STUDIES IN ANIMAL LOCOMOTION

V. RESISTANCE REFLEXES IN THE EEL

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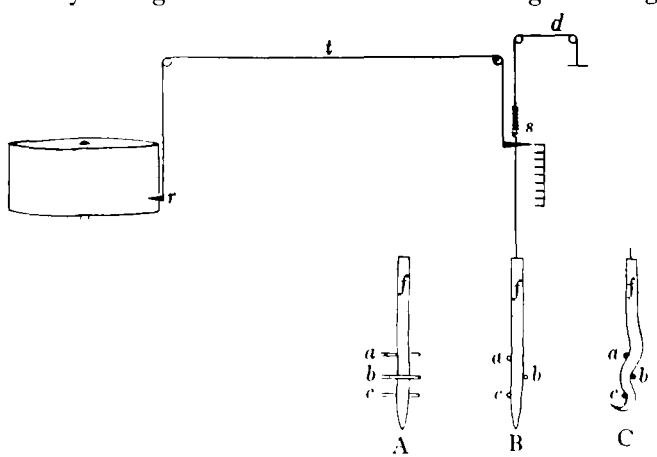
(With One Plate and Seven Text-figures)

In a previous paper (Gray, 1936) it has been shown that the rhythmical movements, characteristic of an eel swimming freely in water, are determined by the spinal cord and not upon impulses reaching the cord from receptors in the skin or muscles. It was also shown that a locomotory rhythm can be elicited from a spinal or decapitate preparation as a response to stimuli applied either to the spinal cord or to exteroceptive sense organs. In all these cases the experimental conditions were such that the muscles of the body were free to contract against the comparatively low resistance of the surrounding water. The present paper deals with the behaviour of the fish when the movements of the muscles are opposed by relatively strong external resistances.

If an intact eel be confined within a glass tube, the animal lies quietly with marked undulatory posture (Plate I, fig. 1 *a*)—the wave-length apparently depending on the diameter of the tube. If the snout of the fish be now stimulated gently by a brush, the eel moves backward in the tube by propagating waves of contraction towards the anterior end of the body as in normal reversed swimming: as soon as the tip of the tail comes into contact with the edge of the glass tube the pattern of response changes abruptly, for the tip of the tail ceases to initiate bilateral waves of contraction but curves sharply towards the side in contact with the glass (Plate I, fig. 1 *b*). The eel then begins to move rapidly out of the tube. It can be seen that the mechanism of withdrawal involves a wave of muscular contraction which passes anteriorly along the side of the body which had come in contact with the edge of the tube. Each region of the body becomes the site of active muscular contraction shortly before reaching the end of the tube. The maximum state of contraction is reached at, or soon after passing, the edge—after which the muscles relax and remain inactive until at least half of the body has emerged. Similar phenomena are observed when an intact eel moves forward out of the tube, but in this case the unilateral contraction is propagated posteriorly over the body. It would appear from observations of this type that if the muscles of an intact eel are constrained to contract against a fixed resistance the rhythmical bilateral type of contraction, characteristic of the freely moving fish, is replaced by a non-rhythmical response which is restricted to the side of the body in contact with the resistance.

The response to external resistance is independent of the higher nervous centres and of a background of rhythmical muscular activity, for it can be elicited from spinal or decapitated preparations. If an active spinal preparation[1] is placed in a tube the animal lies motionless unless the tip of the tail is allowed to come into contact with the edge of the tube; when this occurs, the tail contracts towards the edge of the tube and the eel moves rapidly out of the tube in precisely the same manner as does an intact fish (Plate I, fig. 2). The whole reflex appears to start by a response to tactile stimulation (see Gray, 1936), but its course depends upon the external restraint which is automatically set up when the muscles begin to contract against the relatively strong resistance of the walls and edge of the glass tube. If



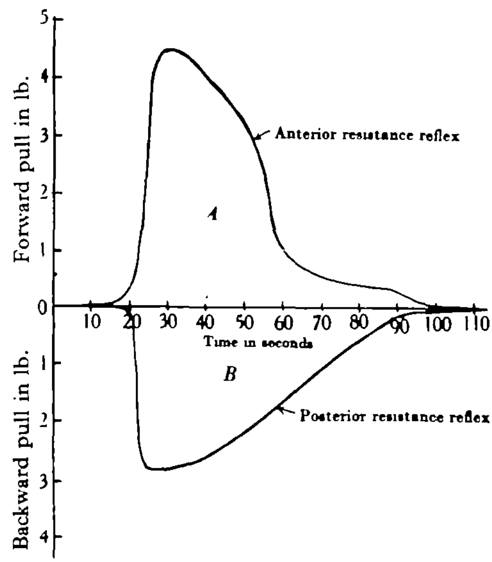
Text-fig. 1. Apparatus for recording resistance reflexes. *a*, *b*, *c*, adjustable pegs (mounted on a mechanical carriage). *f*, fish suspended from spring balance *s*, whose tension is recorded by the string *t* on the revolving drum (*r*). A, lateral view; B, dorsal or ventral view; C, dorsal view showing, diagrammatically, the form of the fish during the elicitation of a posterior resistance reflex. The spring balance is suspended by a cord *d*, the other end of which is attached to a fixed support. By moving the position of the support it is possible to increase or decrease the tension applied to the fish.

a spinal preparation has become fatigued no response occurs to tactile stimulation, but a typical resistance reflex can be elicited by pressing the tail against the edge of the tube by means of a finger or brush placed contralaterally and posteriorly to the edge of the tube (see Plate I, fig. 3). For the sake of convenience the co-ordinated responses elicited by pressure will be referred to as "resistance reflexes".

The ability of a spinal eel to escape backwards from a tube is much more easily demonstrated than is the corresponding movement in a forward direction, for the latter movement has only been observed when a small wire clip has been attached to the caudal fin. It will be shown later in this paper (see p. 187) that the application of such a clip causes complete inhibition of the mechanism which enables the eel to move backwards out of the tube.

[1] This is obtained by transecting the nerve cord at the level of the 2nd–5th vertebra and allowing the animal to remain undisturbed for several days.

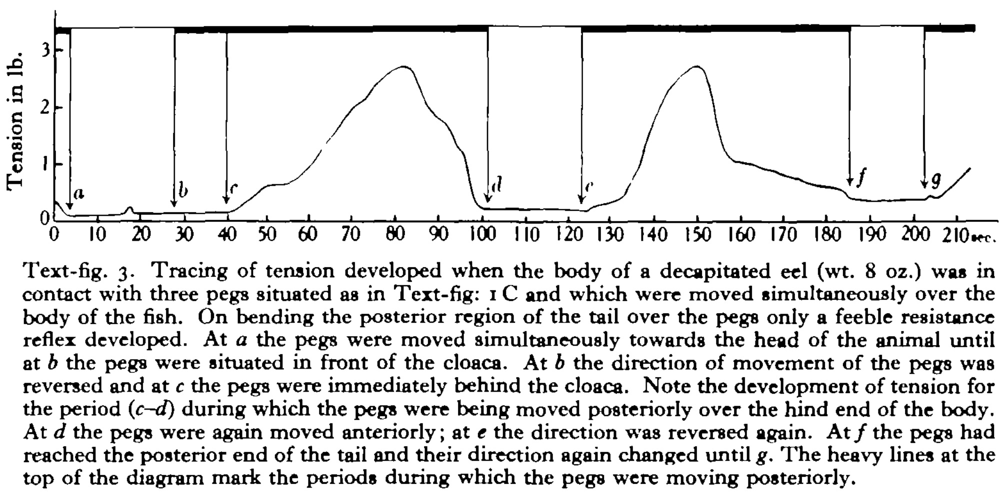
The general nature of the resistance reflexes is most conveniently investigated in freshly decapitated fish, for such preparations display the reflexes very clearly for at least one hour and by means of the apparatus shown in Text-fig. 1 it is possible to elicit resistance reflexes under reasonably controlled conditions. A freshly decapitated eel (*f*) is suspended from a spring balance (*s*) whose indicator is attached by a string (*t*) to a suitable marker (*r*) on a revolving drum. Tactile or pressure stimuli can be applied at any point on the body by means of the adjustable pegs *a*, *b* and *c*, each of which can be moved horizontally or vertically, whilst all three pegs are capable of simultaneous vertical movement. Resistance reflexes can readily be elicited by suspending the preparation in such a position that two of the pegs (3-4 in. apart) are in contact with one side of the body, whilst the third peg is in contact with the other side of the body at an intermediate level. The response of the eel to each of such contacts is essentially the same as that to the end of a glass tube. The response depends on two factors: (i) the sensitivity of the preparation, and (ii) the point of application of the pegs. If, by means of the pegs, tactile or pressure stimuli are applied laterally to the central regions of the body, no response is obtained even in preparations whose general excitability is high. If similar stimuli are applied to the front or hind end of the body an immediate and powerful response is given by fresh preparations. If the anterior end of the fish is attached to the balance, the pegs can be gently brought into contact with the lateral surface of the body immediately in front of the tip of the tail. Under these conditions, the tip of the tail bends sharply round the most posterior peg, and it is easy to see that the muscles at and in front of the points of contact with each of the three pegs are strongly contracted, whereas those on the contralateral side of the body are relaxed, the pattern of muscular contraction near each peg being precisely the same as that near the edge of the tube in Plate I. The pull exerted against the pegs is registered on the balance, and can be seen (Text-fig. 2) to be surprisingly powerful. If, instead of attaching the anterior end of the preparation to a spring balance, the fish is made to pull against a movable weight, the preparation moves actively backwards between the pegs, as soon as the resistance reflex develops. The general course of the reflex is shown by the lower curve in Text-fig. 2, but it must be remembered that, during both the rising and falling phases of tension, the eel is moving between the pegs for a distance equal to the change in the extension



Text-fig. 2. Tracings showing tensions developed by an anterior resistance reflex (*A*) and a posterior resistance reflex (*B*) of a decapitated eel weighing 7 oz.

of the spring of the balance, so that the whole curve does not give a simple picture of the reflex response of a single group of muscles. If, during the height of the reflex, the pegs are suddenly removed it can be observed that the contracted state of the musculature passes off rapidly and shows no tendency to propagate itself along the body of the animal. The propagation seen when the eel is free to move between the pegs or when a spinal eel is moving backwards out of the tube is the mechanical result of the contraction which occurs in the muscles lying ipsilaterally and anteriorly to the points of restraint; the contraction of these muscles draws the fish backwards over the pegs. Successively anterior regions of the body are, thereby, exposed to pressure, and a consequential "wave" of contraction passes towards the head.

Whereas pressure stimuli applied to the hind end of the body result in a backward pull by the somatic muscles, precisely similar stimuli applied to the anterior region of the body elicit an equally distinct forward pull. This can be demonstrated



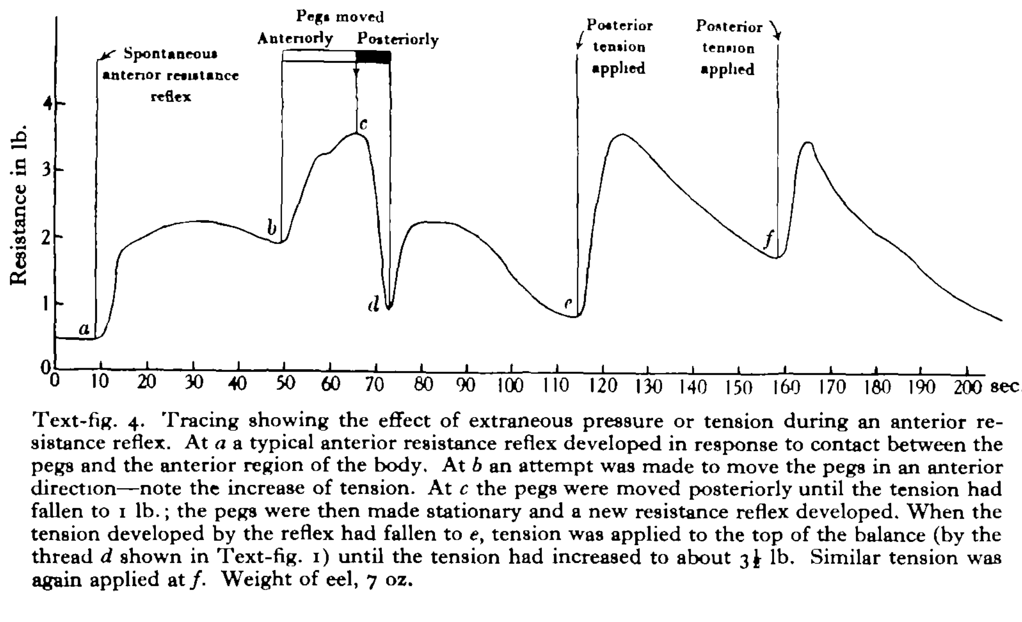
Text-fig. 3. Tracing of tension developed when the body of a decapitated eel (wt. 8 oz.) was in contact with three pegs situated as in Text-fig: 1 C and which were moved simultaneously over the body of the fish. On bending the posterior region of the tail over the pegs only a feeble resistance reflex developed. At *a* the pegs were moved simultaneously towards the head of the animal until at *b* the pegs were situated in front of the cloaca. At *b* the direction of movement of the pegs was reversed and at *c* the pegs were immediately behind the cloaca. Note the development of tension for the period (*c*–*d*) during which the pegs were being moved posteriorly over the hind end of the body. At *d* the pegs were again moved anteriorly; at *e* the direction was reversed again. At *f* the pegs had reached the posterior end of the tail and their direction again changed until *g*. The heavy lines at the top of the diagram mark the periods during which the pegs were moving posteriorly.

by suspending a decapitated fish by the tail and applying the pegs to the anterior end (see upper curve in Text-fig. 2). The course of the reflex is the same as when the conditions are reversed, but in this case the reflex contraction develops ipsilaterally and behind the points of pressure instead of ipsilaterally and in front. It is convenient to refer to the reflex as elicited from the anterior end of the body as the "Anterior resistance reflex" as opposed to the "Posterior resistance reflex" typical of the posterior region of the body.

In a limited number of cases, decapitated preparations when suspended by the anterior end showed little or no response to tactile stimuli applied to the posterior end of the body; in such cases it was possible to bend the posterior region of the body round three pegs into a sigmoid curve without eliciting any apparent muscular contraction.[1] If the pegs were then simultaneously moved anteriorly along the

[1] An active response could sometimes be got by gentle massage applied to the body contralaterally to the position of the pegs.

body, no measurable resistance was observed, but any attempt to move the pegs posteriorly immediately called forth active resistance, and visible contraction took place as long as pressure was exerted by the pegs (Text-fig. 3). Similarly, when the preparation was suspended by the tail, the anterior end could be bent into a sigmoid curve and the pegs moved posteriorly without resistance—but as soon as the pegs were moved in an anterior direction strong resistance was encountered (see Text-fig. 4). The most obvious interpretation of these phenomena seems to be that the response to tactile stimulation did not involve sufficient pressure on the pegs to elicit the resistance reflex although a limited number of muscle fibres lying at and near the pegs were in fact active. When the pegs were moved in a direction which



Text-fig. 4. Tracing showing the effect of extraneous pressure or tension during an anterior resistance reflex. At *a* a typical anterior resistance reflex developed in response to contact between the pegs and the anterior region of the body. At *b* an attempt was made to move the pegs in an anterior direction—note the increase of tension. At *c* the pegs were moved posteriorly until the tension had fallen to 1 lb.; the pegs were then made stationary and a new resistance reflex developed. When the tension developed by the reflex had fallen to *e*, tension was applied to the top of the balance (by the thread *d* shown in Text-fig. 1) until the tension had increased to about 3½ lb. Similar tension was again applied at *f*. Weight of eel, 7 oz.

tended to stretch these fibres, additional pressure was exerted and extensive recruitment from inactive muscle groups took place—when the pegs were moved in the opposite direction the muscles excited by tactile stimuli were allowed to contract freely, no pressure was exerted by the pegs and no recruitment occurred (see p. 189). Responses of this type suggest a resemblance between the resistance reflexes of an eel and the stretch reflexes characteristic of certain limb muscles of the mammals.

In all preparations, the nearer the points of application of unilateral pressure lie towards the tail or head respectively the easier it is to elicit the characteristic reflex. Decapitated preparations, when suitably suspended from a spring balance, exhibit either anterior or posterior resistance reflexes with equal facility, but only in very few cases does a posterior reflex (having been initiated at the hind end of the animal) spread to the anterior end of the body, or an anterior reflex spread to the posterior end of the body. In these respects the suspended fish differs somewhat from an unsuspended preparation for in the latter case the anterior resistance reflex can only be elicited during a short period after decapitation, whereas the posterior reflex

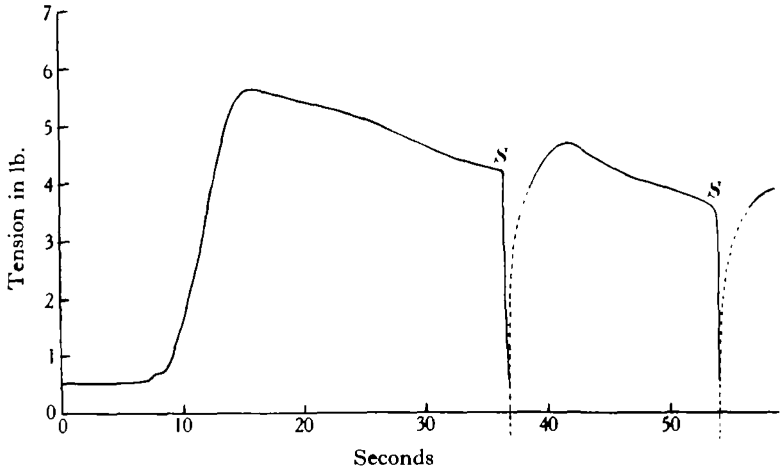


Fig. 5 a

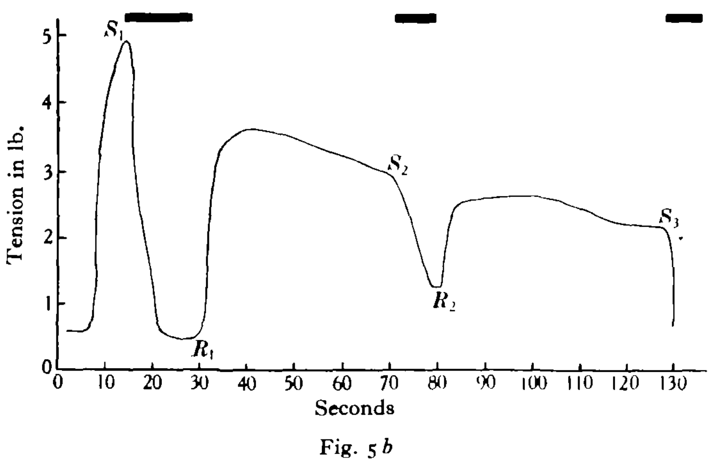
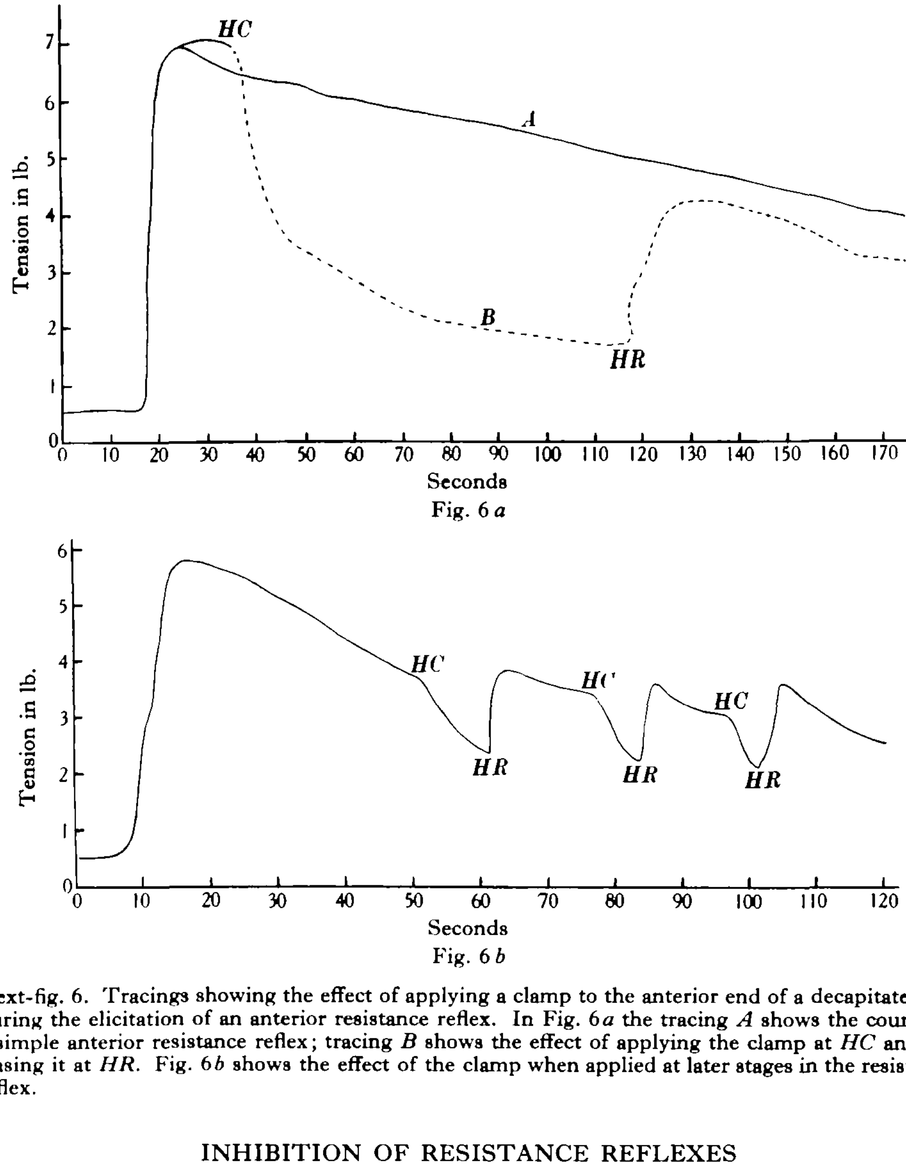


Fig. 5 b

Text-fig. 5. Tracings showing inhibition of posterior resistance reflexes by pinching the tail of a decapitated preparation (total wt. 10 oz.). In Fig. 5*a* a typical resistance reflex was initiated and at *S*, *S*, the tail was momentarily seized by relatively strong forceps. Note the rapid and complete inhibition of the resistance reflex and that the latter rapidly reappears as soon as the tail ceases to be stimulated. In Fig. 5*b* the tail was seized as soon as the resistance reflex had developed its full tension (S_1), and the tail was held for 15 sec. On releasing the tail at (R_1) the reflex again developed and was slowly inhibited by a more gentle seizure of the tail at S_2. The tail was released at R_2 and seized again quickly at S_3. The heavy lines at the top of Fig. 5*b* indicate the periods during which the tail was being stimulated.

remains vigorous for a much longer period. In the unsuspended spinal preparation only the posterior reflex can be elicited. These differences appear to be due to the fact that the anterior reflex can only be elicited under conditions which inhibit the posterior reflex. These conditions are provided by such persistent stimulation to the hind end of the body as occurs when the preparation is suspended from the balance by means of a hook passing through the tail (see below).



Text-fig. 6. Tracings showing the effect of applying a clamp to the anterior end of a decapitated eel during the elicitation of an anterior resistance reflex. In Fig. 6*a* the tracing *A* shows the course of a simple anterior resistance reflex; tracing *B* shows the effect of applying the clamp at *HC* and releasing it at *HR*. Fig. 6*b* shows the effect of the clamp when applied at later stages in the resistance reflex.

INHIBITION OF RESISTANCE REFLEXES

It is possible to inhibit a resistance reflex by stimuli capable of eliciting other types of muscular response. If the tail of a spinal or decapitated eel is momentarily seized by a fine pair of forceps, the tail is rapidly withdrawn by the development of undulatory posture, and, if the stimulus be maintained, a rhythmical response follows which tends to drive the fish forwards (Gray, 1936). Text-fig. 5*a* shows the effect of momentary seizure of the tail of a decapitated fish during a posterior resistance reflex. Very rapid and complete inhibition of the resistance reflex is obvious. The state of inhibition lasts as long as the tail is held, but the resistance reflex reappears as soon as the tail is released (Text-fig. 5*b*).

In an analogous way the response characteristic of pressure applied to the anterior end of the body is influenced by stimuli which elicit other patterns of response. If relatively powerful bilateral pressure is applied to the anterior end of a spinal or decapitated animal by means of a clamp, a rhythmical response ensues

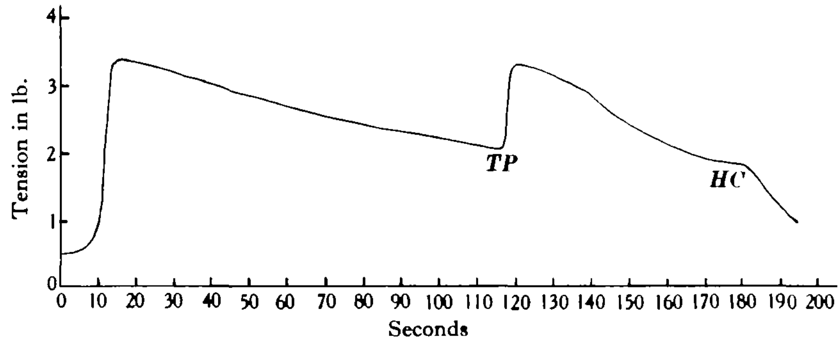


Fig. 7*a*

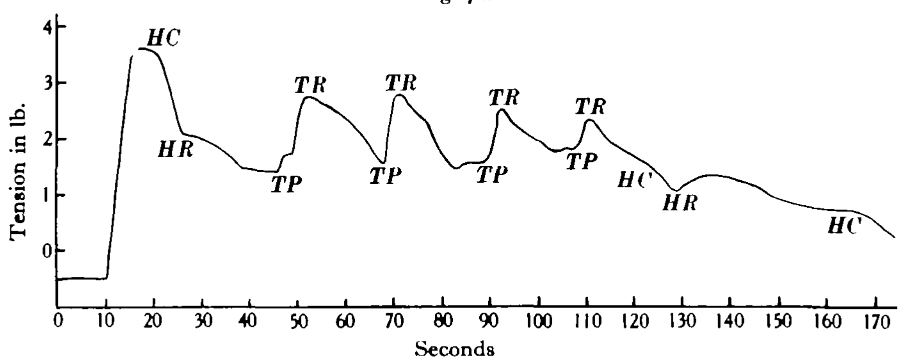


Fig. 7*b*

Text-fig. 7*a*, *b*. Tracings showing the effect of seizing the tail during an anterior resistance reflex. In Fig. 7*a* the tail was seized for about 3 sec. at *TP*; at *HC* a clamp was attached to the anterior end of the preparation. In Fig. 7*b* the symbols denote the following conditions: *HC*, head clamped; *HR*, head released; *TP*, tail seized; *TR*, tail released.

which is characterised by the passage of waves of contraction moving in an anterior direction along the body.[1] The effect of such a stimulus on an anterior resistance reflex is seen in Text-figs. 6*a* and *b*. Inhibition clearly occurs but it develops slowly and is never apparently complete. Both these instances of reflex inhibition seem to be of functional significance. A posterior resistance reflex tends to move the fish backwards and, if the fish is free to move, the characteristic unilateral "wave" of contraction travels mechanically from the hind end of the body towards the

[1] The reversed rhythm is often feeble; this may account for the incomplete inhibition of the anterior resistance reflex.

head; a forward swimming wave tends to move the fish forward and the waves of contraction travel from the front end of the body towards the tail. Complete co-ordination of effort implies mutual inhibition between the individual members of each pair of antagonistic responses; it is of interest to note that this is effected without the intervention of the higher centres of the brain.

AUGMENTATION OF RESISTANCE REFLEXES

Reference to Text-fig. 7 shows that inhibition no longer occurs if, during the elicitation of a resistance reflex, a stimulus is applied which, acting alone, produces a response which moves the fish in the same direction as that effected by the resistance reflex itself. These conditions are fulfilled by pinching the tail during the elicitation of an anterior resistance reflex or by clamping the anterior end of the body during a posterior resistance reflex. In neither case does inhibition occur and in most preparations definite evidence was obtained of additional excitation (Text-fig. 7). These observations are of interest, for they suggest that it may be possible to integrate the spinally determined rhythm with a localised resistance reflex so long as the muscular pattern of both responses are compatible with each other.

A reinforcement of a spinal rhythm by a resistance reflex would only be possible if the rhythmic response involved part of the total available musculature, and it is therefore of interest to compare the force exerted during normal swimming movements with that developed during a resistance reflex. The propulsive force of the locomotory movements can be determined approximately by allowing an intact eel to pull against an extensible spring whilst the eel is actively propagating swimming waves along the body. For this purpose, the spinal cord is cut about 1 in. from the tip of the tail so that a thread from the spring can be attached to the fish without eliciting violent and unco-ordinated movements. After observing the tension developed as the result of very active co-ordinated swimming, the fish is decapitated and the force exerted during a resistance reflex is determined in the usual way. Typical observations are as follows:

Weight of fish, 64 gm.

Total length, 15·5 in.

Maximum tension developed during very active swimming, 100 gm.

Maximum tension developed by anterior resistance reflex, 1475 gm.

It seems clear that, even when swimming very actively, an eel is utilising only a small percentage of its total available musculature, and it seems not unreasonable to assume that the remainder can be brought into action if the muscles encounter extraneous resistance.

It is not easy to determine the precise nature of the stimulus which elicits the resistance reflex. It may be pressure exerted on receptors in the skin or underlying muscles. This view is supported by observations of the effect of moderate bilateral pressure at any point on the body of a spinal eel. If the latero-dorsal surfaces of such a preparation are held firmly between the forefinger and thumb, the fish often moves actively backwards by a curious pulsating movement, which is apparently due to the contraction, on both sides of the body, of the muscles lying anteriorly to the point of restraint.[1] The number of segments which take part in this reflex appears to be smaller than that involved in a typical response to unilateral pressure, but the resemblance between the responses to bilateral and unilateral pressure is quite definite. It must be remembered, however, that even tactile stimuli induce localised reflex contraction in the neighbourhood of the point stimulated (Gray, 1936), and it is therefore possible that a stimulus involving pressure also involves the application of tension to actively contracting muscle fibres; it is conceivable that the effective stimulus may be wholly or in part of a myotactic nature, although the application of passive tension to inactive muscles has no effect.

The observations, recorded in this paper, suggest that the normal movements of an intact eel are determined partly by the inherent properties of the spinal cord and partly by the peripheral reflex arcs which come into action in response to any external resistance which may be encountered by the body. So long as a fish is moving forward in response to a forward spinal rhythm those peripheral arcs which tend to move the eel backwards are completely inhibited, whereas those which operate in the opposite direction are free to come into action should external resistance be encountered; if the resistance is thereby overcome the eel resumes its forward centrally controlled rhythm. Conversely, if an intact eel is swimming backwards, the anterior resistance reflex arcs are inoperative, whereas those of the posterior resistance reflexes can be brought into action. If this conclusion is justified the similarity, already established in other respects (Gray, 1936) between the locomotory processes of the fish and those of the tetrapod vertebrates, becomes even more striking. In both cases the rhythm is determined by purely central processes, but it is adjusted and reinforced to deal with variable environmental conditions by means of peripheral reflexes.

SUMMARY

1. If the actively contracting muscles at the posterior end of an intact, spinal or decapitated eel are subjected to external restraint, a posterior resistance reflex is elicited. This reflex involves very powerful contraction in the muscles lying anteriorly and ipsilaterally to the point of restraint and thereby moves the fish backwards.

2. If the actively contracting muscles at the anterior end of a spinal or decapitated eel are subjected to external restraint (and a persistent stimulus applied simultaneously to the tail), an anterior resistance reflex is elicited. This reflex involves very powerful contraction in the muscles lying posteriorly and ipsilaterally to the point of restraint and thereby moves the fish forwards.

3. The muscular pattern of a posterior resistance reflex is incompatible with that of a forward locomotory rhythm. Sufficiently strong external restraint inhibits a locomotory rhythm; sufficiently strong tactile stimuli (capable, when acting alone, of eliciting a forward locomotory rhythm) rapidly and completely inhibit a posterior resistance reflex. An anterior resistance reflex is slowly and incompletely inhibited by stimuli which evoke a backward locomotory rhythm.

[1] This response is not always obtained, but when it occurs it is unmistakable.

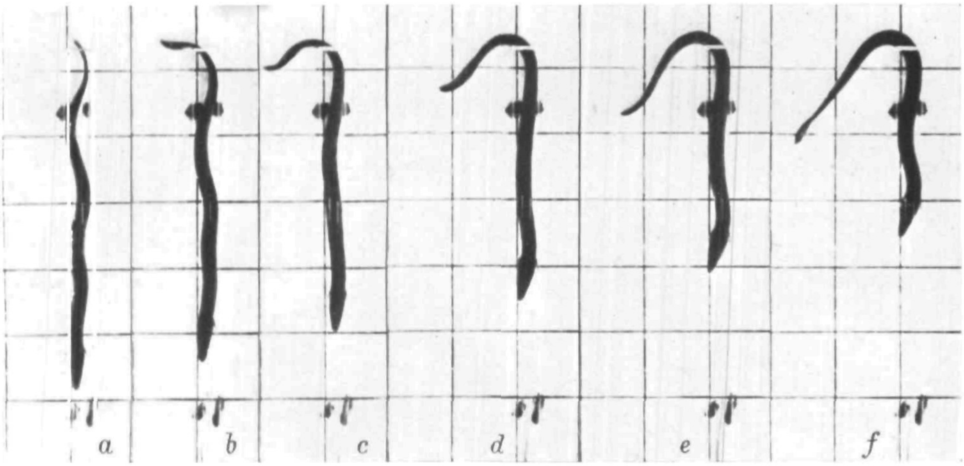


Fig. 1.

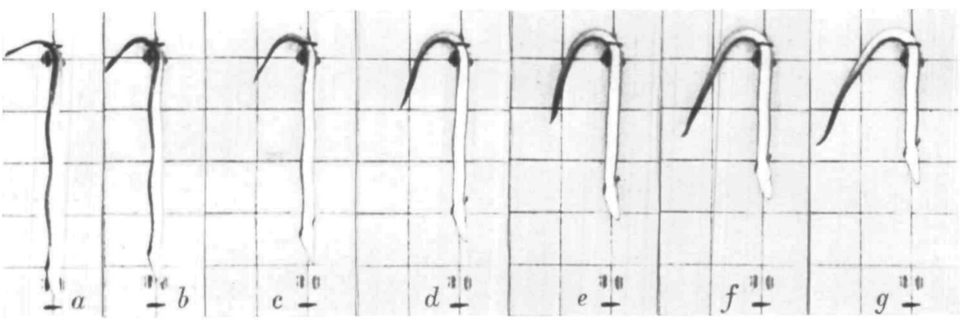


Fig. 2.

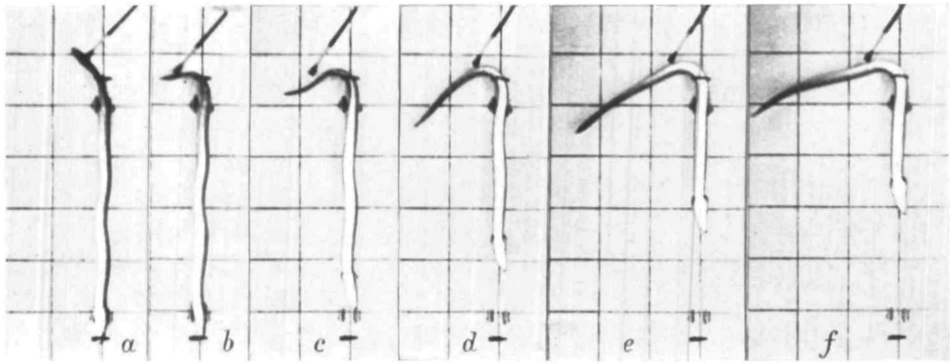


Fig. 3.

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4. If the muscular pattern of a resistance reflex is compatible with that of a locomotory rhythm (*e.g.* an anterior resistance reflex and a forward locomotory rhythm), the two reflexes are not mutually inhibitory but reinforce each other.

5. The resistance reflexes are used by the intact eel when escaping from a confined environment. It is suggested that they may, at other times, adjust and modify the centrally controlled locomotory rhythm which has been shown to involve only a small proportion of the total musculature.

REFERENCE

GRAY, J. (1936). *J. exp. Biol.* **13**, 170.

EXPLANATION OF PLATE I

Fig. 1. Intact eel escaping backwards from a tube 1¼ in. in diameter. The outline of the tube is only shown in photographs *a*, but the hind end of the tube is marked in all the photographs by the white line drawn across the body of the fish. Time interval between each photograph, 0·3 sec.

Fig. 2. An active preparation of a spinal eel escaping backwards from a tube. The ends of the tube were painted black and the hind end can be seen against the ventral surface of the body. Time interval between each photograph, 0·3 sec. The spinal transection was made at the level of the second vertebra.

Fig. 3. A relatively fatigued spinal eel escaping backwards from a tube. Time interval between each photograph, 1·5 sec. Note the brush which has to be applied from time to time to maintain adequate pressure against the tube.