THE TIMING OF MUSCLE STRAIN AND ACTIVATION DURING STEADY SWIMMING IN A SALAMANDER, AMBLYSTOMA MEXICANUM

by

KRISTIAAN D’AOÛT, PETER AERTS and FRITS DE VREE

(Department of Biology, University of Antwerp (U.I.A.), Universiteitsplein 1, 2610 Antwerpen, Belgium)

ABSTRACT

Muscle function during undulatory swimming is commonly described by the relative timing of muscle activity (EMG) in the strain cycle and has been studied for several fish species, ranging from anguilliforms to carangiforms. This paper supplies the basic data for steady swimming at an intermediate speed in a salamander (Ambystoma mexicanum). The strain cycle of the swimming muscles is estimated using high-speed video recordings (500 frames s⁻¹) of an animal swimming in a flow tank. Synchronously, EMG signals of six epaxial myomeres were recorded using bipolar electrodes inserted unilaterally along the body.

The neural stimulation pattern is a head-to-tail travelling wave with a higher speed than the kinematical propulsive wave. The resultant phase delay causes a different muscle recruitment pattern along the body axis, similar to reports for anguilliform fishes like the lamprey (Williams et al., 1989) and the eel (Grillner & Kashin, 1976). The anterior trunk myomeres (up to 45% of the total body length L) are activated purely concentrically (i.e., while shortening). Caudal to the 45% L position, the muscles show an increasing proportion of eccentric activation.

This pattern suggests that there is gross positive work delivery along the body axis, with a limited amount of negative work in the tail tip. This is in agreement with the general conclusions for fish of Wardle & Viderer (1994), where this recruitment pattern is associated with a body shape without a distinct tail blade and with direct and continuous thrust production along the body.

KEY WORDS: swimming, Ambystoma mexicanum, electromyography.

INTRODUCTION

Undulatory swimming is characterised by a propulsion-generating kinematical wave travelling backward along the body. Breder (1926) defined a classification for undulatory swimmers, based on the number of waves on the body. His model ranges from anguilliforms (more than half a wave on the body), via carangiforms (less than half a wave on the body), to ostraciiforms (only the tail shows clear undulations). Although Breder’s (1926)
general classification is prone to criticism since it does not originate from precise kinematic analyses (VIDELER, 1993), it has since then been widely adopted.

Recently, the swimming mechanism of several undulatory swimming fish has been extensively studied, allowing for a more functional understanding of the diversity among undulatory swimmers. The fish species studied so far reflect the continuum from anguilliforms to carangiforms and include (in order of increasing bodywave length): eel (GRILLNER & KASHIN, 1976), lamprey and trout (WILLIAMS et al., 1989), mackerel, saithe (WARDLE & VIDELER, 1993), carp (VAN LEEUWEN et al., 1990) and scup (ROME et al., 1993). All studies used a combination of kinematical data and electromyographical recordings to analyse the muscle recruitment pattern along the body axis. Based on the studies mentioned, and taking also into account the muscle-mechanical data from ALTRINGHAM et al. (1993) and ROME et al. (1993), a general functional model has been proposed by WARDLE & VIDELER (1994). They used the available data to compare the muscle recruitment patterns and linked them to swimming style and body morphology.

It is postulated that fish without distinct tail blades (e.g., eel and lamprey, 'anguilliforms') and with laterally flattened bodies concentrate on local work output, resulting in a direct and continuous thrust production (thus positive work output) in the greater part of the body. Fish with a streamlined body, a narrow caudal peduncle and a well-formed tail blade (e.g., saithe, a 'carangiform') generate thrust mainly in the tail blade, from work produced in the rostral myomeres and transmitted via the caudal myomeres producing negative work (ALTRINGHAM et al., 1993).

This paper presents kinematical and electromyographical data for a salamander, Ambystoma mexicanum, that has no distinct tail blade and shows 'anguilliform' swimming kinematics which largely compare to the eel's and the lamprey's. It has a different phylogeny and shows major myological differences (being a tetrapod) with the fish studied to date. It will be evaluated if, and eventually how, the present results fit into the WARDLE & VIDELER (1994) model.

MATERIAL AND METHODS

During the experiments, an adult specimen of the neotenic mexican axolotl, Ambystoma mexicanum (Amphibia: Caudata; total body length L: 0.205 m; total body mass: 72.4 g) was placed in the working section (0.1 × 0.15 × 0.4 m) of a flow tank with a water speed set at approximately 0.3 m s⁻¹, being the volatile swimming speed of adult axolotl under unstressed conditions (unpublished results).
High-speed video recordings (500 frames per second) were made using a NAC-1000 video system registering a lateral and, by means of a mirror, a ventral view of the swimming animal. Kinematical data were gathered by digitizing the dorsal midline of the animal every fourth frame (resulting in a time resolution of 0.008 s) and further digital and graphical treatment. The exact swimming speed of the animal was determined using its measured speed relative to the fixed camera and the flow speed measured by a posteriori digitization of suspended particles. The muscle strain cycle was determined indirectly by assuming that the maximal lateral deviation of a certain body point represents the longest and shortest muscle fibre length on the convex and concave side, respectively. The relatively simple architecture of the epaxial myomerite with nearly parallel running fibers in *Ambystoma mexicanum* gives morphological evidence for this direct link.

Electromyography (EMG) of six unilateral (left) epaxial myomerites at 30, 45, 65, 70, 75 and 80% L was performed by implantation of bipolar NiCr electrodes. The signals were amplified 2000 x using Tektronix 26A2 differential pre-amplifiers and Honeywell Accodata 117 DC amplifiers and stored on a 14-channel tape recorder (Honeywell 96 FM). The EMG on- and offset times were determined on the raw EMG's. Synchronisation of kinematics and EMG was done using a high-luminance LED giving a synchronous optical signal on the video frames and an electrical signal stored on the EMG tape.

The spatial propagation of both kinematical and electromyo graphical waves as a function of time was modelled by a significant linear regression (p < 0.05 in both cases).

The epaxial muscle mass along the body axis was estimated by measuring the epaxial muscle surface on 3 mm thick transversal slices of an individual similar to the experimental animal.

From the best sequence, five complete swimming cycles were selected for further detailed analysis. The results were compared with and confirmed by three shorter sequences at a similar swimming speed.

**RESULTS**

**Kinematics**

During the analysed sequence of five complete cycles, the animal swam at a virtually uniform speed of 0.308 m s\(^{-1}\) (specific swimming speed 1.50 bodylengths s\(^{-1}\) (L s\(^{-1}\))), a normal swimming speed under unstressed circumstances. It had a body wave length of 0.180 m (88% L) and a swimming frequency of 3.79 Hz. The swimming kinematics compare to those from 'anguilliform' fish, but with a longer wavelength (59% L for eel and lamprey, GRILLNER & KASHIN, 1976; WILLIAMS et al., 1989). This general similarity seems surprising since the axolotl's swimming muscles are much more concentrated in the trunk region (see Fig. 2B).

Figure 1B shows the muscle strain cycle for the six studied body positions. The strain cycles will further be described using ALTRINGHAM & JOHNSTON’S (1990b) definitions. In one complete cycle of 360° the following stages are recognised: 0°/360°: muscle at resting length and lengthening; 90°: muscle at maximum length; 180°: muscle at resting length and shortening; 270°: muscle at minimum length. The temporal succession
of strain phases from head to tail reflects the backward travelling of the propulsive wave, here at a speed of 0.668 m s$^{-1}$ (3.25 L s$^{-1}$) relative to the body.

Fig. 1. Representation of the EMG- and kinematical cycles during steady swimming in Ambystoma mexicanum. The time axis is the same for both data types. A. The phase of EMG activity in the studied body positions, indicated by black bars. B. The lateral amplitudes at the studied body positions, as an estimate of the strain cycle. Positive values: fibres relatively long. Negative values: fibres relatively short. Notice the difference in ordinate scaling.
Fig. 2. Steady swimming in *Ambystoma mexicanum*. A. Diagram showing the strain cycle (oblique solid and dashed lines) and EMG activity (grey surface) by means of linear regressions through the data points. The meaning of the strain phases is explained in the text and indicated in the inset. B. Transverse surfaces of epaxial muscle (both sides) along the body, measured from 3 mm thick slices. The muscle distribution shows a sharp decline in the tail region, which is in contrast to the much smoother profile for lamprey and eel (Hess, 1983).
Electromyography

Figure 1A shows the on- and offset of EMG activity at the six studied body positions. Like the kinematical wave, the muscle activation also shows a backward travelling wave, with a higher speed of 1.06 m s\(^{-1}\) (5.17 L s\(^{-1}\)). The on- and offset times run parallel, i.e., the EMG duration remains constant along the body and occupies 19.1% of the total cycle duration, which corresponds to 68.8° of the strain cycle.

Muscle recruitment

The difference in backward speed of the kinematical and EMG cycles inevitably results in a difference in muscle recruitment pattern, the muscles at different longitudinal body positions being activated during a different phase in their strain cycle. This phenomenon is shown in Fig. 2A, where the significant linear regressions of muscle strain and EMG on- and offset of the second wave in Fig. 1 are used for simplicity. The solid and dashed oblique lines represent the iso-strain lines (see inset for a schematic representation), while the grey area indicates the period of EMG activity.

At the rostralmost positions (up to about 45% L) the muscles are activated while their strain passes from 90° to 270°, thus while shortening (i.e., concentric activation). More caudally an increasing part of their activation occurs while lengthening, i.e., the muscles are partially activated eccentrically. Caudal to the 80% L body position, no electromyograms could be recorded for experimental reasons (i.e., very few fibres are present in this area, see also Fig. 2B). However, if we assume that the observed linear relationship between 30% L and 80% L remains valid, we expect the muscles to be purely eccentrically activated.

DISCUSSION

Determination of the timing of muscle stimulation in the strain cycle for different longitudinal body locations is a powerful tool to investigate muscle function during swimming. One must however be aware that the complete picture can only be drawn by incorporating muscle mechanical data, allowing for quantitative power determination. This type of data is recently getting available for slow and fast fish muscle under sinusoidal strain cycles, mimicking the in vivo situation (Altringham & Johnston, 1990a, b; Altringham et al., 1993; Curtin & Woledge, 1993a, b, c; Davies & Johnston, 1993; Davies et al., 1995; Johnson et al., 1994; Johnston et al., 1993; Mutungi & Johnston, 1993; Rome et al., 1993).
The aim of this study was not to measure exact power output, but to get a qualitative estimation by using the strain-stimulation relationship in epaxial muscle at different locations. It is likely that the rostral muscles produce positive work while the more caudal muscles produce an increasing fraction of negative work. However, three aspects must be considered. First, the region where eccentrical activation is found contains very few muscle (see Fig. 2B) and the resulting negative work, if present at all, will therefore be small in absolute terms. Second, the eccentrical activation takes place just before maximal strain, thus with a minimal displacement. This adds to the production of little work, since work = force × displacement. Third, the muscle fibres (both 'red' and 'white', Willemse, 1977) will have a certain latency resulting in a greater amount of positive work than estimated on the basis of muscle recruitment only (with the assumption of zero latency). From the experimental data and these three aspects we expect that there will be a major positive work production over the body, with eventually a limited amount of negative work in the tail tip.

Wardle & Videleer (1994) evaluated the relative timing of muscle stimulation in the strain cycle for seven fish species, two of them (eel and lamprey) being anguilliforms. As explained in the introduction, they relate the muscle recruitment pattern in these species (where they expect it to give gross positive work output along the body) to the 'anguilliform' body shape without distinct tail fin. Our results concern a species from a different Class (Amphibia) with a (compared to fish) simpler epaxial muscle architecture as found for tetrapods in general. However, it has a tapering tail with few muscles (see Fig. 2B), a wide finfold over the entire tail and most of the trunk (see Fig. 2B) and a considerably greater body wave length. For this species we found a pattern that is in general accordance with the conclusions of Wardle & Videleer (1994).

Thus, our results confirm the validity of this model for the 'anguilliform' swimming mechanism.

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REFERENCES


