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SHORT COMMUNICATION

LOCOMOTION IN LAMPREY AND TROUT: THE RELATIVE TIMING OF ACTIVATION AND MOVEMENT

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Most fish swim by the rhythmic passage of a wave of lateral displacement from head to tail, thereby developing a reactive thrust from the water which pushes the fish forward (Marey, 1894). Breder (1926) classified this type of swimming into different modes according to how much of the body performs undulations. In the anguilliform (eel-like) mode most or all of the body is flexible and participates in the passage of the wave, whereas in the carangiform mode the amplitude of the lateral movement becomes significant only as the wave approaches the tail. Anguilliform swimmers tend to have a fairly constant lateral projection along the length of the body, whereas the carangiform swimmers have the more familiar fish shape, with the body tapering to a minimum in the caudal peduncle and then widening again in the caudal fin. The hydrodynamic models appropriate for the theoretical analysis of these two types of swimming reflect these differences in form and function (Lighthill, 1969).

The kinematics of swimming are well documented for several species. Less attention has been given, however, to the role of muscle activation in the production of the observed movements. In the static case, activation of the lateral musculature at a point along the body will develop a local curvature concave to the active side (see Gray, 1933; Alexander, 1969; Wainwright, 1983). During swimming, however, activation does not, in general, coincide with concave curvature, because of the time-dependent interactions of the physical properties of the fish and the water (see Blight, 1977).

It has been shown in the early newt embryo (Blight, 1976) and for escape swimming in the carp (Kashin *et al.* 1979) that a propagated mechanical wave can be produced by muscle activation which simply alternates on the two sides of the body. In this case, energy stored elastically is released as a passively propagated wave that performs work against the water (see Blight, 1976).

Key words: lamprey, locomotion, phase coupling, swimming trout.

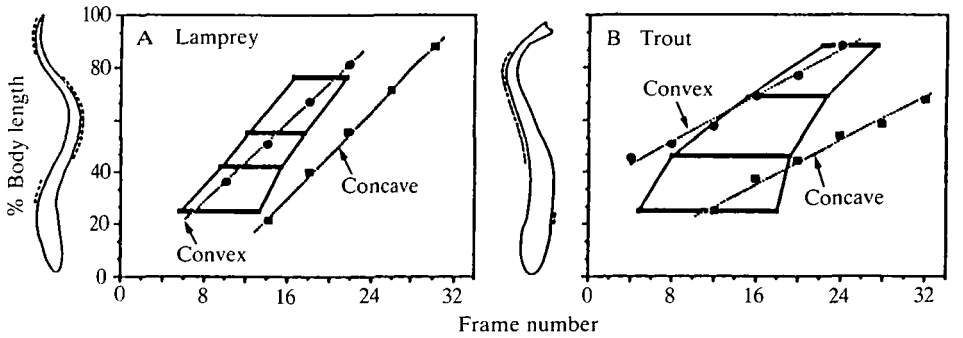

Fig. 1. Passage of the neural (EMG) and mechanical activity during one swimming cycle. Squares indicate maximum concave curvature on the side from which the EMG was recorded, circles maximum convex curvature. Dotted lines show linear regressions through these points. Horizontal bars represent time during which activity occurred at each electrode position along one side of the body only; solid lines connect onset or termination of activity at the four electrode positions. The slope of each line is equal to the respective speed of travel down the body. Body outlines demonstrate activity at frame 16 in the lamprey, frame 19 in the trout. Dashed lines alongside body outline represent active muscle. Water velocity: 0·70 m s^{-1}, lamprey, 0·18 m s^{-1}, trout; body length: 0·35 m, lamprey; 0·28 m, trout.

In the usual case, however, a wave of muscle activation does indeed travel from head to tail, as first shown by Grillner (1974), who recorded electromyograms simultaneously at different positions along the body in dogfish. It has also been shown, however, in the eel and dogfish (Grillner & Kashin, 1976) and in the tench (Blight, 1976, 1977) that this wave of activation travels faster than the mechanical wave. The significance of the relative timing of activation and movement is not known (see Blight, 1977). In this paper we describe the quantitative relationship between muscle activation and lateral curvature in two fish which use different swimming styles, the lamprey (an anguilliform) and the trout (a carangiform).

Experiments were performed on three lampreys (*Lampetra fluviatilis*, 28–30 cm) and three rainbow trout (*Salmo gairdneri*, 26–28 cm). The animals were anaesthetized (tricaine methyl sulphonate, approx. 100 mg l^{-1}), and fine-wire intramuscular electrodes were placed superficially in the lateral musculature along the midline at four positions along one side of the body. Reflective markers were glued along the dorsal midline (trout only). Synchronized electromyographic and cinematographic recordings were made while an animal swam in a swim-mill against water flowing at constant velocity, over a range of 0·16 to 2·6 m s^{-1} (Grillner & Kashin, 1976). Filming speed was 80 frames s^{-1}, and a digital pulse from the camera was recorded on a separate channel of the EMG record for synchronizing (Grillner *et al.* 1977). Each ciné frame was projected and the positions of the points of maximal concave and convex curvature were estimated. The distance (arc length) along the body of these points from the head (lamprey) or the nearest reflective marker (trout) was determined with a digitizing tablet.

Fig. 1 shows the relative timing of electromyographic and mechanical activity

during approximately one locomotor cycle. It can be seen that in both species the mechanical wave (e.g. maximal concave curvature) travels at nearly constant speed along the body. The wave of activation, as measured by the EMG, also propagates but at a faster speed than the mechanical wave. This is particularly noticeable in the trout: the points of maximal curvature in Fig. 1B are travelling at approximately 1·7 body lengths s^{-1}, whereas the midpoint of the burst of EMG activity is travelling at an average speed of about 4·0 lengths s^{-1}.

When expressed as body lengths per cycle (i.e. wavelength), both the electrical and the mechanical waves travelled independently of the swimming frequency, confirming earlier results in several species (e.g. Bainbridge, 1963; Grillner & Kashin, 1976; Videler & Wardle, 1978; Videler & Hess, 1984). The average wavelength of the mechanical wave was $0{\cdot}72 \pm 0{\cdot}07$ (SD) body lengths in the lamprey and $0{\cdot}82 \pm 0{\cdot}04$ in the trout. The latter value is similar to that found by Webb *et al.* (1984) for trout of the same body length. The speed of propagation of the EMG was nearly constant over the length of the lamprey (see Fig. 1A). Calculated from the travel of the midpoint of the EMG burst, the average wavelength was $1{\cdot}05 \pm 0{\cdot}10$ body lengths. For the trout, however, the speed of EMG propagation changed considerably along the body (see Fig. 1B). Thus the wavelength calculated by passage of the midpoint of the EMG burst between the two most rostral electrodes (at 25% and 45% of the body length) was $6{\cdot}0 \pm 1{\cdot}5$ body lengths, whereas the value between the two most caudal electrodes (at 68% and 86%) was $1{\cdot}1 \pm 0{\cdot}2$ body lengths.

As a consequence of the different speeds of travel of the electrical and mechanical activity, the phase relationship between them changes along the body length. This is illustrated in Fig. 2, which is constructed from average values at several swimming speeds. It gives the average phase lag (expressed as a fraction of the cycle) between electrical activity on one side of the body and the maximal concave curvature towards that side during one wave passage. Thus zero on the y-axis would represent EMG activity occurring at the time of maximal concave curvature towards the active side, whereas ±0·5 would represent activity coincident with maximal convex curvature. Values of ±0·25 or ±0·75 would represent the occurrence of EMG activity when the body is straight.

Near the head of the lamprey, the EMG activity on one side of the animal begins just before maximal curvature convex to the active side (0·50) and ends just before maximal curvature concave to the same side (0·00) (Fig. 2A). About halfway down the body, however, the EMG activity begins approximately as the body is straight (0·75) and continues as convex curvature develops further, ending just before the body is straight once more (0·25).

The timing in the trout is quite different (Fig. 2B). Near the head, the EMG activity begins after the body has begun to develop concave curvature towards the active side, continues as the active side passes through maximum concave curvature, and ends when the body is straight again. Near the tail, the timing approaches that seen in the lamprey, i.e. EMG activity is approximately coincident with convex curvature.

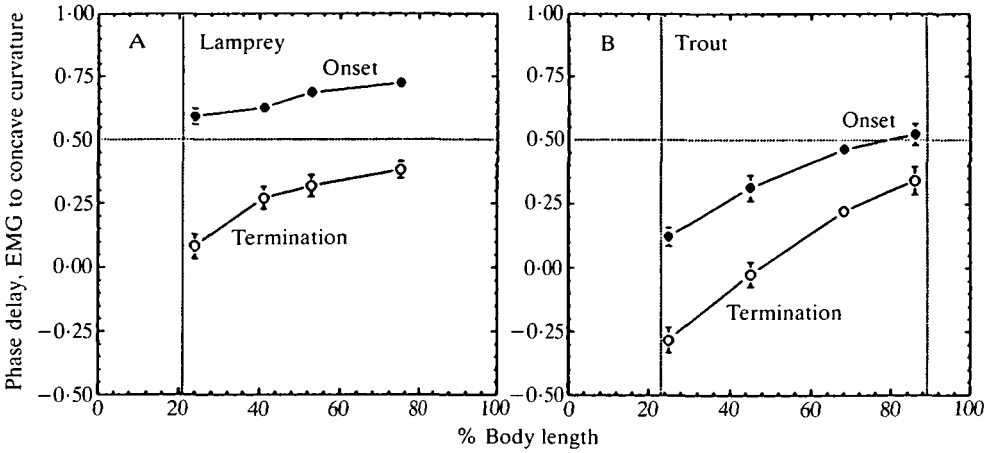

Fig. 2. Phase coupling between muscle activation and movement in lamprey (A) and trout (B). Abscissa, position along the body, measured from the rostral end. Ordinate, phase delay (as fraction of cycle duration) between onset (filled circles) or termination (open circles) of EMG activity and maximal concave curvature towards the side from which recordings were made. Mean values are given for three swimming speeds (error bars are standard errors of the mean): lamprey, 1·6–2·2 body lengths s^{-1}; trout, 0·65–9·2 body lengths s^{-1}. Vertical dotted lines show boundaries with the head and gill region (both lamprey and trout) and the caudal fin (trout only). Horizontal dotted lines represent time of maximal convex curvature of the active side.

Blight (1977) has suggested that muscle activation can contribute to the thrust developed by a passively travelling wave only if the contractile elements add tension along the convex side of the curvature, i.e. a phase coupling of 0·5 as defined in this study. At this time the straight portion of the body one-quarter wavelength caudal to the curvature (the leading edge of the travelling wave) is crossing the line of motion with maximum velocity towards the convex side (see Gray, 1933). Tension along the convex curvature would assist the propulsive force developed here (Blight, 1977). The dotted horizontal lines in Fig. 2A,B represent the timing of such maximum velocity, and it can be seen that for most of the length of the lamprey (but not the trout) this occurs near the midpoint of the EMG burst. Thus, in the lamprey the muscle activation is approximately in phase with the velocity of that portion of the body which is performing work against the water.

In the carangiform, however, the most significant thrust is developed in the tail, and Lighthill (1977) has predicted that the development of force by the body musculature should be in phase with the velocity of the caudal fin. In view of this, we have used the same data as that in Fig. 2 to calculate the phase relationships between the onset and termination of muscle activation at each electrode position and the arrival of the wave of maximal convex curvature at the tip of the caudal fin. These results are presented in Fig. 3 for both lamprey and trout.

Since the maximal lateral velocity of the caudal fin to one side occurs 0·25 cycles later than the maximal curvature concave to that side, values of −0·25 in

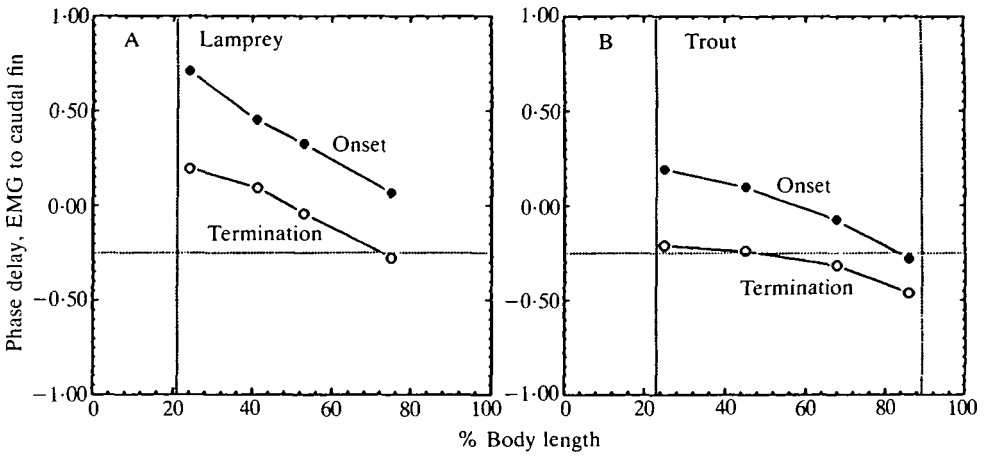

Fig. 3. Phase coupling between muscle activation (EMG) and caudal fin movement. Ordinate, phase delay (as fraction of cycle duration) between EMG activity at each electrode position and arrival of wave of maximal convex curvature at the tip of the caudal fin. Same sequences as in Fig. 2. Horizontal dotted lines represent time of maximal velocity of trailing edge of caudal fin towards side from which EMG was recorded.

Fig. 3A,B would represent coincidence of muscle activity with maximal velocity of the caudal fin towards the active side. In the lamprey (Fig. 3A), only near the tail does the phase approach this value. In the trout, however, almost all the body musculature is activated approximately in phase with the maximum caudal fin velocity (Fig. 3B), as suggested by Lighthill (1977).

The study of how the patterns of neural activity generated by the spinal cord produce swimming can conveniently be divided into two questions. (1) How does activation of the contractile filaments of muscle interact with the physical properties of the body and the water to produce the observed pattern of movements of portions of the body relative to each other? (2) How do such changes in the shape of the body interact with the water to provide forward movement of the entire fish? The latter question falls in the realm of fluid dynamics, and much progress has been made in recent years in the analysis of carangiform swimming (see Webb & Weihs, 1983), even though anguilliform swimming remains intractable (Lighthill, 1983). In this study we have collected data bearing on the first question, for which no relevant models yet exist.

We have examined the relative timing of muscle activation and movement along the length of the body at different swimming speeds in two different types of fish. The timing of muscle activation is, of course, not identical to the timing of force development in the muscle attachments. The delay between the EMG and the onset of tension in the contractile filaments is only a few milliseconds and can be neglected. However, the additional delays introduced by the elastic and inertial properties of the muscle will be at least tens of milliseconds (Wardle, 1975) and will

not decrease in proportion to the cycle length. Hence, at the slower swimming speeds in the trout (2·5 Hz) the additional delay may be of the order of 10% of a cycle, but at the highest frequency (15·8 Hz) it may constitute half a cycle or more. And yet the phase relationship between muscle activation and movement is independent of swimming speed, in both lamprey and trout. This is a finding which has no obvious explanation but which must be taken into account in any mechanical model relating muscle force development to body movements. Our results do not bear directly on hydrodynamic theories of swimming, but the observation that the activation of the contractile filaments is approximately in phase with the velocity of that part of the body which is doing the most work against the water (Fig. 3A, lamprey; Fig. 3B, trout) may reflect a functional similarity in the two species.

If the activation along the entire length of the trout were exactly in phase with the velocity of the caudal fin, the muscle activation would occur as a standing wave, alternating left and right. Theoretical calculations from kinematic data for saithe and mackerel (Hess & Videler, 1984) led these authors to conclude that muscle force occurs as a standing wave. In contrast, the experimental data reported here clearly show that the activation of the contractile elements occurs as a travelling wave. However, the large burst duration in the rostral part of the trout, coupled with the high velocity of propagation of the EMG wave (Fig. 1B), produces some of the features of a standing wave, in that most of the musculature is active at the time of maximal caudal fin velocity (dotted line in Fig. 3B).

In the lamprey (Grillner *et al.* 1981) and the dogfish (Grillner & Wallén, 1982) studies with paralysed or *in vitro* preparations have demonstrated a powerful system of movement-generated sensory feedback which ensures the appropriate timing between activation and movement (see Wallén & Williams, 1985; Williams, 1986; Sigvardt, 1989). It is not known whether such a system also exists in the teleosts but it would seem likely that it does, especially in view of the very tight coupling demonstrated here in the trout. In the lamprey such feedback is mediated, at least in part, by intraspinal mechanoreceptors (Grillner *et al.* 1982, 1984). It is therefore not possible by deafferentation to discover what the relative timing between activation and movement would be without such feedback. It would seem unlikely that the sensory feedback would be required to oppose the mechanical system except for correcting errors. We could thus assume that in steady constant swimming the mechanical system of the body of the fish and the water are well matched to the neurally generated pattern so as to provide approximately the appropriate timing without the need for sensory feedback. The differences in such relative timing in these two species reflect the different swimming strategies that have evolved.

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