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ELECTROMYOGRAPHY OF THE FIN MUSCULATURE OF THE CUTTLEFISH *SEPIA OFFICINALIS*

BY WILLIAM M. KIER

Department of Biology, CB no. 3280, Coker Hall, University of North Carolina, Chapel Hill, NC 27599-3280, USA

KATHLEEN K. SMITH

Department of Biological Anthropology and Anatomy, Duke University Medical Center, Durham, NC 27710, USA

AND JALEEL A. MIYAN

Department of Zoology, University of Edinburgh, King's Building, West Mains Road, Edinburgh EH9 3JT, Scotland

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Summary

The musculature of the fins of the cuttlefish *Sepia officinalis* (Mollusca, Cephalopoda) was studied with electromyography to test predictions of the functional role of the various muscle masses. Previous research had shown the fins to consist of a tightly packed, three-dimensional array of muscle with distinct zones of anaerobic glycolytic and oxidative muscle fibres. In addition, a network of crossed oblique connective tissue fibres was observed within the musculature. In a previous paper a model of the function of the muscle and connective tissue was presented. In the present paper, we present recordings of electrical activity from the various muscle bundles in the fin, in conjunction with the output from an electronic movement-monitoring device, and correlate muscle activity with both the phase and the intensity of the fin-beat cycle. The results obtained here support the hypothesis that the oxidative muscle fibres produce gentle fin movements and are consistent with the hypothesis that the network of crossed oblique connective tissue fibres provides skeletal support. The results also support predictions that the anaerobic glycolytic muscle fibres both produce vigorous fin movements and provide support for that movement. This study provides a critical test of models of the role of the tightly packed, three-dimensional array of muscle found in muscular hydrostats such as the arms and tentacles of cephalopods and tongues of mammals and lizards.

Introduction

A tightly packed, three-dimensional array of musculature characterizes the

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musculoskeletal system of many molluscs, especially cephalopods (Kier, 1988). In previous research on the arms and tentacles of squid (Kier, 1982, 1985), nautilus (Kier, 1987) and octopus (Kier & Smith, 1985; Kier, 1988), the morphology of these appendages was analysed from the stand-point of biomechanics. Predictions were made concerning the role of the muscle arrangements in producing movement and providing skeletal support. Experimental tests of the predictions are difficult to perform, however, because movement of these appendages is neither cyclical nor stereotyped, and the animals, in particular squid and nautilus, are difficult to maintain in captivity (Bidder, 1950). A recent study (Kier, 1989) examines the functional morphology of the musculature of the lateral fins of squid and cuttlefish. The fins are of interest because they also consist of a tightly packed, three-dimensional array of muscle, yet they produce rhythmic undulatory waves used in locomotion and hovering. This stereotyped movement makes the fins particularly amenable to experimental analysis. In addition, cuttlefish are more tractable experimental animals than squid or nautilus.

An analysis of the functional morphology of the fins of cuttlefish and squid (Kier, 1989) generated a number of specific predictions of the role of the various muscle and connective tissue arrangements in producing movement and providing skeletal support. The present study is designed to test these predictions with an electromyographic analysis of the muscles of the fins of the cuttlefish *Sepia officinalis*.

Materials and methods

Experimental animals

Specimens of *Sepia officinalis* were supplied by the Marine Biological Association Laboratory, Plymouth, England, and the Stazione Zoologica, Naples, Italy. The dorsal mantle length of the animals studied ranged from 100 to 175 mm. Electromyographic (EMG) electrodes (see below) were implanted in animals anaesthetized with a 1:1 mixture of 7·5% magnesium chloride in sea water (Messenger *et al.* 1985) or 1·0–1·5% ethanol in sea water. The magnesium chloride anaesthetic was found to be more reliable and was used for the majority of the experiments. After a successful experiment, the animal was killed by over-anaesthesia. Portions of the fin containing the EMG electrodes were then removed and fixed in 10% formalin in sea water for later dissection to determine precise electrode location.

Experimental tank and movement monitor

Experiments were performed in a 30·5 cm long × 25·5 cm wide × 12 cm deep Perspex aquarium equipped with running sea water input and variable-level exit. The vertical displacement of the fin was monitored by generating an electrical field in the tank and detecting the voltage measured on a sampling electrode mounted on the fin. Dr Douglas M. Neil, Department of Zoology, Glasgow University, Scotland, provided the design for the circuits used in the movement-monitor

system, which was based on a system used for measuring joint angles in arthropods (Marrelli & Hsiao, 1976). The base of the aquarium was covered by a 1 mm thick stainless-steel plate and an identical plate was placed at the water surface once the animal was in the tank. The upper plate was wired to an Advance Electronics SG 65A function generator which was used to produce a 200–300 mV, 40 kHz sine-wave signal. Approximately 1 mm of insulation was removed from the end of 0·075 mm diameter Teflon-insulated, annealed stainless-steel wire, and the bared end of the wire was attached to the fin margin at the location of the EMG electrodes with a drop of tissue adhesive (Histoacryl, B. Braun Melsungen AG). The wire was also attached to a miniature plastic clamping block (5 mm × 5 mm × 10 mm, design courtesy of Professor K. Liem, Harvard University, Cambridge, MA) that was sutured to the dorsal surface of the mantle, leaving sufficient wire between the attachment point on the mantle and that on the fin so that fin movement was not restricted or affected. This sensing electrode was attached to a circuit that served to filter, rectify and amplify the signal detected at any vertical location in the field, producing an output voltage that was proportional to the distance above the bottom plate in the aquarium. The movement monitor therefore provided a continuous measure of fin location that was recorded on an instrumentation tape recorder along with the EMG signals (see below).

Electromyography

An initial attempt was made to use bipolar, fine wire electrodes for EMG recordings (Basmajian & Stecko, 1962; Gans & Gorniak, 1980; Loeb & Gans, 1986). The thinness and flexibility of the fins, however, made electrode placement with this technique difficult and unreliable. Instead, pairs of fine tungsten wire electrodes were individually implanted in the musculature of the fin.

The electrodes were made as follows. Tungsten wire (0·250 mm diameter, Clark Electromedical Instruments, Reading, UK) was etched in a sodium nitrite solution with electrical current to form a sharp tip. The wire was then cut approximately 3–4 mm from the tip and a tight loop was formed at the cut end. The stripped end of 0·075 mm Teflon-insulated annealed stainless-steel wire was tied to the loop and then soldered (immersion in orthophosphoric acid aided soldering). The joint was then painted with silver paint, encapsulated in a small bead of epoxy resin and then coated with insulator resin (Epoxylite Resin, Clark Electromedical Instruments, Reading, UK). The insulator resin was removed from the tip of each electrode by scraping with a fine scalpel blade, forming a bared tip approximately 1 mm long. The wire leads of each bipolar electrode were then glued together with cement along their length and soldered to a twin lead connector.

The electrodes were implanted in the fin musculature with the animal under anaesthesia (see above). A small (1 cm diameter) patch of epidermis and dermis was removed from the fin, exposing the fin musculature. The electrodes were then inserted into the muscle until the bead of epoxy was level with the surface of the fin and then covered with a thin layer of tissue adhesive (Histoacryl). Electrode pairs were inserted in such a way that their tips were separated by approximately

2–4 mm. Two bipolar electrodes were typically implanted in each experiment. The leads were anchored to the dorsal surface of the mantle in the same clamp used for the movement-monitor electrodes. Sufficient length was left between the anchoring point and insertion point in the musculature so as not to restrict or affect fin movement.

The EMG electrodes were connected either to a Neurolog NL104 a.c. preamplifier or to an Isleworth Electronics A103 pre-amplifier. Output from the preamplifiers was further amplified with Neurolog NL104 a.c.–d.c. amplifiers, filtered with Neurolog NL125 filters (typically set to pass a 20 Hz to 50 kHz bandwidth) and recorded on magnetic tape with a Hewlett Packard 3960 Instrumentation FM tape recorder. The signals were monitored with a Tektronix 5111 storage oscilloscope. All recordings were made at a tape speed of 15 inches s^{-1}. Chart recordings of sequences on tape were made on a Gould Brush chart recorder using a tape recorder play-back speed of 15/16 inches s^{-1}, thereby transforming the input to lie within the recorder bandwidth.

Quantitative comparisons of EMG activity were made as follows. The FM tape recordings of sequences of EMG activity were first passed through a full wave rectifier and then through a low-pass RC filter. The time constant for the RC filter was set at 400 ms and the tape recorder was played back 16 times slower than real time, resulting in an apparent time constant of 25 ms. Both the raw EMG signal and the averaged EMG signal were reproduced on the chart recorder along with the movement-monitor recordings of fin position. The movement-monitor trace was used to determine the beginning of the up and the down phases of fin movement. The records were placed on a Numonics model 2210 digitizing tablet (Numonics Corp., Montgomeryville, PA) interfaced with a microcomputer, and the area under the averaged EMG trace, the duration and the amplitude were calculated for each up and down phase using Sigma-Scan software (Jandel Scientific, Corte Madera, CA). Statistical comparisons between various parameters were made using routines available in Sigma-Scan. The graph shown in Fig. 3 was plotted using Statgraphics software (Rockville, MD) for a microcomputer.

Cuttlefish fin functional morphology

Fin microanatomy and ultrastructure

A detailed description of the morphology, microanatomy and ultrastructure of the fins of the cuttlefish is provided by Kier (1989). The following summarizes the major features of this description.

The fins extend laterally on each side along the length of the mantle. The fins lack both hardened skeletal support elements and fluid-filled cavities and consist of tightly packed muscle fibres arranged in three mutually perpendicular directions (Fig. 1). The muscle fibres principally originate and insert on three collagenous connective tissue fasciae: a dorsal and a ventral fascia each situated immediately beneath the dermis on the dorsal and ventral surface of the fin and a median fascia

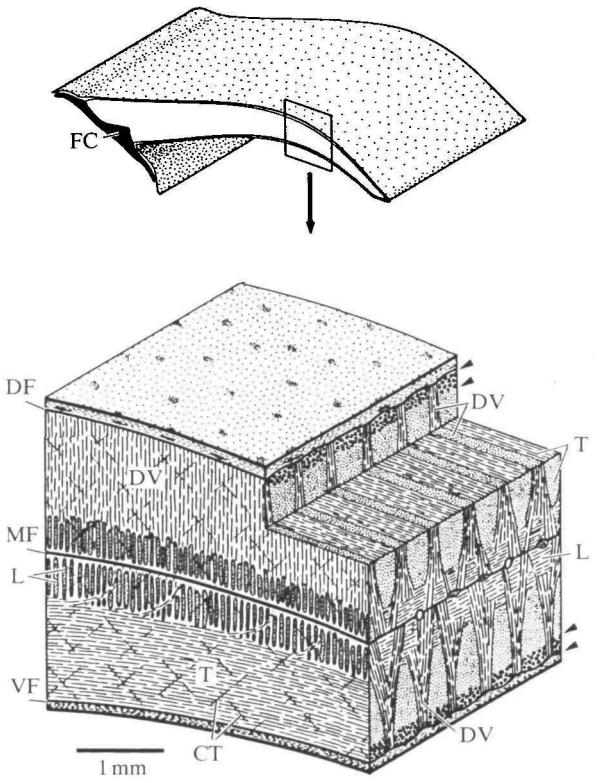

Fig. 1. Schematic diagram of the fin of *Sepia officinalis* showing the arrangement of the muscle and connective tissue fibres. CT, crossed oblique connective tissue fibres; DF, dorsal connective tissue fascia; DV, dorsoventral muscle; FC, fin cartilage; L, longitudinal muscle; MF, median connective tissue fascia; T, transverse muscle; VF, ventral connective tissue fascia. The arrowheads delimit the dorsal and ventral zones of transverse muscle fibres with more extensive mitochondrial cores (the oxidative fibres). The scale bar indicates the scale for the lower portion of the diagram. The figure is adapted from Kier (1989).

that divides the fin into dorsal and ventral portions. Dorsal and ventral transverse muscle bundles extend laterally towards the fin margin from their origin on the fin cartilage at the base of the fin. As they extend towards the margin, muscle fibres branch off from the transverse muscle bundles to insert on the median fascia. The transverse muscle bundles are separated from one another by dorsoventral muscle fibres that have their origin and insertion on the connective tissue fasciae of the fin. The dorsoventral muscle fibres in the dorsal portion of the fin have their origin and insertion on the dorsal and median fasciae whereas those of the ventral portion have their origin and insertion on the ventral and median fasciae. Longitudinal muscle layers are situated adjacent to the dorsal and ventral surface of the median fascia (Kier, 1989).

The transverse muscle bundles contain two distinct zones of muscle fibres (Kier,

1989). In a narrow zone adjacent to the dorsal and ventral fasciae of the fins are cells with a significantly larger mitochondrial core than that of the other muscle cells of the transverse muscles (Fig. 1). These two zones resemble the analogues of red and white muscle previously reported in the mantle musculature of squid and cuttlefish (Bone *et al.* 1981; Mommsen *et al.* 1981). In the mantle, muscle fibres with a more extensive mitochondrial core are specialized for oxidative metabolism whereas those with a less extensive core primarily use anaerobic glycolysis. The cells of the dorsoventral and longitudinal muscles lack zones of muscle fibres with the larger mitochondrial core.

A meshwork of crossed collagenous connective tissue fibres is present within the transverse and dorsoventral muscle masses of the fin. These fibres extend from the median fascia to the superficial fasciae at an angle of approximately 45° relative to the muscle fibres in which they are embedded (Fig. 1). The fibres are only present in transverse planes, i.e. vertical planes perpendicular to the long axis of the mantle and fins.

Proposed function of muscle and connective tissue

While a cuttlefish is swimming or hovering, undulatory waves travel along the length of the fin. The waves may travel in either direction, depending on whether the animal is swimming backwards or forwards. When it is resting on the substratum or hovering, small-amplitude waves are common. Undulatory waves of higher frequency and amplitude are observed during feeding or rapid locomotion and manoeuvring.

The fins of cuttlefish resemble other muscular hydrostats (Kier & Smith, 1985) in which the musculature serves as the effector of movement and in addition provides the support for movement. The fin is a structure that is constant in volume; muscle tissue is essentially incompressible, there is no significant flow of fluid into or out of the fin, and there are no compressible gas-filled spaces in the fin. Because the fin is constant in volume, support for movement can be provided by the various muscle arrangements of the fin by virtue of the fact that a decrease in one dimension must result in a compensatory increase in another dimension (Kier, 1989).

Movement of a given portion of the fin during the passage of a wave involves sequential bending dorsally and then ventrally. To bend the fin dorsally, the musculature must reduce the width of the dorsal portion of the fin relative to the ventral portion. Contraction of the dorsal transverse muscle bundles will provide the lateral compressional force required to reduce the width of the dorsal portion of the fin. This contraction will cause significant dorsal bending of the fin only if the compression is resisted on the ventral portion of the fin; otherwise, this force will simply pull the fin margin medially, reducing the width of the fin. Because the fin is a constant-volume structure, a decrease in width must result in an increase in the thickness, the length, or both. The longitudinal muscles are arranged such that they could resist increase in length and the dorsoventral muscles are arranged such

that they could resist increase in thickness. Without support from some other component of the fin, bending requires simultaneous contractile activity of all three muscle orientations.

The role of the various muscle arrangements in producing movement and providing support for movement can be predicted on the basis of the above analysis. Dorsal bending of the fin probably involves simultaneous contractile activity of the dorsal transverse muscle bundles and ventral dorsoventral muscle bundles. Ventral bending requires simultaneous contractile activity of the ventral transverse muscles and dorsal dorsoventral muscles. These movements also require contractile activity in the longitudinal muscles, providing control of the longitudinal dimension of the fin.

These simple predictions must be refined and expanded to incorporate the additional observations of the ultrastructure of the muscle cells and the connective tissue fibres embedded in the muscle. The two muscle fibre types in the transverse muscles probably serve different functional roles, as in the mantle (Kier, 1989). We hypothesize that transverse muscle cells with a more extensive mitochondrial core are oxidative and are responsible for creating the almost constant, low-amplitude undulatory fin waves used during hovering or while the animal is resting on the substratum. The transverse muscle fibres with a less extensive mitochondrial core are probably recruited during brief bursts of rapid locomotion and manoeuvring.

Zones of muscle fibres with an extensive mitochondrial core are not present in the longitudinal and dorsoventral muscle masses. The lack of such zones of fibres suggests that some other component of the fin provides the resistance to lateral compression caused by contraction of the oxidative transverse muscle fibres during gentle fin beating. Kier (1989) suggests that the obliquely oriented connective tissue fibres of the fin may provide this support. A simple mechanical analysis of a block of muscle fibres of constant volume with connective tissue fibres oriented at an angle of 45° to the muscle fibres suggests that shortening or lengthening of the muscle fibres of the block will place the connective tissue fibres in tension. Thus, lateral compression of the fin due to contraction of the oxidative muscles during gentle fin beating may be resisted by the obliquely oriented connective tissue fibres of the fin. During vigorous fin beating, it is likely that all three muscle orientations are active.

The predictions of the above analysis of the functional morphology of *Sepia* fins can be summarized as follows. The gentle fin beating is produced by contraction of the putative oxidative muscle fibres of the transverse muscle masses. EMG activity would be expected in the musculature of the dorsal portion of the fin in the up phase of the fin beat but not in the down phase. Musculature of the ventral portion of the fin would be active in the down phase of the fin beat but not in the up phase. During vigorous fin beating, however, EMG activity would be expected in the musculature of the fin during both the up and the down phases of the fin beat, as the dorsoventral and longitudinal muscles provide support for contraction of the transverse muscles on the opposite side.

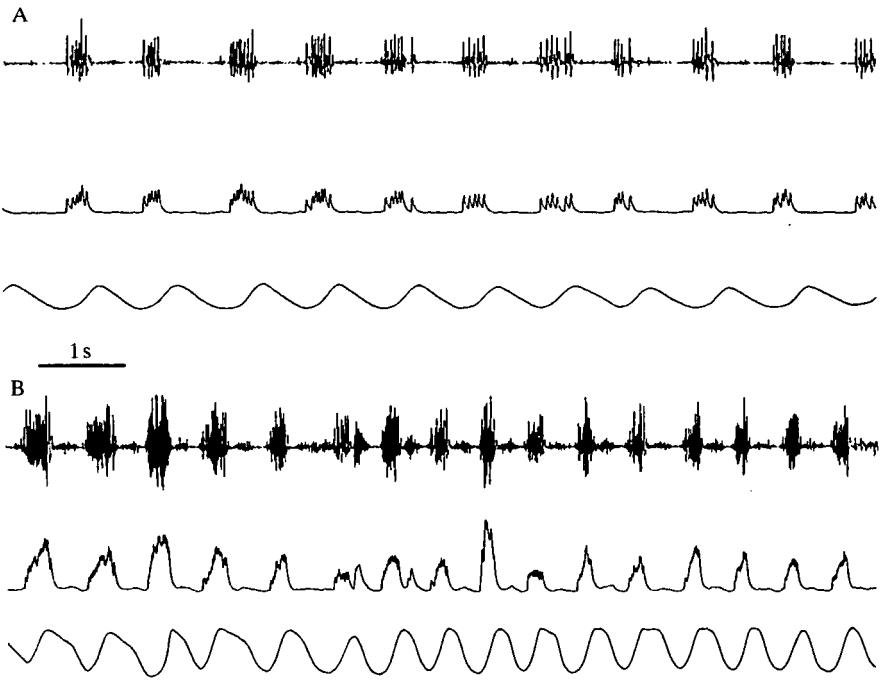

Fig. 2. Chart recordings of EMG activity from dorsal dorsoventral and dorsal transverse muscle bundles of fin (top tracing), a tracing of the same EMG signal following rectification and filtering (middle tracing), and a tracing of the output from the movement-monitor circuitry indicating the vertical position of the edge of the fin at the approximate location of the EMG electrodes. The recordings shown in A and B are from the same bipolar electrode and all filter, amplifier, recorder, etc. settings are identical in the two sequences. Note that the frequency and amplitude of fin movement are greater in the tracing in B than in A and significant EMG activity is recorded on the down phases of the cycles in B but little EMG activity is recorded on the down phase of the cycles in A. The dorsal mantle length of the specimen was 175 mm.

Results

Recordings of approximately 1400 fin-beat cycles were made from 11 experiments, with two bipolar electrodes and one or two movement-monitor electrodes per experiment. In most recordings the fin beats ranged from gentle undulatory waves when the animal was hovering during low rates of water flow into the experimental tank to vigorous, high-amplitude and high-frequency waves when the flow rate was increased. The specific amplitudes and frequencies varied from animal to animal and we therefore make quantitative comparisons only within single specimens. In general, these differences were size-related, with larger animals showing lower-frequency and higher-amplitude fin waves.

Fig. 2 shows EMG recordings from an electrode located in the dorsal portion of the fin within the transverse and dorsoventral muscle bundles but not within the dorsal longitudinal muscle. (The thinness of the various muscle bundles precluded reliable electrode placement within a single muscle orientation. For instance, the

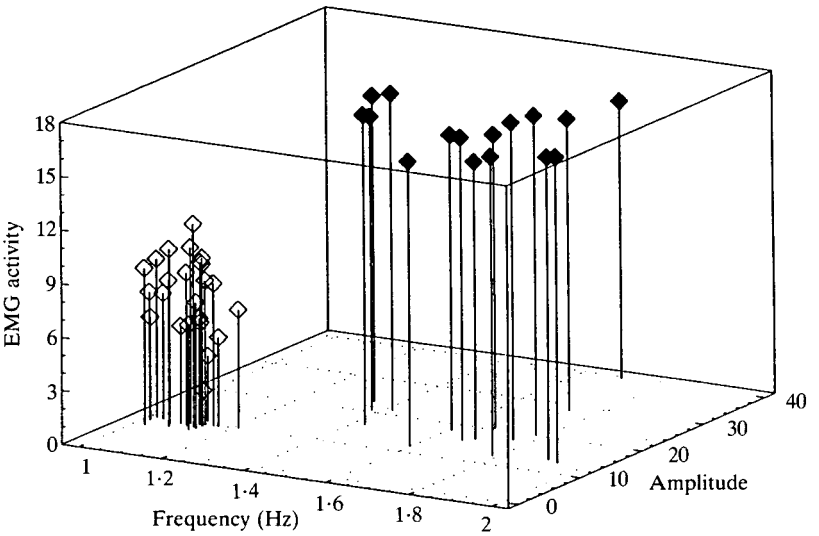

Fig. 3. Graph showing quantification of gentle and vigorous fin-beat sequence parameters from the same electrode as illustrated in Fig. 2. Note that the lower-amplitude and lower-frequency cycles from the gentle sequence (◇) show a smaller area under the rectified, averaged EMG trace for the down phase of the cycle than the higher-frequency and higher-amplitude cycles (◆) from the vigorous sequence. The units of amplitude and area under the rectified, averaged EMG trace are arbitrary.

dorsoventral muscle bundles in the fins of the animal from which the recordings illustrated in Fig. 2 were obtained were approximately 0·2 mm thick and the transverse muscle bundles were approximately 0·5 mm thick.) The figure shows a sequence of gentle fin beats and a sequence of more vigorous fin beats from a continuous recording session. The two sequences are from the same electrode and all amplifier, filter, tape and chart recorder settings are identical. The records also include the rectified, averaged EMG signal and movement-monitor output, also with identical settings. During the series of gentle fin beats (Fig. 2A), significant EMG activity of the dorsal muscles is observed only on the upward phase of each fin-beat cycle. During the sequence that included vigorous fin beats (Fig. 2B), significant EMG activity is also observed during the downward phase of the fin-beat cycle. Note that both the amplitude and the frequency of the fin beat are increased in the sequence shown in Fig. 2B relative to those shown in Fig. 2A.

The EMG activity of the dorsal muscle and other parameters of 16 cycles from the vigorous sequence and 25 cycles from the gentle sequence were compared quantitatively. Fig. 3 shows that the amplitude and frequency of the fin-beat cycles of the gentle and vigorous sequences are distinct. More significantly, the area under the rectified, averaged EMG trace for the down phase of the cycle is highly differentiated in the two sequences. A Student's *t*-test of the area under the rectified, averaged EMG curve for the down phases of the gentle *versus* vigorous sequences confirms that the means of the samples are different ($t = 7{\cdot}826$,

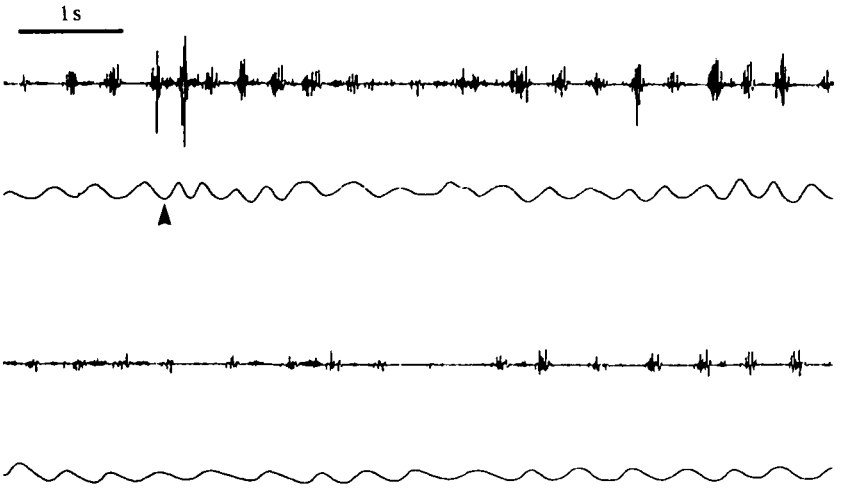

Fig. 4. Chart recordings of EMG activity from the dorsoventral and transverse muscle bundles of the ventral portion of the fin (top tracing), and a tracing of the output from the movement-monitor circuitry indicating vertical position of edge of fin at approximate location of the EMG electrode (bottom tracing). Note that, in contrast to the recordings from the dorsal portion of the fin (e.g. Fig. 2), significant EMG activity is recorded on the down phase of the gentle fin-beat cycles. The EMG activity recorded during the up phase of the cycle is greater in the higher-amplitude and higher-frequency cycles (arrowhead). The dorsal mantle length of the specimen was 123 mm.

$P \ll 0{\cdot}001$). To demonstrate that the increase in EMG activity during the down phase of the vigorous cycles relative to that of the gentle cycles is more than simply a general increase in EMG activity for the entire fin musculature, the EMG activity recorded during the down phase of the cycle was expressed as a percentage of that recorded during the previous up phase. The means of these two samples are indeed significantly different $\{t = 2{\cdot}869,\ P \ll 0{\cdot}001$ [mean of gentle = 17·0 % (S.D. = 7·4 %); mean of vigorous = 30·4 % (S.D. = 21·1 %)]}. The means of the amplitude and frequency of the two sequences are also different (amplitude: $t = 28{\cdot}905,\ P \ll 0{\cdot}001$; frequency: $t = -16{\cdot}266,\ P \ll 0{\cdot}001$).

Fig. 4 shows EMG recordings from an electrode implanted in the ventral portion of the fin. This sequence is of interest in comparison with the recordings from the dorsal portion of the fin because a significant burst of EMG activity is observed primarily on the down phase of the fin-beat cycle. Note that the cycles of higher frequency and amplitude show greater EMG activity during the up phase of the beat than that observed during the up phase of the lower-frequency and lower-amplitude cycles.

Fig. 5 shows EMG recordings from an electrode implanted in the dorsal portion of the fin. Dissection revealed that one of the electrode tips extended down through the dorsoventral and transverse muscle bundles into the dorsal longitudinal muscle. The other electrode tip was located within the dorsal transverse and dorsal dorsoventral muscle bundles. This sequence includes a range of amplitude

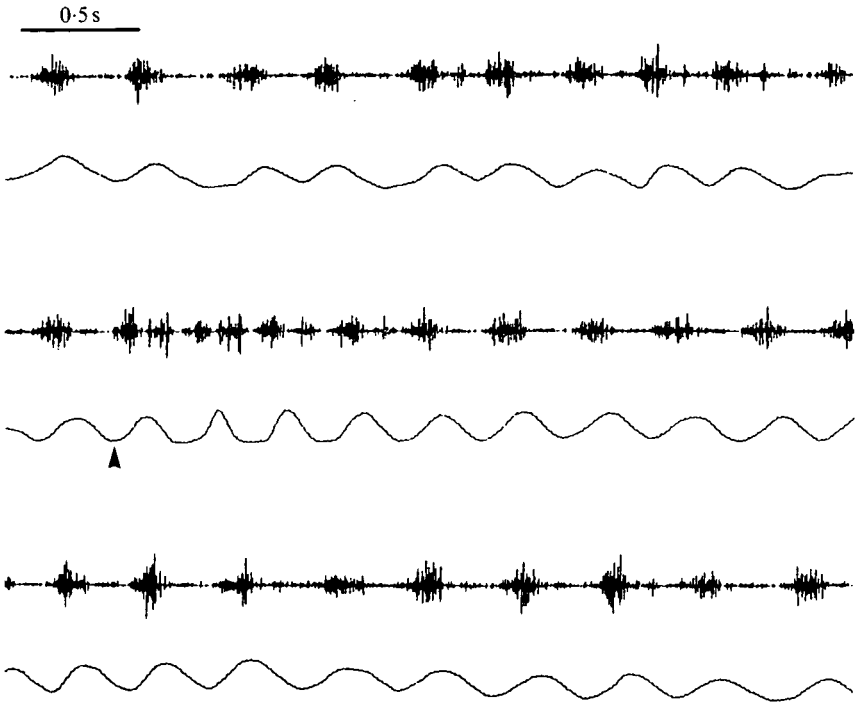

Fig. 5. Chart recordings of EMG activity from the dorsoventral, transverse and longitudinal muscle bundles of the dorsal portion of the fin (top tracing), and a tracing of the output from the movement-monitor circuitry (bottom tracing). Note that the sequence begins with low-amplitude and low-frequency fin movements that show little EMG activity on the down phase of the fin beat. Several higher-frequency and higher-amplitude fin-beat cycles (arrowhead) occur in the middle of the sequence and show a dramatic increase in EMG activity during the down phase. The dorsal mantle length of the specimen was 126 mm.

and frequency of fin beating. Note that the less vigorous fin-beat cycles at the beginning and the end of the sequence show significant EMG activity on the up phase of the cycle but little EMG activity during the down phase. However, several vigorous cycles in the middle of the sequence show a remarkable increase in EMG activity during the down phase of the cycle.

A consistent pattern of activity of the dorsal and ventral musculature of the fin was observed in this study. During gentle fin movements, significant electrical activity was only recorded from the dorsal musculature when the fin moved upwards and from the ventral musculature when the fin moved downwards. During vigorous fin movement, however, the EMG activity became biphasic; electrical activity was recorded from the dorsal or ventral fin musculature during both the upward and the downward phases of the cycle. In summary, the major difference between the gentle and vigorous sequences is the increased electrical activity during the phase of the cycle when the muscle is providing support.

Discussion

These recordings demonstrate two distinct patterns of EMG activity and confirm the earlier predictions of the function of the fin musculature. During gentle fin movements, the burst of EMG activity in the dorsal portion of the fin during the up phase is probably contractile activity of the oxidative fibres of the dorsal transverse muscle bundles. Little EMG activity is recorded in the ventral portion of the fin during this phase. The lack of EMG activity in the ventral portion of the fin is consistent with the prediction that a component other than the musculature provides support for gentle fin movements. This prediction is based on the observation that a zone of oxidative muscle fibres is present only in the transverse muscles (Kier, 1989), and muscular-hydrostatic (Kier & Smith, 1985) support for these fibres would require muscle fibres with similar aerobic capacity in the longitudinal and dorsoventral muscle bundles. Kier (1989) suggests that the crossed oblique connective tissue fibres provide this support. The EMG recordings are consistent with this prediction (see also Gosline & Shadwick, 1983*a*,*b*; Gosline *et al.* 1983). Likewise, recordings during the down phase of a gentle fin-beat cycle show EMG activity in the ventral portion of the fin but little EMG activity in the dorsal portion.

During rapid locomotion and manoeuvring, the fin-beat amplitude and frequency are increased. EMG recordings of these more vigorous fin movements showed activity during both the up and the down phase of the fin-beat cycle for both the dorsal and the ventral portion of the fin. The large burst of EMG activity observed in the dorsal portion of the fin musculature during the up phase is probably due to contractile activity of the dorsal transverse muscle bundles and presumably involves a larger proportion of the fibres, including the anaerobic glycolytic muscle fibres of the dorsal transverse muscle bundles (Kier, 1989). EMG activity is recorded simultaneously in the ventral portion of the fin. This is interpreted to be contractile activity of the dorsoventral and longitudinal muscles of the ventral portion of the fin, providing increased support for contraction of the dorsal transverse muscles. This increased support is necessary as the force and amplitude of the fin beat increase. Similarly, EMG activity was observed in the ventral portion of the fin during both the down and the up phases of vigorous fin-beat cycles.

This discussion implies that the dorsoventral musculature of the fin is responsible simply for maintaining the thickness of the fin. However, this musculature may serve a more active role in bending the fin during vigorous fin movements (Kier, 1989). For example, bending the fin upwards could result from lateral extension of the ventral portion of the fin relative to the dorsal portion. Contraction of the ventral dorsoventral muscle bundles would create lateral extension of the ventral surface and bending would occur as long as dorsal transverse muscle activity prevented lateral extension of the dorsal surface. It is likely that these two conditions (transverse muscle shortening with dorsoventral muscle activity for support and dorsoventral muscle shortening with transverse muscle activity for support) represent two end points in a continuum of relative

contraction of the transverse and dorsoventral muscle bundles. Of significance for this study is the fact that simultaneous shortening of both muscle orientations would create a more pronounced bend than either shortening of one orientation with contractile activity of the other for support or, as in the gentle fin movements, contraction of transverse muscle bundles with the crossed oblique connective tissue fibres providing support.

This study has thus provided evidence to support general hypotheses on the production of movement in muscular-hydrostats. It is the first EMG study that tests models of the role of muscle in both producing and supporting bending movements. Furthermore, it corroborates hypotheses on intramuscular differential function proposed by Kier (1989): two distinct patterns of muscular activity exist in the transverse muscles. As yet it cannot be demonstrated that this reflects recruitment of the two fibre types, but the present results are entirely consistent with this hypothesis.

It is possible that our interpretation of the observed EMG activity during vigorous fin beating might be complicated by 'cross-talk' (Mangun *et al.* 1986) from muscles on the opposite fin surface. For example, the burst of EMG activity recorded during the down phase of the cycle from the transverse and dorsoventral muscles of the dorsal portion of the fin might simply be volume-conducted electrical activity from the ventral fin musculature. Several methods are available for determining whether EMG signals are contaminated with cross-talk, but they did not prove feasible in our study (Loeb & Gans, 1986; Mangun *et al.* 1986). Although we cannot eliminate the possibility of cross-talk in our recordings, the presence of the median fascia separating the dorsal and ventral portions of the fin makes cross-talk less likely.

The discussion above has focused on the EMG activity at one point in the fin as that portion undergoes dorsal and ventral bending movements. Creation of an undulatory wave in the fin requires sequential contraction along the length of the fin. Recordings from adjacent EMG electrodes showed a shift in phase either in advance of or behind that of the adjacent electrode, depending on the direction of propagation of the undulatory wave. Observations of swimming cuttlefish (Russell & Steven, 1930; Bidder & Boycott, 1956; Boycott, 1958; Kier, 1989) reveal not only that waves pass in either direction along the fin but also that during yawing movements the direction of propagation on one side of the animal may be opposite to that of the other side. In addition, hovering animals are sometimes observed to initiate waves at each end of the fin simultaneously, which then meet and cancel in the middle of the fin. Clearly the control and coordination of the fin-beat amplitude, force and direction are complex. The neural control of fin movement has not been addressed in this study. Preliminary evidence for the existence of mechanoreceptors in the fin has been reported by Kier *et al.* (1985). The distribution of these putative mechanoreceptors along the entire length of the fin is consistent with their suggested role in coordination of the undulatory waves of the fin and they deserve further study in the context of the analysis of fin mechanics outlined above.

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