

## THE LOCOMOTORY RHYTHM OF THE DOGFISH (*SCYLLIUM CANICULA*)

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(With Three Text-figures)

RECENT experimental work (v. Holst, 1935; Gray, 1936) has shown that the locomotory rhythms of certain teleostean fishes are determined by the intrinsic activity of the central nervous system, for they remain unaffected when the intervention of peripheral reflexes from the skin or muscles has been eliminated. This conclusion is at variance with that of ten Cate (1933) who removed all the muscles in the neighbourhood of the anterior dorsal fins of the dogfish (*Scyllium canicula* and *S. catulus*) and having transected the nerve cord, observed that a locomotory rhythm was propagated over the site of the operation thereby maintaining co-ordinated movement between the head and the posterior region of the body; the activity of the posterior region depends, according to ten Cate and ten Cate-Kazejewa (1933), on tensile stimuli applied to the posterior musculature whenever an active contraction occurs in the head region. If this conclusion be justified, the normal locomotory rhythm of the dogfish involves the activity of a chain of peripherally controlled reflexes whereas that of the eel is determined by a mechanism entirely independent of such reflexes. The situation appeared to be sufficiently anomalous to justify further investigation, and an attempt has been made to confirm ten Cate's observations. The work was performed at Plymouth and *Scyllium canicula* was used as the most convenient material; a few observations made on *S. catulus* indicated that there is no essential difference in the behaviour of the two species.

According to ten Cate and ten Cate-Kazejewa (1933, p. 18) a spinal dogfish,<sup>1</sup> at rest, closely resembles the normal animal. It remains immobile at the bottom of the tank with the body slightly curved, the posterior region of the body showing no movement. When the fish begins to swim, either spontaneously or by excitation of the anterior end of the body, undulatory movements start at the head and are propagated over the whole body. After simple spinal transection, ten Cate and ten Cate-Kazejewa (p. 20) never observed any lack of co-ordination between the two halves of the body. As these observations form a curious contrast with those about to be described, it is well to emphasise the fact that we have found it impossible to

<sup>1</sup> The nerve cord being transected at the level of the fifth or sixth vertebra.

assess the degree of active co-ordination between two regions of a spinal fish by means of visual observation of preparations lying freely in water; under such conditions all movements which originate in one region of the body (or indeed of any vibrating system) automatically induce apparently co-ordinated movements in another region although, in the case of the fish, the muscles of this region may be entirely inactive; the movements are of a passive mechanical nature and provide, of course, no evidence of active co-ordination although they may help to propel the fish. Similarly if each of two regions of a spinal fish is exhibiting an independent rhythm, the degree of independence is obscured by the mechanical effects which each part excites on the movements of the other. For these reasons the observations described in this paper were made under conditions in which mechanical interferences of the above type can be shown to be absent; in all cases the movements have been recorded by means of a cinematograph.

A spinal preparation, as used in these experiments, was prepared by anaesthetising the fish in 1 per cent. ethyl urethane in sea water; the dorsal surface of the nerve cord was exposed by a deep transverse incision, and the spinal cord cut with a sharp scalpel. The wound was then stitched up and the animal allowed to recover from the anaesthetic.

A preliminary series of preparations revealed the fact that within a few hours of the operation (in some cases, a few minutes) every spinal fish exhibited, when lying on the bottom of the tank, a marked and persistent rhythm. The amplitude of these movements was usually less than those of an intact fish swimming freely in water and the propulsive powers of the rhythm were low. Since the rhythm of the spinal fish can be accelerated by superficial stimulation to the ventral surface (Gray and Sand, 1936), it seemed possible that the activity seen when the fish is lying on the bottom of the tank was dependent upon tactile stimulation. This interpretation is, however, eliminated by the observation that when a spinal fish was suspended in water in such a way that the spinal region was isolated from contact with a solid surface, the locomotory rhythm persisted for many hours, after which observation was discontinued. Such a preparation can be made by suspending the fish (by the snout) vertically in a deep tank of water or horizontally after denervating a dorsal or caudal fin in such a way as to provide a second insensitive point of suspension.

The persistent activity of the spinal preparation is not characteristic of an intact fish, for the latter tends to swim intermittently with periods of rest. Apart from the persistent rhythm, we have never observed, in a spinal fish, any movements which may be interpreted as "spontaneous"; on the other hand, the spinal fish exhibits two unmistakable differences in behaviour to the unoperated animal. Firstly, all labyrinthine reflexes are absent, and the fish can be placed with its dorsal side downwards without eliciting any righting response; secondly, the region of the body posterior to the spinal section fails to respond to stimuli applied to the snout. The only instances in which the behaviour of spinal fish appeared to approximate to that described by ten Cate proved to be cases in which the cord had been incompletely severed during the initial operation.

As mentioned above, the spontaneous activity of an intact dogfish is of an intermittent type, and it seems therefore improbable that the persistent activity of the spinal preparation is directly dependent upon the activity of muscles which retain their connection to the higher centres of the brain. The following observations confirm this view. A dogfish was anaesthetised, and, all the somatic muscles at the level of the anterior dorsal fin were completely denervated for twelve segments ( $2\frac{1}{2}$  in.). This fish was then held firmly by a clamp fixed to the denervated region. After the effect of the anaesthetic had worn off, the fish exhibited the intermittent type of rhythm characteristic of the normal fish, and during periods of activity it was possible to observe that the posterior region of the body exhibited a rhythm in strict co-ordination with that of the anterior region (Fig. 1).<sup>1</sup> Waves of activity started at the anterior end of the body and passed to the tail of the fish without any disturbance of the difference in phase typical of the intact fish. Any modification in the rhythmic activity of the anterior region (as could be induced by persistent stimulation of the pectoral or pelvic fins) was immediately accompanied by a corresponding modification of the activity of the posterior region; similarly, excitatory stimuli applied to the tail excited both anterior and posterior regions of the body.<sup>2</sup> Precisely similar results were obtained with preparations of spinal fish (transected immediately behind the medulla, and denervated as above at the level of the anterior dorsal fin). In these cases the rhythm was persistent—and complete co-ordination was observed between the anterior and posterior regions of the body (Fig. 2). It is to be noted that purely mechanical movements of an inactive region of the body are, under the conditions of these experiments, completely eliminated, since if the hind end of the animal be pithed, it remains absolutely motionless whilst movements occur in the anterior region (Fig. 2E): similarly, after the fish has been killed even intense mechanical movement of the posterior region of the body fail to elicit any movement of the head.

That the intact spinal cord provides an effective mechanism for the maintenance of a co-ordinated rhythm between two regions of the body separated by a peripherally denervated gap is shown by the effect of cutting the spinal cord at the level of the gap. Under these circumstances co-ordination between the anterior and posterior regions breaks down, and if both regions of the body are composed of an adequate number of segments (see p. 206) each of them maintains a rhythm whose frequency is independent of that of the other, and the effect of a stimulus is no longer transmitted to the region of the body lying beyond the site of spinal transection (see Fig. 3).

It seems very improbable that a rhythm which is dependent on the activity of peripheral reflexes could pass over twelve or more inactive segments, and the above

<sup>1</sup> The diagrams shown in Figs. 1–3 have been prepared by an analysis of photographic records. The vertical lines *ab*, *a<sub>1</sub>b<sub>1</sub>* represent the approximate antero-posterior axis of movement. The frequency and duration of each beat can be judged by the time scale on the left of the diagrams and the amplitude by the total excursion from left to right. The records read from top to bottom. The positions of the tail as shown by individual points on the curves have not, in these figures, been recorded for the same instants of time as those defining the position of the head. Records of the latter type exhibit equally well the essential characteristics of the movement.

<sup>2</sup> The behaviour of these fish is strikingly similar to those described by ten Cate, but the two sets of experiments are not comparable since the spinal cord in our experiments was intact.

results strongly suggest that the mechanism of transmission of the locomotory rhythm in the dogfish is essentially of the same central type as that of the eel (see Gray, 1936). If segmentally organised peripheral reflexes play an essential role, the

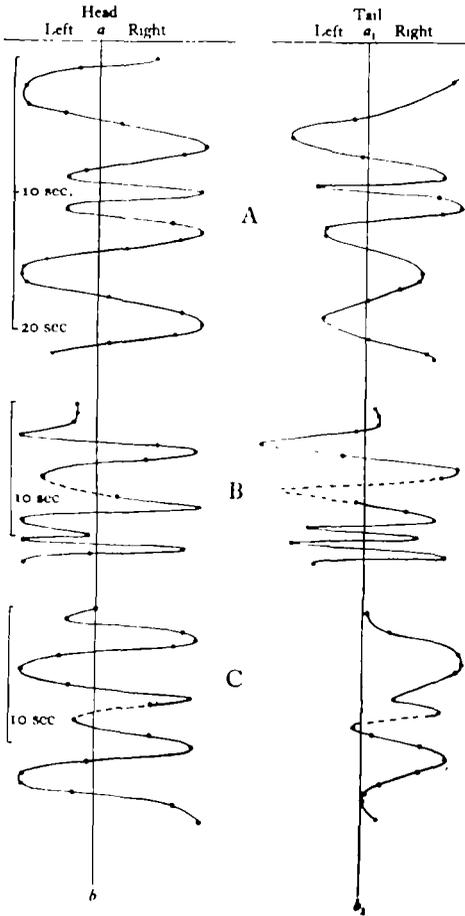


Fig. 1.

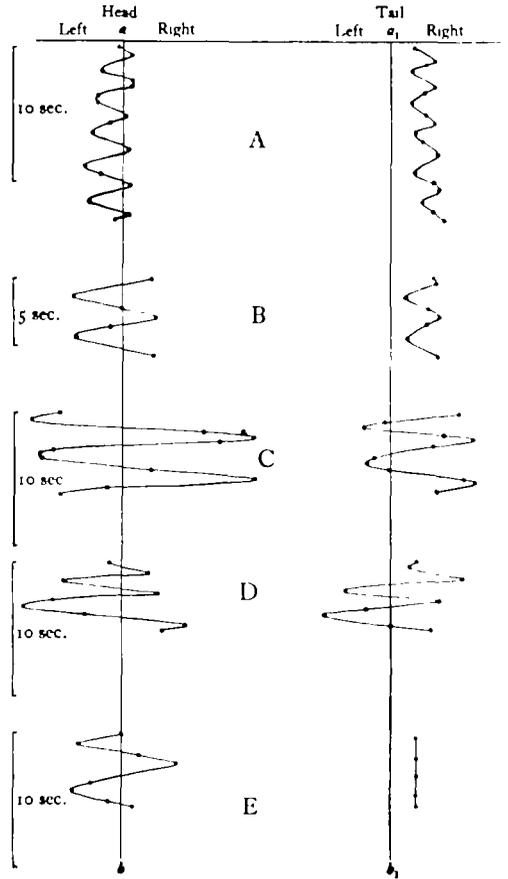


Fig. 2.

Fig. 1. Record (see footnote, p. 202) of the movements of anterior and posterior regions of a dogfish (with intact brain and spinal cord) held by a central denervated region of twelve segments. Note the co-ordination of the two regions (A) during spontaneous swimming movements; (B) movements during application of a clip to the tail; (C) movements during application of a clip to the pectoral fin.

Fig. 2. Record of the movements of regions of a dogfish anterior and posterior to a denervated area of twelve segments of a dogfish whose spinal cord has been transected behind the medulla only. Note the co-ordination of the two regions (A) during normal spontaneous rhythm; (B) when a clip is attached to the pectoral fin; (C) when a clip is attached to the pelvic fin; (D) when a clip is attached to the tail; (E) when the posterior region has been pithed.

resultant rhythm should be inhibited by transection of a number of dorsal spinal nerves. v. Holst has shown that the severance of the dorsal spinal roots in the tench (*Tinca vulgaris*) does not abolish the locomotory rhythm, and our experiments with the dogfish confirm this observation. When the dorsal roots were cut either on

one or both sides over a length of 5 in. in the region of the pectoral fins, the animal remained at rest at the bottom of the tank unless excited by tactile stimulation, in which case it exhibited a normal swimming response. The sluggish behaviour of the fish is not surprising in view of the fact that a substantial length of the spinal

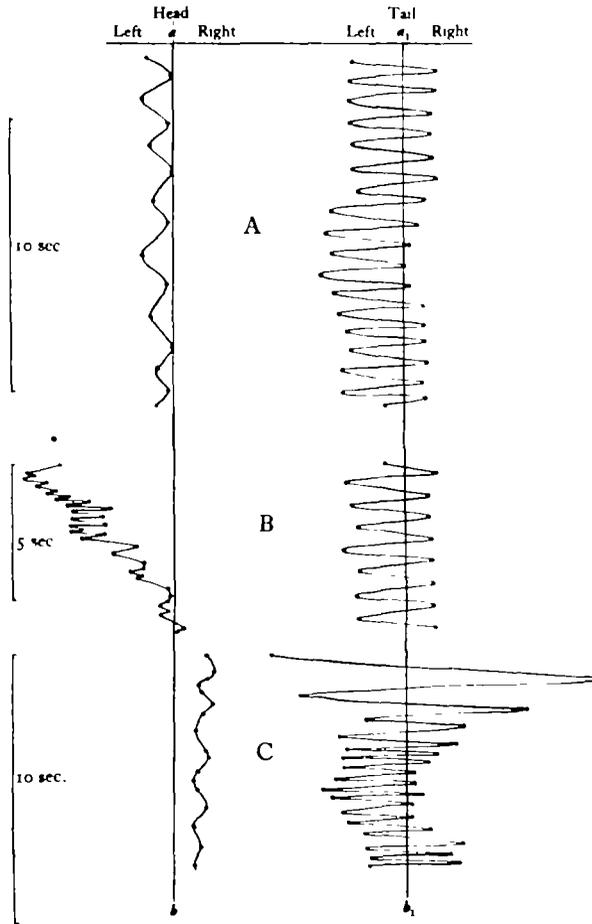


Fig. 3. Record of the movements of the anterior and posterior regions of a dogfish whose spinal cord has been transected behind the medulla and also at the level of the denervated region by which the animal has been clamped. Note the absence of co-ordination (A) during normal spontaneous rhythm; (B) during application of a clip to the pectoral fin; (C) during application of a clip to the tail.

cord had been exposed in order to sever the dorsal roots without injury to the motor nerves.

In view of the above results we find it difficult to avoid the conclusion that peripheral reflexes play no essential role in the maintenance of a locomotory rhythm in the dogfish.

At first sight the persistent rhythmical activity of the spinal dogfish appears in marked contrast to the typically inactive state of the spinal teleost. If an eel be

rapidly decapitated behind the medulla, the body not infrequently exhibits rhythmical movements for a brief period (Gray, 1936), and it seems reasonable to associate these movements with nervous impulses set up at the site of the injury inflicted by the operation. It is, however, difficult to associate the very persistent rhythm of the spinal dogfish with phenomena of this type. It is not easy to be certain that the site of injury exerts no lasting influence on the general level of spinal activity, but it can be shown that the frequency and amplitude of the spinal rhythm depend upon conditions which are essentially the same in the dogfish and in the teleost, in which the excitatory effect of actual transection is limited to a few minutes. The responses of the spinal dogfish to exteroceptive stimuli form the subject of another paper (Gray and Sand, 1936), but it is of interest to note that the rhythm so characteristic of complete spinal transection is sensitive both in frequency and amplitude to tactile and nociceptive stimuli. If the fish be stroked on the ventral surface (particularly in the neighbourhood of the cloaca) with a fine brush, the rhythm is greatly enhanced in frequency; alternately, if the spinal fish be placed on its back, the rhythm tends to subside and is not infrequently abolished. If, on the other hand, a small clip be attached to the caudal fin the amplitude of the rhythm is greatly increased; in the case of the eel, a stimulus of this type elicits a rhythm which is otherwise absent (Gray, 1936). We conclude from these observations that the presence of a locomotory rhythm in the body of a spinal fish depends on the general level of excitation of the spinal cord. A stimulus applied locally on the surface of the body increases or decreases the general excitatory state of the whole cord. As soon as the state of excitation reaches a critical level, a locomotory rhythm emerges and is sustained until the excitatory level falls below the threshold value. In view of ten Cate's observations, it is of interest to record that we have not infrequently observed that the spinal rhythm of a dogfish transected immediately behind the medulla can be accentuated by bending the snout in such a way as to exert a tension on the posterior region of the body. This is not, in our opinion, due to the activation of local reflex arcs but to an exhalation of spinal excitation, induced by peripheral stimulation, which has spread to all parts of the cord and which is comparable to the effect of stimulation in the region of the cloaca or elsewhere.

It is obvious that rhythmical activity involves co-ordination between the right and left musculature of each segment, and that the mechanism which controls the rhythm must be such that the motor neurones of both sides of the same segment should not be active simultaneously. An attempt has been made to determine how far each segment of the spinal cord controls the rhythmical activity of the muscles belonging to that segment, or how far the rhythm of one segment is determined by regions of the cord lying outside that segment. For this purpose, varying lengths of cord were isolated in the following way. The cord was cut in two places: (i) immediately behind the medulla, and (ii) at a position varying from twelve to thirty segments from the site of the first transection. The whole of the cord posterior to the second transection was pithed to eliminate confusion of interpretation due to spontaneous movements of the posterior region of the body. The preparations were

then suspended by their snouts in a deep tank, thus eliminating any extraneous source of excitation or inhibition. Tables I and II show that no spontaneous persistent rhythm was displayed by any preparation comprised of fewer than twenty-seven intact segments; preparations composed of approximately twenty-four segments showed no spontaneous rhythm, but when stimulated by pressure on a fin or by a brush applied to the cloaca, a rhythmical response occurred which persisted for some time after the removal of the stimulus. Preparations of approximately seventeen segments only exhibited a rhythm during the period of application of relatively strong extraneous stimulation. So far as we could determine, the level at which the cord was isolated did not influence the number of segments requisite for spontaneous rhythm (compare Tables I and II).

We conclude from these observations that the power to sustain a state of spontaneous and persistent rhythm is a property peculiar to a considerable length of the spinal cord and is not of a strictly segmental nature. This observation is in harmony with the conception of the rhythmical mechanism advanced elsewhere (Gray, 1936) and which is based on the conclusion that, under appropriate conditions, a unilateral region of localised spinal activity automatically induces a secondary region of activity lying anteriorly and contralaterally to itself.

Bethé (1899) showed that if the brain of the dogfish be transected in front of the medulla, the fish retains its normal powers of active locomotion. It may therefore be concluded that the powerful but intermittent rhythm characteristic of the intact fish is the result of medullary influence on the weaker but persistent rhythm which is an inherent property of the isolated spinal cord. The typical spinal preparation of an eel (*Anguilla vulgaris*)<sup>1</sup> can, in the absence of extraneous peripheral stimuli, only exhibit rhythmical activity if appropriate electrical stimuli are applied to the surface of the spinal cord (Gray, 1936), and it therefore seems reasonable to assume that during locomotion the medulla of the eel is exciting an excitatory influence on the cord. The removal of medullary control in the case of the dogfish effects a change in the opposite direction, for it enables the cord to express more readily its inherent rhythmical properties and it seems possible that the intact dogfish begins to swim when medullary inhibition is removed. It must not be forgotten, however, that, in the absence of strong peripheral stimulation, the propulsive powers of the spinal dogfish are very much lower than those of an intact fish, and the amplitude of the movements is often low. How far these effects are due to a general lowering of muscular "tone" due to the removal of medullary influences is uncertain. Attempts to modify the rhythmic activity of a decapitated or spinal dogfish by the application of electrical stimuli to the spinal cord did not give definite results, and usually evoked somewhat violent and non-rhythmical movements of the body.

The influence of the higher nervous centres on the spinal activity of a dogfish

<sup>1</sup> A spinal preparation of the conger (*Conger vulgaris*) appears to exhibit rhythmical activity much more readily than that of the fresh-water eel. During the first few weeks after spinal transection behind the medulla, a single specimen readily exhibited prolonged rhythmical activity in the hinder end of the body after gentle stimulation; three months after the operation the rhythm became persistent. von Holst (1934) has reported spontaneous spinal activity in some specimens of *Anguilla vulgaris*.

Table I

Dogfish	Total length cm.	Position of anterior spinal transection	Position of posterior spinal transection	No. of segments between anterior and posterior transections	Spontaneous rhythm	Remarks
S	—	Immediately behind medulla	Level with posterior incision of pelvic fins	> 27	Present	Persistent rhythm
T	—	Immediately behind medulla	At posterior incision of anterior dorsal fin	> 27	Present	Persistent rhythm
U	—	Immediately behind medulla	At posterior incision of anterior dorsal fin	> 27	Present	Persistent rhythm
V	56.5	5 cm. from snout	18 cm. from snout	> 27	Present	Persistent rhythm
W	60	6 cm. from snout	16 cm. from snout	—	Absent	Persistent rhythm
X	65	7.5 cm. from snout	25 cm. from snout	27	Present	Persistent rhythm
Y	61	6 cm. from snout	19 cm. from snout	21	Absent	Rhythmic response only during stimulation of pelvic fins
Z	62	6 cm. from snout	20 cm. from snout	23	Absent	Rhythmic response only during, and for brief period after, stimulation of pelvic fin

Table II

Dogfish	Total length cm.	Position of anterior transection		Position of posterior transection	No. of segments between spinal transections	Spontaneous rhythm	Remarks
		Cm. from snout	From anterior insertion of pelvic fin				
L	63	21	4 cm. anterior	37	29	Present	Rhythm during, and for a brief period after, pelvic stimulation
M	65	25.5	(Level)	39	24	Absent	
N	57	22	(Level)	31	17	Absent	Rhythm during pelvic stimulation only
O	63	24	—	39	—	Absent	As in M

can, to some extent, be followed in preparations in which the spinal cord has been transected, behind the medulla, on one side only. This operation was performed on four fish, two of which survived the operation for many weeks. If the latter fish can be regarded as typical examples of spinal hemisection, the effect of the operation is as follows. For a variable period after the operation, the locomotory movements are normal but somewhat weaker than those of the intact fish; the animal swims without marked deviation from a straight course but is unable to execute a turning movement towards the operated side. If the fish be held by the snout, violent muscular response is restricted to the intact side. When at rest the fish lies in a normal posture, but this condition lasts only for a limited period and is gradually changed by the acquisition of a marked excess of tone on the intact side; about 14 days after the operation, the fish can no longer swim normally but exhibits circus movements towards the intact side, and when at rest lies with a marked curvature towards that side. When a fish of this type is in motion it can be seen that the regularity of the locomotory waves is only disturbed to the extent that the contractions on the intact side are very much greater than those on the operated side. The state of unilateral hypertonicity gradually subsides and has completely disappeared after two months. The interpretation of the effects of spinal hemisection must await definite information on the degree of spinal regeneration which takes place, but the inability of these fish to execute a turning movement towards the operated side, although displaying the power to transmit muscular waves down that side, is in harmony with the view that a muscular wave, having been initiated on the intact side automatically induces a wave down the operated side (see Gray, 1936). It is also, perhaps, significant that a hemisected fish exhibits no signs of persistent rhythm—presumably because any rhythmical activity which might be induced in the intact side by the spontaneous activity of the operated side is suppressed by medullary influence.

#### SUMMARY

1. The locomotory rhythm of an intact or spinal dogfish resembles that of other fish in that it is determined by the intrinsic activity of the spinal cord without the participation of proprioceptor arcs.

2. The persistent rhythm characteristic of the spinal dogfish can be accelerated or inhibited by peripheral stimuli. So long as the spinal cord is intact, localised stimuli elicit co-ordinated responses from all intact segments of the body although at least twelve intermediate segments may have been deprived of their spinal innervation. Co-ordinated responses no longer occur if two regions of the body are isolated from each other by a second spinal transection; if both such regions are of adequate length, each exhibits an independent spontaneous rhythm and responds independently to peripheral stimulation.

3. In order that a spinal preparation should exhibit spontaneous and persistent rhythmical activity, in the absence of extraneous stimuli, approximately twenty-five segments of the nerve cord are necessary.

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