movements from a decapitate or spinal preparation by purely peripheral stimulation. If the tip of the caudal fin of a decapitate preparation be gently seized by a pair of forceps the tail is actively withdrawn, but if such withdrawal from the source of stimulation be prevented by adequate pressure of the forceps, the preparation shows marked rhythmical and propulsive movements, which in some cases may persist for a considerable period. This response will be considered in greater detail when the properties of the chronic spinal fish are described.

For obvious reasons the decapitate fish is not an entirely suitable preparation in which to study the effect of the removal of the brain on the locomotory rhythm. A more suitable preparation is provided by the spinally transected fish. In accordance with the observations of other authors, complete transection of the brain in front of the medulla caused no obvious disturbance of locomotion; if the medulla itself be cut, locomotion ceases, but the respiratory movements also cease and the fish do not survive the operation for more than 2 days.¹ In the following experiments the nerve cord was transected immediately behind the medulla or between the 1st and 4th vertebrae. In all cases the fish survived the operation for many weeks. It may be mentioned that when the cord is severed at these high levels there is no danger of confusing active movements of the spinal fish with mechanical movements induced by the region of the body in communication with the medulla.

In shallow water a spinal eel lies motionless on its side with the body straight or curved to one or other side; the undulatory curvature, typical of the intact fish, no longer persists. In no case have active and well-defined spontaneous movements

¹ During this period the fish did not show any signs of spontaneous locomotory movements.

been observed, although in some cases feeble rhythmical contractions (approximating to but not absolutely of the same frequency as the respiratory rhythm) may be present. These contractions do not involve the whole of the body but are frequently maintained for prolonged periods in preparations exhibiting the phenomenon (see von Holst, 1934). The typical absence of spontaneous movements in these spinal fish is in contrast to the observations of Bickel (1897)¹ and it is of interest to note that the spinal preparation of the Conger appears to show spontaneous activity much more readily.

Although the spinal eel does not normally exhibit any sign of spontaneous activity, well-marked rhythmical movements can readily be elicited by mechanical stimulation of the tip of the tail. As in the case of the intact or decapitated fish, gentle pressure applied to the tip of the tail causes a rapid withdrawal response (Pl. I, fig. 2). If, however, the stimulation is made continuous by the attachment of a small clip, well-defined rhythmical movements are elicited which are capable of propelling the fish through the water (Pl. II, fig. 3). In some preparations the rhythm is sustained for some time after the removal of the clip, in others the rhythm may subside whilst the clip is still in position. These observations are of importance, for they show that the level of spinal excitation necessary to produce a swimming response can be provided by peripheral stimulation as well as by stimuli applied directly to the cord by electrical stimulation (p. 172).

By means of cinematograph records it is possible to analyse the rhythmical movements elicited by seizing the tail of the spinal fish. These records are of interest, for they show clearly that there are two phases in the response. The first phase of the response is the development of undulatory tone whereby the posterior end of the fish is thrown into a wave form (Pl. I, fig. 2). If the stimulus be removed at this stage the wave form is gradually lost and the body resumes its normal form; there is no evidence that the waves are transmitted along the body. If, however, the stimulus be maintained, the waves begin to move towards the posterior end of the body and new waves are formed in front of the original ones. This phenomenon can be seen in Pl. II, fig. 4. The simplest interpretation of these facts appears to be that if a region on one side of the body near the hind end of the fish is reflexly stimulated to contract it induces a contraction on the other side of the body over a region lying anteriorly to the original area of contraction thus throwing the body into a wave-like form. If the stimulus is maintained these regions of contraction pass posteriorly backwards, each inducing contralaterally and anteriorly situated contractions as they move. Such an interpretation obviously leads to a definite picture of the normal swimming mechanism (see p. 178), and at present it must be regarded as extremely tentative although some confirmation is forthcoming from a study of certain tactile reflexes well exhibited by the spinal eel.

RESPONSE OF SPINAL FISH TO UNILATERAL TACTILE STIMULATION

If the surface of a spinal eel be gently touched by a blunt needle or by a camel's hair brush, a localised contraction occurs at the point stimulated, and the surface of

¹ Bickel described active movements in spinal preparations two months after the operation; there is evidence which suggests that such movements were dependent on spinal regeneration.

the body is removed from contact with the needle. If, before this contraction has subsided, contact with the needle or brush be again established at the same point, the degree of contraction is increased, and is now accompanied by a more extensive contraction on the contralateral side of the body anteriorly to the point of contact (Pl. III, fig. 5) (see also Tracy (1926); von Holst (1934, Fig. 1)). This secondary contraction develops slowly and dies away slowly after the source of the stimulus is removed. Both phases of the reflex appear to be of functional significance, for in both cases the surface of the body tends to be removed from the source of irritation. For the present purpose, however, the significant feature of the reflex is the development of the contralateral contraction which follows an ipsilateral contraction which is itself the reflex response to tactile stimulation. Under normal circumstances the response is of a static postural type, but if the stimulus is persistent and relatively intense, as is the case when a thin loop of wire is attached to the body,¹ the spinal eel responds by swimming actively forwards (Pl. II, fig. 3). The initiation of swimming in the spinal eel in response to persistent exteroceptive stimuli appears to resolve itself into two phases: firstly, the development of a state of undulatory tone which throws the body into a wave-like form, and secondly, the transmission of this state of tone posteriorly over the body of the animal.

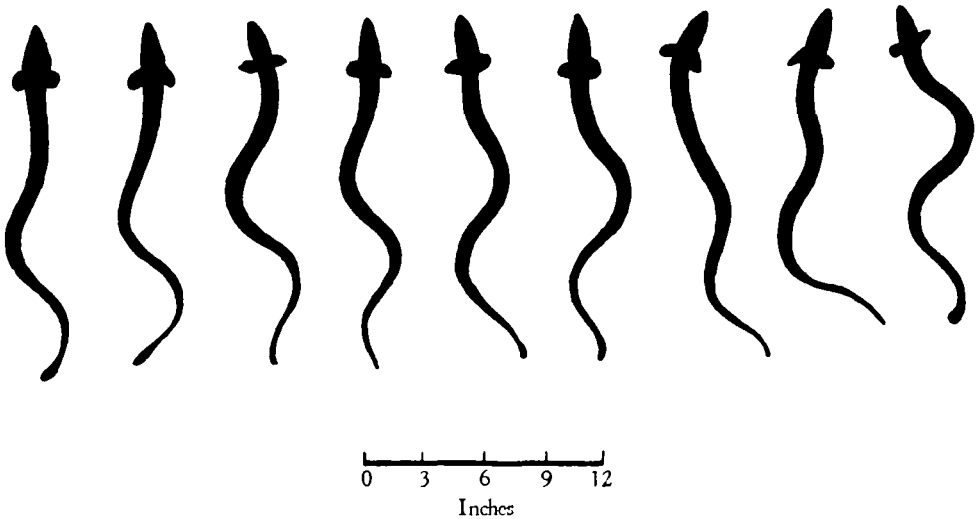
UNDULATORY POSTURE

It may be recalled that an intact eel, when at rest, seldom exhibits uniform tone on the two sides of the body. The fish, almost invariably, lies with the body curved to one side or curved into a wave-like form. The latter state of undulatory tone is particularly characteristic of young specimens (see Gray, 1933*a*); it is also well marked in older specimens after any operation on the central nervous system which has not involved complete section of the spinal cord behind the medulla. In decerebrated animals, for example, the increase of undulatory tone is very noticeable, and persists for several days (Text-fig. 1). The interest of this state of accentuated postural tone lies in the observation that when such animals swim forwards the waves already present move backwards over the body of the animal; when the animal swims backwards the waves move forwards (Pl. III, fig. 6). Since a wave of contraction passing along the body of a fish can stop in any position (just as a tetrapod limb can be fixed at any phase of its movement), it is clear that the passage of a locomotory wave over the body of an eel is not the expression of a simple series of excitatory stimuli passing down the spinal cord from the medulla and activating the muscles as it passes; such a mechanism could hardly produce a stationary wave. For this reason the scheme suggested by Coghill (1929) for *Amblystoma* seems inapplicable to the eel. A more satisfactory analysis of the activity of the fish's body might be based on the conception of a definite pattern of posture capable of being transmitted along the body. If the level of postural activity at any one point on the body is upset, definite and co-ordinated changes appear to be induced at other levels and on both sides of the body.

¹ The response to a stimulus of this type is not dependent on bilateral stimulation since it remains after denervation of the skin and muscles beneath one side of the loop.

HEMISECTION OF THE SPINAL CORD

Although complete transection of the spinal cord behind the medulla typically abolishes all spontaneous movements in the eel, this effect is absent if the cord is cut on one side only. A hemisected preparation exhibits, at first, feeble but definite swimming movements in which the contractions appear to be somewhat greater on the intact side; apart from the weakness of the movements, the most distinctive feature of such fish is an inability to turn towards the operated side. This suggests that the fish is unable to initiate a wave down the operated side (see Gray, 1933*b*), although a wave can be induced in this side behind the point of operation by one which has arisen on the intact side. Within a few days of the operation, a hemisected fish shows a marked excess of tone on the intact side and swims in close circles towards



Text-fig. 1. Positions of rest of an individual eel after transection of the brain behind the optic lobes. Note the variation in the positions of the regions of maximum muscular contraction.

this side; the difference in tone gradually passes off until at the end of 3 weeks the swimming has become almost normal, although the fish is still unable to initiate a turning movement towards the injured side. Until it is known how far the injury to the cord is capable of undergoing regeneration, it is perhaps unwise to consider the theoretical implications of the effect of hemisection.

DISCUSSION

It is of interest to note that the locomotory rhythm of an eel shares certain fundamental properties with that of the limbs of the mammalia. Contrary to the views of Philippson (1905), it is now known that the stepping reflex of the mammals is determined by the spinal cord, for it persists after all afferent impulses from the limbs have been removed by section of the sensory nerves (Graham Brown, 1912*a*

and *b*; Sherrington, 1931). Neither the swimming rhythm of the eel nor the stepping rhythm of the cat are dependent on proprioceptor systems; how far such systems can modify the centrally controlled rhythms of the fish (as is probably the case in mammals) is at present unknown.

Our knowledge of the mechanism of the co-ordination of mammalian limb muscles is largely based on the effect of stimuli applied to specific spinal nerves under conditions in which it is possible to observe the response of individual muscles. In the case of the fish such a procedure seems impossible on account of the extreme difficulty of isolating the muscles and their individual nerve supply. We can, however, safely regard the right and left sides of the musculature of each segment as mutually antagonistic and in this sense comparable with the flexor and extensor groups of the tetrapod limb. If we accept this view, the elicitation of swimming in the decapitated eel by electrical stimulation of the surface of the nerve cord finds a remarkable parallel in the stepping reflex of the decapitated cat. In the latter case "an ipsilateral rhythm is obtainable by weak stigmatic unipolar faradisation of the cut transverse face of the spinal cord at a tiny area in the lateral column. It tends to be accompanied by feebler stepping of the opposite hindlimb in the same frequency but oppositely tuned. If both left and right spots on the cord are simultaneously stimulated, a subliminal stimulus on one side becomes effective on applying a subliminal stimulus to the other" (Sherrington, 1931). In the case of the mammal it seems clear that simultaneous stimulation of antagonistic muscles is an essential condition for the elicitation of a rhythmic stepping response. Using the tibialis anticus and the gastrocnemius (a flexor and extensor of the ankle) Graham Brown (1912*b*) showed that in the low spinal or decerebrate preparation a simple contralateral stimulus from the saphenous nerve gives a steadily maintained extensor contraction, while a simple ipsilateral stimulus gives maintained flexor contraction, whereas when both sides are stimulated a rhythmic response ensues. The similarity of the results obtained by unilateral and bilateral stimulation of the spinal cord of the eel to those obtained by Graham Brown strongly suggests that the resultant rhythms in the two cases are controlled by similar mechanisms, since the right and left halves of the musculature of each segment of the fish are to be regarded as mutually antagonistic.

It will be recalled that a definite rhythm can be elicited in the spinal eel by the application of peripheral stimuli, for example, by the application of a clip to the caudal fin. In an analogous way stepping can be elicited from a spinal cat by the application of a clip to the limb (Sherrington, 1931). In both fish and mammal the requisite level of spinal activity can be reached either by stimuli applied direct to the spinal cord (either artificially or through the higher centres of the brain) or by stimuli of purely peripheral origin.

The striking similarity between the locomotory rhythm of the fish and the mammal suggests the possibility of attributing to both movements the same intrinsic mechanism. The most effective picture of the stepping rhythm appears to be that of Graham Brown (1912*b*). "The cell bodies and processes of the efferent neurones of antagonistic muscles form centres which mutually inhibit each other.

A stimulus falling on one inhibits the other. If this inhibition reduce the activity of the second centre, that will inhibit the first less, and so the process will proceed till a limit is set to this 'progressive augmentation of excitation'. If a stimulus falls more or less equally on the two antagonistic centres, or if two equal stimuli fall on them, that which is most activated will have its excitability increased by progressive augmentation up to a point—the limit being set by a process of inhibitory fatigue. If this proceeds the balance will be swung in the other direction till this also reaches its limit, and the process sets in in the opposite direction again" (Graham Brown, 1912*b*). It does not seem possible to apply this scheme to the swimming mechanism of a fish without substantial modification. In the first place, it fails to explain the existence of standing "waves" of posture, and secondly it is difficult to see why the states of inhibitory fatigue in the successive segments of the body should be so harmoniously adjusted as to enable the rhythms of all segments to have exactly the same frequency as each other.

The formulation of a definite theory of the mechanism of swimming in the eel must await a detailed analysis of the properties of the spinal cord but the facts described in this paper suggest that there is a relationship between the mechanism which maintains a static state of undulatory posture in the resting fish and that which maintains the difference in phase between successive segments of the freely swimming fish. The response of the spinal eel to unilateral stimulation suggests that a localised unilateral state of spinal activity induces a secondary region of activity lying contralaterally and anteriorly to itself; it is possible that typical undulatory posture is determined in this way. A sustained swimming rhythm would result if one such localised unilateral state of spinal activity were propagated along the body for it would automatically induce the formation of an anterior contralateral wave travelling at the same speed as itself. If this interpretation of the facts be correct, the possibility of eliciting a self-generating rhythm would be dependent on the integrity of an adequate length of spinal cord. This has been found to be the case in the dogfish (Gray and Sand, 1936), but it must be remembered that more than one interpretation of the facts is possible.

Although the spinal cord contains all the properties necessary for the elicitation of a locomotory rhythm it is quite clear that any conception of the normal spontaneous swimming mechanism which leaves out of account the activity of the medulla must be inadequate. So far as can be judged by the effect of electrical stimulation of the exposed spinal cord, the inherent rhythm of the latter can, in the absence of persistent peripheral stimuli, only express itself when the cord is conditioned by a stream of appropriate impulses from the medulla, although the rhythm of these impulses has no direct relationship to that emerging from the cord. If both sides of the cord receive conditioning stimuli of approximately equal effectiveness, normal forward (or backward) swimming results; if, on the other hand, one side of the cord receives more effective stimuli than the other the response made by this side (when the spinal mechanism expresses itself) is greater than that of the other side, and the effect is that seen in the hemisected fish or in the intact fish executing a turning movement to one side (see Gray, 1933*b*).

SUMMARY

1. The integrity of the peripheral sensory nervous system, associated with the skin, muscles, and connective tissue, is not essential for the transmission of a locomotory rhythm along the body of the eel (*Anguilla vulgaris*). The rhythm is determined by the intrinsic activity of the spinal cord.

2. The spinal cord only expresses its inherent locomotory rhythm when conditioned by stimuli of either peripheral or central origin. In the latter case the requisite level of excitation is effected by the medulla.

3. The body of a decapitated eel can be induced to swim forward by the application of appropriate electrical stimuli to the cut end of the spinal cord; the frequency of the applied stimuli bears no direct relationship to that of the emergent muscular rhythm. If the intensity of the applied stimuli be increased the direction of the resultant muscular waves is reversed.

4. A localised unilateral tactile stimulus induces a primary contraction at the point of stimulation and a secondary contraction lying contralaterally and anteriorly to itself. If the primary stimulus is persistent and of adequate intensity the postural response is replaced by a well defined locomotory rhythm.

5. If the brain of an eel is transected in front of the medulla, the fish exhibits, when at rest, marked undulatory posture. It is suggested that there is a relationship between the mechanism maintaining this posture and that which maintains the phase difference between the successive segments of the actively moving fish.

6. The mechanisms which determine locomotion in an eel are strikingly similar to those which control a stepping rhythm in the limbs of mammals.

Most of the observations on which this paper is based have been recorded photographically and I have to acknowledge my indebtedness to Mr K. Williamson for his very valuable co-operation.

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EXPLANATION OF PLATES

The time interval between successive photographs is 0.1 sec.; the background of all the figures is divided into 3" squares

PLATE I

Fig. 1. Waves of contraction (indicated by the symbols •, ×, †) passing over the body of an eel from which the skin and all the muscles have been removed for a length of 3 in. and replaced by a splint. Except in the last photograph the fish is prevented from moving forwards by pressing the splint firmly on to the bottom of the tank.

Fig. 2. The response of a spinal eel (transected through the 2nd vertebra) to a momentary tactile stimulus applied to the tip of the tail. Note the acquisition of an undulatory posture.

PLATE II

Fig. 3. A spinal eel swimming forward in response to the stimulus provided by a small wire clip. Note that the waves of contraction (indicated by the symbols •, ×, †, □) pass posteriorly over the body and alternate on the two sides of the body. The position of the clip is approximately 3" from the tip of the tail and is marked by a white circle.

Fig. 4. The response of a spinal eel to a persistent stimulus applied to the tip of the tail. Note the formation and movement of active waves of contraction (indicated by the symbols •, ×, †).

PLATE III

Fig. 5. The response of a spinal eel to unilateral and localised tactile stimulus from a camel's hair brush. Note the development of a contraction near the site of stimulus and of a secondary contraction (indicated by the symbol •) lying anteriorly and contralaterally to the site of stimulation. The movements of the head are in no way associated with the stimulus applied to the body.

Fig. 6. An eel, after transection of the brain behind the optic lobes, swimming backwards in response to stimulation of the snout. Photographs 1 and 2 show the original position of rest. Note the subsequent movement of the original postural waves (indicated by the symbols • and ×) towards the anterior end of the body.

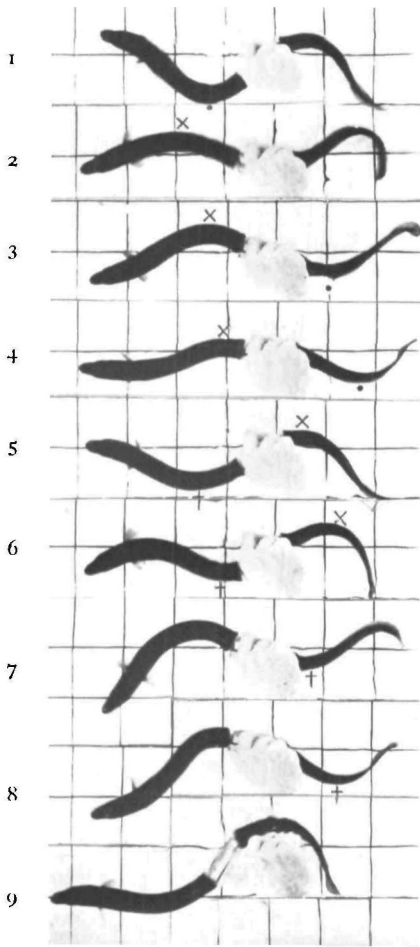


Fig. 1.

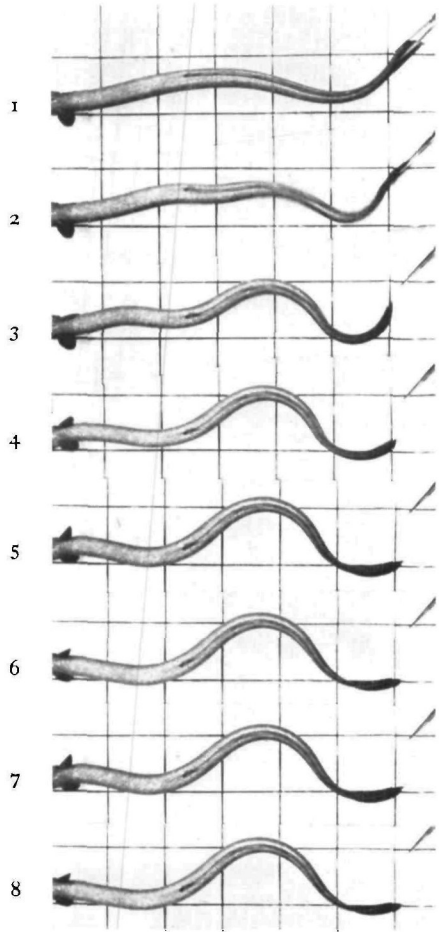


Fig. 2.

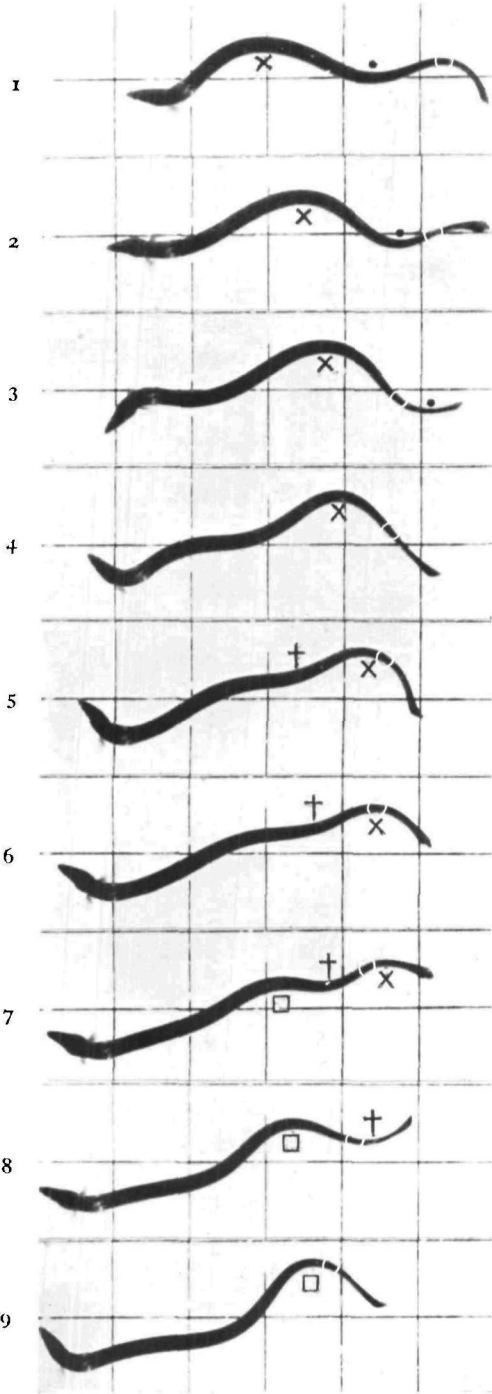


Fig. 3.

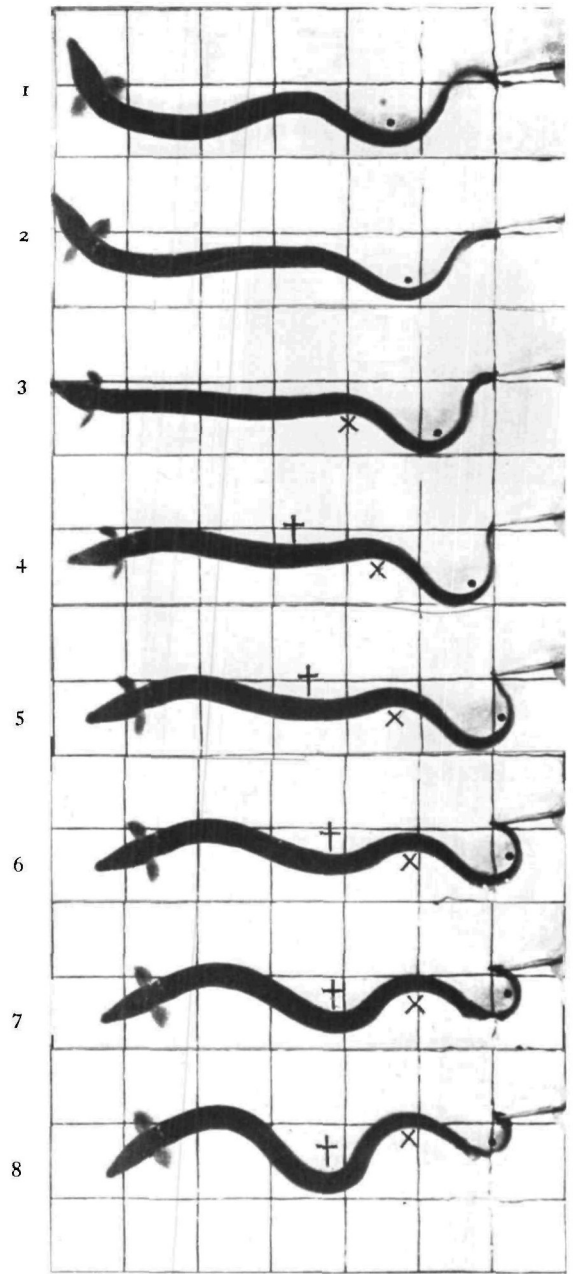


Fig. 4.

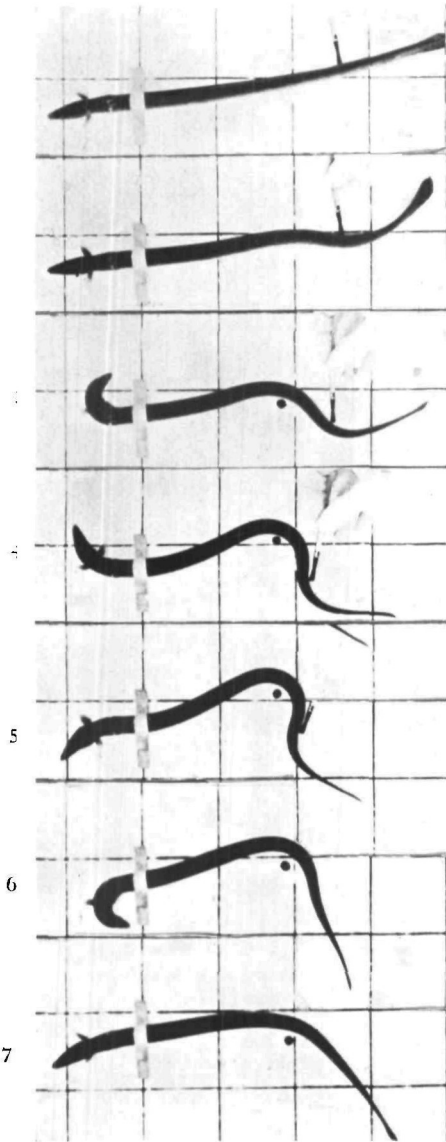


Fig. 5.

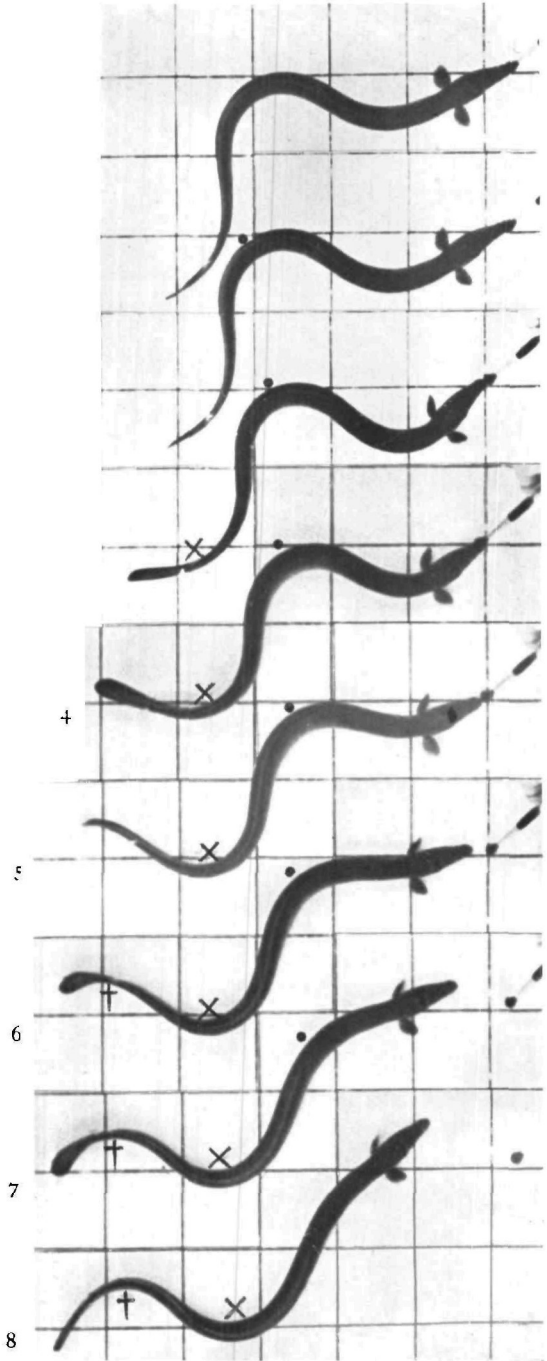


Fig. 6.