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Function of the Dorsal Fin in Bluegill Sunfish: Motor Patterns During Four Distinct Locomotor Behaviors

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ABSTRACT The median fins of fishes are key features of locomotor morphology which function as complex control surfaces during a variety of behaviors. However, very few studies have experimentally assessed median fin function, as most workers focus on axial structures. In particular, the dorsal fin of many teleost fishes possesses both spiny anterior and soft posterior portions which may function separately during locomotion. We analyzed the function of the soft region of the dorsal fin and of the dorsal inclinator (Di) muscles which are the primary muscles responsible for lateral flexion. We used electromyography to measure in vivo Di activity, as well as activity of the red myomeric muscles located at a similar longitudinal position. We quantified motor patterns during four locomotor behaviors: braking and three propulsive behaviors (steady swimming, kick and glide swimming, and C-starts). During the three propulsive swimming behaviors, the timing of Di activity was more similar to that of ipsilateral red myomeric muscle rather than to contralateral myomeric activity, whereas during braking the timing of activity of the Di muscles was similar to that of the contralateral myomeric musculature. During the three propulsive behaviors, when the Di muscles had activity, it was consistent with the function of stiffening the soft dorsal fin to oppose its tendency to bend as a result of the body being swept laterally through the water. In contrast, activity of the Di muscles during braking was consistent with the function of actively flexing the soft dorsal fin towards the side of the fish that had Di activity. Activity of the Di muscles during steady speed swimming was generally sufficient to resist lateral bending of the soft dorsal fin, whereas during high speed kick and glide swimming and C-starts, Di activity was not sufficient to resist the bending caused by resistive forces imposed by the water. Cumulative data from all four behaviors suggest that the Di muscles can be activated independently relative to the myomeric musculature rather than having a single phase relationship with the myomeric muscle common to all of the observed behaviors.

The median fins of most fishes are large, conspicuous structures whose evolutionary origin within the chordate clade probably preceded that of appendicular structures, and yet we presently know remarkably little about how the median fins function during fish locomotion. This is unfortunate because hydrodynamic modeling suggests that interspecific variation in median fin morphology is related to differences in the longitudinal distribution of surface area that tend to correlate with different locomotor tasks such as fast steady swimming, rapid acceleration, and maneuvering (Webb, '84). Our current knowledge of the median fins of teleosts is derived mainly from a small number of studies which are mostly structural and evolutionary in nature, such as Winterbottom's ('74) comparative descriptions of the median fin muscles. With the exceptions of the papers by Arita ('71) and Roberts ('69), the overview of Harris ('53), and the work of Geerlink and Videler ('87), who focused on the relation between fin ray structure and its mechanical

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properties, we have virtually no idea of how median fins are used by fish during locomotion.

In contrast to the scant data available for the function of the median fins, function of the myomeres has been studied intensively for diverse species of fishes that swim using lateral undulations of the vertebral column (Grillner, '74; Blight, '76; Grillner and Kashin, '76; Wallén and Williams, '84; Williams et al., '89; van Leeuwen et al., '90; Rome et al., '93; Jayne and Lauder, '94, '95a). A recurrent finding of these studies of axial muscle function is that myomeric muscle activity during steady lateral undulatory swimming is unilateral, propagates posteriorly, and alternates between left and right sides. Patterns of lateral bending of the vertebral column appear to be a complex result of the timing and amount of muscle activity and complicated interactions between the mechanical properties of the axial structures and the resistive forces of the fluid.

The dorsal inclinator muscles of the dorsal fin consist of many individual segments which collectively extend along a large portion of the entire length of the fish (Winterbottom, '74), in a similar general design to myomeric segmentation. Thus, in light of the motor patterns used by myomeres during swimming and the segmented architecture of both the myomeres and dorsal inclinator muscles, it is useful to examine how dorsal inclinator muscle activity is coordinated with that of the myomeres. For example, one expectation for activity of the dorsal inclinator muscles could be that these muscles are simply activated simultaneously with underlying myomeric muscle at the same longitudinal position. Given the patterns of bending that have been found for the vertebral column of swimming fishes, one might also predict that movements of the compliant soft dorsal fin involve a combination of active (muscle activity) and passive (fluid resistance) mechanisms.

The overall objective of this study is to analyze the locomotor function of the median dorsal fin in a percomorph teleost fish, the bluegill sunfish, *Lepomis macrochirus,* during locomotion. Specifically, we measure both fin movement and the activity of major muscles controlling the fin (dorsal inclinators) during four distinct locomotor behaviors: steady swimming, kick and glide swimming, C-start, and braking. We analyze electromyograms (EMGs) from dorsal inclinator muscles for each of the four behaviors in order to document the diversity and generality of activity patterns of the dorsal fin musculature and to test three specific pairs of alternative hypotheses. First, are the ipsilateral Di muscles activated simultaneously or sequentially? Second, is activity of the Di muscles in or out of phase with the activity of the underlying myomeric muscle? Third, does activity of the Di muscle bend the soft dorsal fin or oppose the tendency of water resistance to bend the fin?

MATERIALS AND METHODS

Animals

Our experiments used six *Lepomis macrochirus* (bluegill sunfish), for which we analyzed the data in detail from the four individuals with the most complete recordings. These four individuals had a mean total length (TL) of 17.3 cm (range 17.0–17.5 cm) and a mean mass of 90.5 g (range 78–102 gm). Bluegill were maintained in separate 40 l aquaria with a 12D:12N photoperiod, and the water temperature was the same as that used for all experiments (19.5 ± 1.5°C).

Image acquisition and analysis

We videotaped all experiments using a NAC HSV-400 high speed video system that recorded 200 images/s. The flow tank used for all experiments had a working section with a cross-sectional area of 19 × 19 cm and a length of 46 cm which was parallel to the direction of the flow of the water. We varied the flow from 0 to approximately 3 TL/s using a variable speed motor to drive a propeller in the tank. We used two cameras to obtain direct lateral and ventral (via a mirror) views of the swimming fish. A 100 Hz square wave generator simultaneously sent output to the video unit and the tape recorder that stored the EMGs; hence, we were able to synchronize movements with EMGs. All experiments involved simultaneous video and electromyographic recording.

We played back the videotapes to a computer which had custom image analysis software that allowed us to superimpose a measuring cursor onto the image of the fish. We expected the dorsal inclinator muscles to resist passive bending as the body of the fish was swept from side to side through the water. Thus, we primarily recorded the kinematic events indicating the times of movement to the left or right for the region of the fish at the base of the most posterior ray of the soft dorsal fin (Fig. 1). We also noted

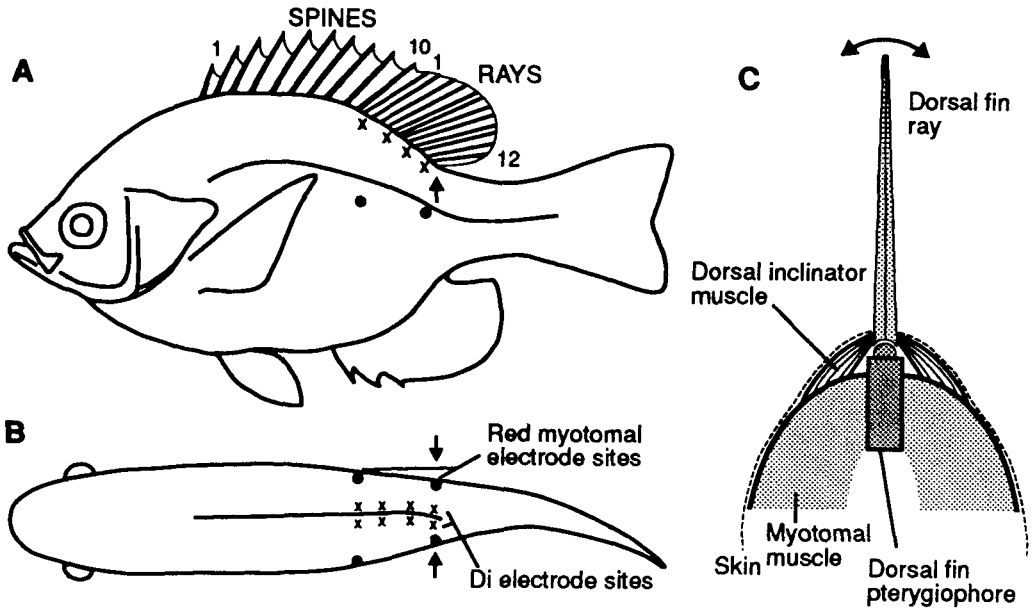


Fig. 1. Lateral (**A**), ventral (**B**), and cross-sectional (**C**) views of a bluegill (*Lepomis macrochirus*) showing the electrode sites and the anatomical position of the dorsal inclinator (Di) muscles. In A and B, x's indicate electrode positions in the four Di muscles on each side of the fin, and the dots indicate electrodes implanted into the red myomeric musculature on each side. Numbers above the dorsal fin in panel A indicate the average number of spines and rays in each portion of the fin. Arrows indicate the longitudinal position of the body that was used as a reference point to determine when lateral displacement was to the right and left.

when the fin protruded laterally beyond the silhouette of the body. Detailed kinematics of swimming behaviors are complex and beyond the scope of this study, and we have presented or will present additional details of kinematics elsewhere for steady swimming (Jayne and Lauder, '95b), kick and glide swimming (in preparation), the escape response (Jayne and Lauder, '93), and braking (in preparation).

Electromyography

To record muscle activity, we used bipolar electrodes made from 0.051 mm diameter stainless steel wire with an uninsulated portion of about 0.5 mm. Additional details of electrode construction and implantation can be found elsewhere (Jayne, '88; Jayne and Lauder, '93). After anesthetizing bluegill with a standard dose of tricaine methanesulfonate, we removed a few scales near the basal region of the soft dorsal fin rays in order to facilitate implanting electrodes percutaneously into the dorsal inclinator (Di) muscles. On each side of the fish (Fig. 1A,B), we placed four electrodes in the Di muscles so that there were at least two fin rays between adjacent sites, and the longitudinal extent of the sites approximately encompassed the entire soft portion of the dorsal fin. We also implanted electrodes into the superficial red portion of two myomeres on each side of the fish with locations that corresponded longitudinally to our most anterior and most posterior electrodes in the Di muscles (Fig. 1A,B) and did not implant electrodes into white myotomal fibers for two reasons. First, centrarchid fishes recruit the superficial red myomeric fibers for both low and high speed undulatory movements (Jayne and Lauder, '93, '94), whereas white fibers in the portions of the myomere that are nearest the Di muscles are recruited only for high speed kick and glide swimming and C-starts (Jayne and Lauder, '95c). Second, when both red and white muscle are recruited, the offset times of red and white fibers within a single myomere are synchronous (Jayne and Lauder, '94). Hence, placing electrodes in the superficial red myomeric muscle allowed us to maximize use of our 12 electrode channels to monitor the timing of myomeric muscle

activity over the entire range of locomotor behaviors involved in the present study. After the experiments, we killed bluegill with an overdose of anesthetic and then dissected the EMG electrodes to verify location. For the Di muscles we analyzed only data from sites in which dissections revealed that both poles of a bipolar electrode were confined entirely to a single segment of the Di associated with one soft dorsal fin ray.

The EMGs were amplified 20,000 times with Grass P511K preamplifiers using a 60 Hz notch filter and a half-amplitude low and high filter settings of 100 Hz and 3 kHz, respectively. To record the analog EMG data, we used a Teac XR-7000 FM tape recorder operating at a recording speed of 9.5 cm/s. We generated a digital file of the EMGs using 12 bit Keithley analog-to-digital converter with an effective sampling rate of 8,000 Hz per channel (Jayne et al., '90). We then filtered the digital EMG data using a finite impulse response filter that reduced frequencies of below 250 Hz to less than 10% of their original amplitude. The digital filtering proved especially important for reducing cable movement artifacts during rapid locomotor behaviors such as C-starts and kick and glide locomotion.

We used custom software (Jayne and Lauder, '93) to digitize the times of onset and offset and the rectified integrated areas of EMGs. For each EMG burst, we also determined EMG duration and calculated intensity as the rectified integrated area divided by duration.

To facilitate pooling data from different trials, we standardized the times of EMG onset (ON) and offset (OFF) using the times of key events (T_0, T_1, and T_2) described in more detail below. We also calculated the lag times between onsets (ONMYLAG) and offsets (OFFMYLAG) of the Di and myomeric muscle at the corresponding longitudinal location. When a Di site was not directly medial to an electrode in the myomeric muscle on the ipsilateral side, we interpolated the myomeric times from the anterior and posterior sites in order to correct for the number of intervening body segments. Negative values of ONMYLAG and OFFMYLAG indicate that Di activity preceded that of the corresponding myomere, whereas positive values indicate that the Di was activated later than the corresponding myomere. The amount of time for which an EMG overlapped with the time of lateral displacement (of the body near the posterior base of the dorsal fin) towards the ipsilateral side was expressed as a percentage of EMG duration (%DUR). For example, %DUR would equal 70% if the body at the posterior base of the dorsal fin moved from left to right during 0–100 ms and a right side muscle was active from 30–130 ms.

Because each behavior involved different patterns of muscle activity and kinematics, we discuss the additional methods and terminology below separately for the four behaviors. Initial events of interest could occur on either the left or right sides of the fish. Hence, for unsteady swimming behaviors, we use *primary side* to refer to the side of the fish with the initial event of interest, and *secondary side* refers to the contralateral side associated with a subsequent event. We use subscripts of 1 and 2 to refer to data from the primary and secondary sides, respectively, for the following EMG variables: ON, OFF, ONMYLAG, OFFMYLAG, and %DUR.

We were unable to obtain EMGs for each longitudinal position of each individual for each behavior; hence, these missing cells in our experimental design precluded performing an ANOVA with longitudinal location as a categorical variable. Furthermore, the longitudinal positions (segmental number) of EMG electrodes differed slightly among different individuals. Thus, to determine if electromyographic variables varied longitudinally, we calculated the least squares regressions of various EMG variables (pooled for all individuals) vs. the segmental number of the site from which data were obtained. For the regressions of ON and OFF vs. segmental number, one should note that a significant slope would indicate propagated muscle activity, and the value of such a slope would indicate the rate of propagation. Unless stated otherwise, we used $P < 0.01$ as the criterion for statistical significance of the regressions. We used this P value to partly account for the fact that we were usually making multiple comparisons of five EMG variables within each of the four locomotor behaviors. All significant regressions are shown in the figures with the bivariate plots of EMG variable vs. segmental number of the dorsal inclinator. We do note a few marginally nonsignificant results to draw attention to potential trends in our data that might emerge with larger sample sizes.

Data analysis

We analyzed only trials for which fish were generally 2 cm away from the left and right

sides of the flow tank and for which neither the fish nor the electrode wires contacted the additional surfaces surrounding the working section of the flow tank. The resulting data set included 16 steady swimming cycles (4 individuals), 18 kick and glides (4 individuals), 5 C-starts (3 individuals), and 13 braking events (3 individuals).

Steady swimming

By definition, steady swimming involves alternating oscillations of the tail to the right and left for which both the amplitude and time course of successive tail beats are constant. Consequently, we could pool observations meaningfully from contralateral sides from each individual. We restricted our analysis to sequences with four beats of the caudal fin for which the fish had less that a total of 3 mm of change in upstream-downstream position as the water speed of the flow tank remained constant. Furthermore, for this behavior, we used only sequences for which the fish was a minimum of 2 cm away from the surface of the water and all boundaries of the working section of the flow tank (i.e., in the region of well-characterized steady water flow in the calibrated flow tank; see Jayne and Lauder ('93, '94, '95b) for further information on flow tank methods). For this behavior, the activity of red myomeric muscles alternates between the left and right sides, and we use *primary side* to refer to the side having red myomeric activity, and the *secondary side* refers to the contralateral side of the fish (the initial designation of primary side is arbitrary). T_0 indicates the time of maximum lateral displacement of the reference point towards the secondary side, and T_1 indicates the time of maximum lateral displacement towards the primary side.

Kick and glide swimming

Unlike steady swimming, the time course and amplitudes of both EMGs and kinematics may vary considerably as the tail is swept from side to side during kick and glide swimming, and this behavior is used to attain speeds that cannot be sustained with steady swimming behavior. To facilitate pooling data, we use *primary side* to designate the side with the first of two high intensity myomeric EMGs that we digitized for each trial, and *secondary side* will refer to the contralateral side with the second myomeric EMG associated with a kick and glide episode. Kick and glide swimming always involves at least one vigorous and rapid movement of the tail from one side towards the opposite side. However, a kick and glide episode may or may not have additional, subsequent, rapid, large-amplitude sweeps of the tail. Furthermore, initial myomeric EMGs with high intensity may have very different apparent effects ranging from a seemingly preparatory flexion of the body with minimal forward acceleration (similar to C-start stage 1 below) to other instances with a large tail beat amplitude that rapidly accelerates the fish forward (similar to C-start stage 2 below). Thus, compared to the other swimming behaviors, the collective kinematic data for the primary side were extremely variable. T_0 indicates the time of maximal lateral displacement of the reference point towards the secondary side. T_1 indicates the subsequent time of maximum lateral displacement towards the primary side as a result of the myomeric activity on the primary side, and T_2 is the subsequent time of maximum lateral displacement towards the secondary side.

C-starts

We induced the C-start behavior from slowly swimming fish by dropping a small (size C) battery onto the surface of the water slightly lateral to the caudal fin (as in Jayne and Lauder, '93). During stage 1 of the C-start, all of the myomeric muscle along one side of the body is activated synchronously (within 1 ms), resulting in a C-like curvature of the body (concave towards the stage 1 myomere EMG) with little forward progression of the fish (Jayne and Lauder, '93). During stage 2 of the C-start, the myomeres of the contralateral side are activated, causing tail extension that propels the fish forward (Jayne and Lauder, '93). For the present study, we designate the side with the stage 1 myomeric EMG as the primary side and the contralateral side with the stage 2 myomeric EMG as the secondary side. T_0 indicates the onset of the stage 1 EMG, and T_1 indicates the end of lateral displacement of the reference point towards the primary side. Thus, the time interval from T_0 to T_1 encompasses the time of lateral movement of the reference point towards the primary side as well as an initial period (approximately 7 ms) during which there is muscle activity but no discernible lateral displacement. T_2 indicates the time of maximum lateral displacement towards the secondary side which occurs after the stage 2 myomeric EMG.

Braking behavior

Finally, we studied braking behavior of fish that was associated with capturing prey in still water. We dropped pieces of earthworm into the flow tank near the front grid of the working section of the flow tank. Fish rapidly accelerated towards the prey, glided forward with a relatively straight body, and then rapidly decelerated in order to capture the prey by suction feeding and to avoid colliding into the front grid of the working section. During the rapid deceleration, the body was generally flexed into an S shape such that the caudal fin and region of the soft dorsal fin were displaced towards opposite sides. For this behavior, the primary side refers to the side of the fish for which the Di muscles had a prolonged high amplitude EMG associated with flexing the dorsal fin towards the side of muscle activity, and the secondary side is the contralateral side. T_s refers to the time at which the fish came to a complete stop after prey capture.

RESULTS

Anatomy

Lepomis macrochirus (Fig. 1A) has a dorsal fin that can be partitioned into a rostral portion having spiny rays with restricted lateral mobility and a caudal portion with flexible, segmented, soft rays that are capable of considerable lateral movement. The number of soft dorsal fin rays of the *L. macrochirus* used in our study range from 11–13. The dorsal inclinator (Di) muscles of the soft dorsal fin originate from the fascia between the skin and the epaxial myomeric musculature and insert onto the lateral base of each fin ray via a tendinous insertion (Fig. 1C) (Winterbottom, '74). Contraction of the Di muscles can control the lateral movement and curvature of the soft dorsal fin rays (Arita, '71).

EMGs and kinematics

Before we present the individual accounts of each behavior, it is useful to clarify the meaning of key electromyographic variables. For the three propulsive behaviors (steady, kick and glide, and C-start), if the values of onset and offset relative to the times of maximum lateral displacement (ON_1–T_0, ON_2–T_1, OFF_1–T_1, and OFF_2–T_2) all equal zero, this would indicate a perfect correspondence between muscle activity of the Di and the times during which the body is being swept laterally towards the side of the active muscle. If the values of $\%DUR_1$ and $\%DUR_2$ equal 100%, then this indicates that all of the Di activity is confined to the interval when the body is being moved toward the side of Di muscle activity, but it is important to note that values of 100% may include EMGs of the Di with durations shorter than the time taken to move the tail from one side to the opposing side. If the values of $ONMYLAG_1$, $ONMYLAG_2$, $OFFMYLAG_1$, and $OFFMYLAG_2$ all equal zero, then the Di activity would be perfectly synchronous with that of the ipsilateral red myomeric muscle at the same longitudinal location. Significant correlations between ON_1–T_0, ON_2–T_1, OFF_1–T_1, or OFF_2–T_2 and Di segment number would indicate that muscle activity propagates longitudinally rather than occurring in a standing pattern.

Steady swimming

For the slowest speeds of steady swimming, *Lepomis macrochirus* frequently uses only pectoral fin movements and no lateral undulation of the axial structures, and during such swimming no activity of the Di muscles is apparent. Over a wide range of slow to moderate speed steady undulatory swimming, the Di muscles generally lack activity of sufficient amplitude to allow the times of onset and offset to be quantified. When the tail beat frequencies equal or exceed approximately 4 Hz in some individuals, Di activity is observed occasionally.

Figure 2 illustrates body position and EMGs from the Di and red myomeric muscle during steady swimming. As indicated by the values of $\%DUR_1$, Di activity on the primary side is strongly associated with the lateral movement of the body of the fish (near the base of the soft dorsal fin) from the secondary side towards the primary side. For all observations (N = 35) from the Di muscles, $\%DUR_1$ has a mean value of 83% (range 42–100%, SD = 15%), whereas for the red myomeric muscle (N = 64) $\%DUR_1$ has a mean value of only 44% (range 0–100%, SD = 30%).

As the body moves laterally though the water from the secondary towards the primary side, water presumably exerts a component of force that tends to flex the compliant soft dorsal fin towards the secondary side. Hence, much of the observed Di activity on the primary sides appears to prevent the fin from being pushed towards the secondary side rather than actively flexing the soft dorsal fin towards the primary side. For example, during the sequence shown in Figure 2, the Di muscles on the right side of the fish

have no detectable activity, and the soft dorsal fin bends noticeably towards the left side. Conversely, the left side Di muscles are active as the tail moves from right to left, and the soft dorsal fin does not bend enough to protrude noticeably beyond the right side of the body of the fish (Fig. 2). Briefly, near the end of the EMG burst of the left-side Di muscles and during the transition from left to right movement, the soft dorsal fin does protrude laterally towards the side of the active Di muscle. Hence, some Di activity also appears to be associated with lateral flexion of the fin as well as preventing passive bending towards the opposite side.

For the pooled data, the mean value of Off_1–T_1 (Fig. 3B) is 0 ms (range −44 to 73 ms, SD = 32 ms), indicating that offset of Di activity on the primary side is generally coincident with the maximum lateral displacement of the body towards the primary side. The mean value of ON_1–T_0 is 29 ms (range −143 to 133, SD = 50 ms), indicating that the Di muscles of the primary side are usually activated slightly after the time of maximal lateral displacement of the body towards the secondary side. Neither ON_1–T_0 nor OFF_1–T_1 is significantly correlated with longitudinal position (Fig. 3A,B). Consequently, there is no consistent pattern of longitudinal propagation of the EMGs of the Di muscles.

The mean value of the duration of Di activity (Fig. 3C) is 123 ms (range 64–186 ms, SD = 35 ms), which is similar to that of the mean value of 113 ms (range 69–160 ms, SD = 22) for the duration of the red myomeric EMGs. Durations of EMGs from the Di tend to decrease posteriorly (Fig. 3C) ($P = 0.014$), but this is not significant after correcting for multiple comparisons of the data.

Both the onset and offset of Di activity usually precede those of the red myomeric muscle at the corresponding longitudinal location. Mean values of $ONMYLAG_1$ and

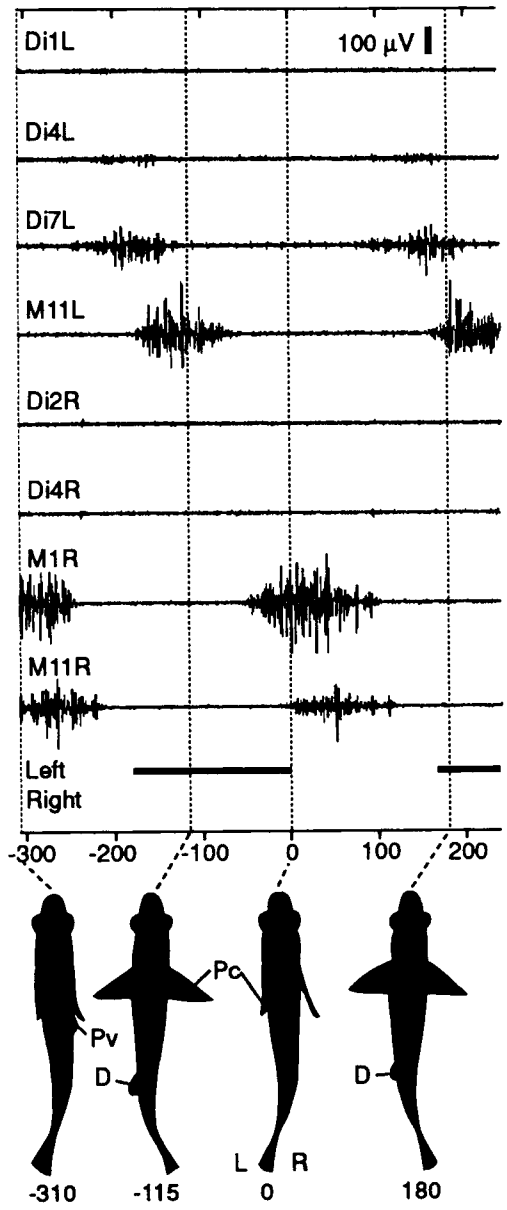
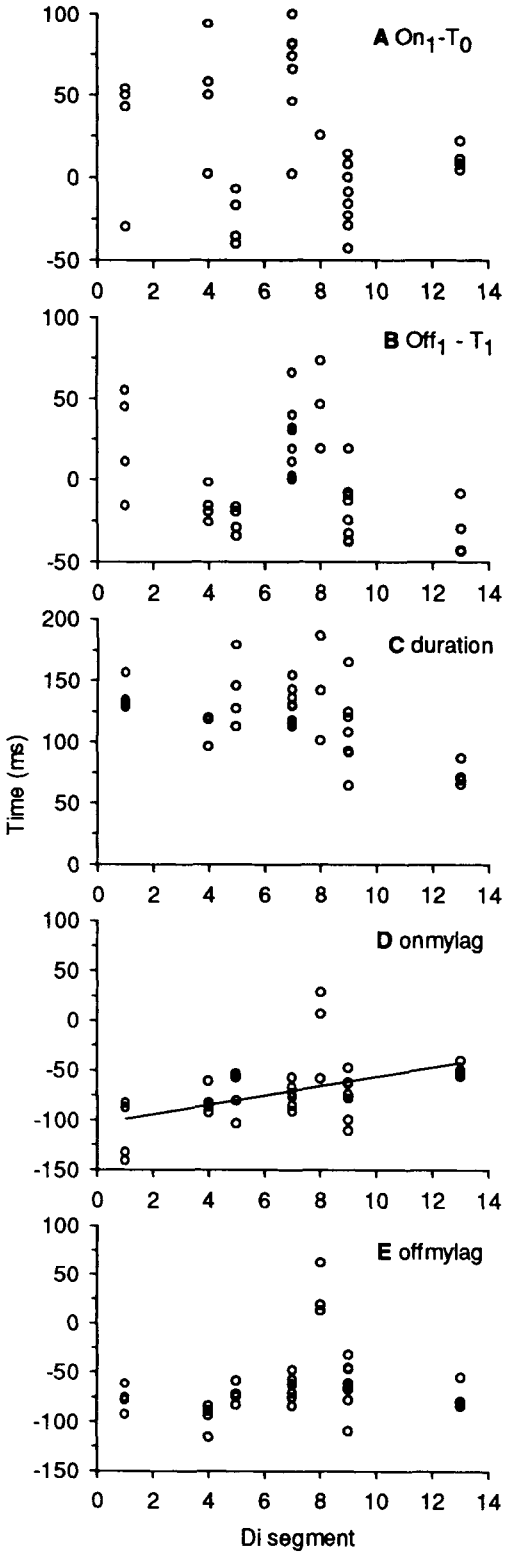


Fig. 2. *Lepomis macrochirus*. EMGs from the dorsal inclinators (Di) and red myomeric muscle (M) and fish position during steady swimming. The silhouettes of the fish were made directly from videotaped ventral-view mirror images, and the vertical dashed lines indicate the time for each fish image. Below each silhouette, elapsed time is indicated in milliseconds, and time scales are included above and below the EMGs. The thick horizontal bars indicate time intervals when the soft dorsal fin was visible lateral to the left (L) and right (R) sides of the body. The numbers after each muscle abbreviation beside the EMGs indicate the number of the body segments counting from the most anterior soft dorsal fin ray and proceeding posteriorly (Fig. 1A). For example, Di1L indicates an electrode in the dorsal inclinator lateral to the first soft dorsal fin ray on the left side, and M1R indicates an electrode in the red myomeric muscle on the right side at the same longitudinal position as Di1L. D, Pv, and Pc indicate the dorsal, pelvic, and pectoral fins, respectively. For the left side of the fish, 0 ms and 180 ms correspond to T_0 and T_1, respectively. Note that in the absence of right-side Di activity, the soft dorsal fin bends noticeably to the left as the posterior region is swept from left to right through the water.



OFFMYLAG$_1$ are −71 ms (range −141 to 28, SD = 32 ms) and −63 ms (range −16 to 62, SD = 36 ms), respectively. ONMYLAG$_1$ has a significant posterior increase (Fig. 3D), whereas OFFMYLAG$_1$ is not significantly correlated with longitudinal position (Fig. 3E). As shown in Figure 2, the timing of Di activity generally is more closely associated with the timing of red myomeric activity from the ipsilateral rather than the contralateral side.

Kick and glide

Figure 4 illustrates EMGs and body positions during an episode of kick and glide swimming, and Figure 5 indicates how the EMG variables vary between primary and secondary sides and among different longitudinal positions. None of the EMG variables shown in Figure 5 is significantly correlated with longitudinal position for either the primary or secondary sides.

Figure 4 shows a large burst of left side Di activity that occurs as the tail is swept from the right to the left side, suggesting that Di activity tends to resist lateral forces imposed on the soft dorsal fin as a result of the water resisting the lateral movements of the fish. For the Di muscle, the corresponding mean values of %DUR$_1$ and %DUR$_2$ are 84% (N = 39, range 38–100%, SD = 16%) and 69% (N = 38, range 11–100%, SD = 22), respectively. The timing of red myomeric muscle activity also overlaps considerably with the time during which the body is being displaced towards the side of the active muscle with mean values of %DUR$_1$ and %DUR$_2$ of 89% (N = 36, range 54–100, SD = 12) and 94% (N = 35, range 48–100%, SD = 12%), respectively.

Although the high values of %DUR are consistent with activation of the Di muscles in order to resist passive bending of the fin by the water, high intensity EMGs of the Di muscles (Fig. 4, 15–30 ms) could also precede

Fig. 3. Values of EMG variables vs. the longitudinal location of the Di muscle for data pooled from the left and right sides for four individuals of *Lepomis macrochirus* during steady swimming. Di onset relative to the time of maximal lateral displacement towards the secondary (**A**) and primary (**B**) sides. **C:** Duration of dorsal inclinator activity. The time lags between EMG onsets (**D**) and offsets (**E**) of the Di muscle relative to the ipsilateral red myomeric muscle at the corresponding longitudinal location. The lag time between onsets of the Di and red myomeric muscles (D) increased significantly with increased Di segment number ($Y = -104 + 4.71 * X$, $r^2 = 0.24$, $P = 0.003$), and the duration of Di activity (C) almost declined significantly with increased Di segment number ($Y = 151 - 4.09 * X$, $r^2 = 0.17$, $P = 0.014$).

or overlap with time intervals during which the soft dorsal fin bends noticeably towards the contralateral side (Fig. 4, 25–65 ms). Thus, Di activity probably stiffens the soft dorsal fin but not by an amount sufficient to resist the forces imposed by the water as the body is swept laterally towards the side of muscle activity.

Figure 4 also illustrates that the major activity of the Di is more closely associated with that of the ipsilateral myomeric muscle than that of the contralateral myomeres. Most of the power of the EMGs from contralateral sites of the Di (Fig. 4, Di7L vs. Di7R) tends to be out of phase; however, low amplitude portions of the EMGs from the Di muscles occasionally do overlap with EMGs from the contralateral site. Hence, although much of the activity of the Di muscles is unilateral, the Di muscles do have much more bilateral activity compared to that of the red myomeric musculature (Fig. 4, M10L vs. M10R).

Descriptive statistics further support the above conclusions. For the pooled data from the primary side, the mean values of ON_1–T_0 (Fig. 5A) and OFF_1–T_1 (Fig. 5B) are 30 ms (range −29 to 121 ms; SD = 39 ms) and 0 ms (range −30 to 22 ms; SD = 14 ms), respectively. For the secondary side, the mean values of ON_2–T_1 (Fig. 5A) and OFF_2–T_2 (Fig. 5B) are −12 ms (range −33 to 26 ms; SD = 15 ms) and −31 ms (range −89 to 15 ms; SD = 24 ms), respectively.

Mean values of $ONMYLAG_1$ and $ONMYLAG_2$ are −20 ms (range −105 to 40 ms, SD = 27 ms) and −23 ms (−44 to −3 ms, SD = 11 ms), respectively, and mean values of $OFFMYLAG_1$ and $OFFMYLAG_2$ are −2 ms (range −28 to 30 ms, SD = 27 ms) and −9 ms (range −37 to 23 ms, SD = 11 ms), respectively. Consequently, the onset of Di activity noticeably precedes that of the red myomeric activity at the same longitudinal location, whereas the offset of Di activity and that of the red myomeric muscle are nearly synchronous.

The mean durations of activity of the Di muscle on the primary and secondary sides are 55 ms (range 21–121, SD = 24 ms) and 48 ms (range 25–92 ms, SD = 14 ms), respectively, and the corresponding mean durations of activity of the red myomeric muscle are 37 ms (range 18–92 ms, SD = 18 ms) and

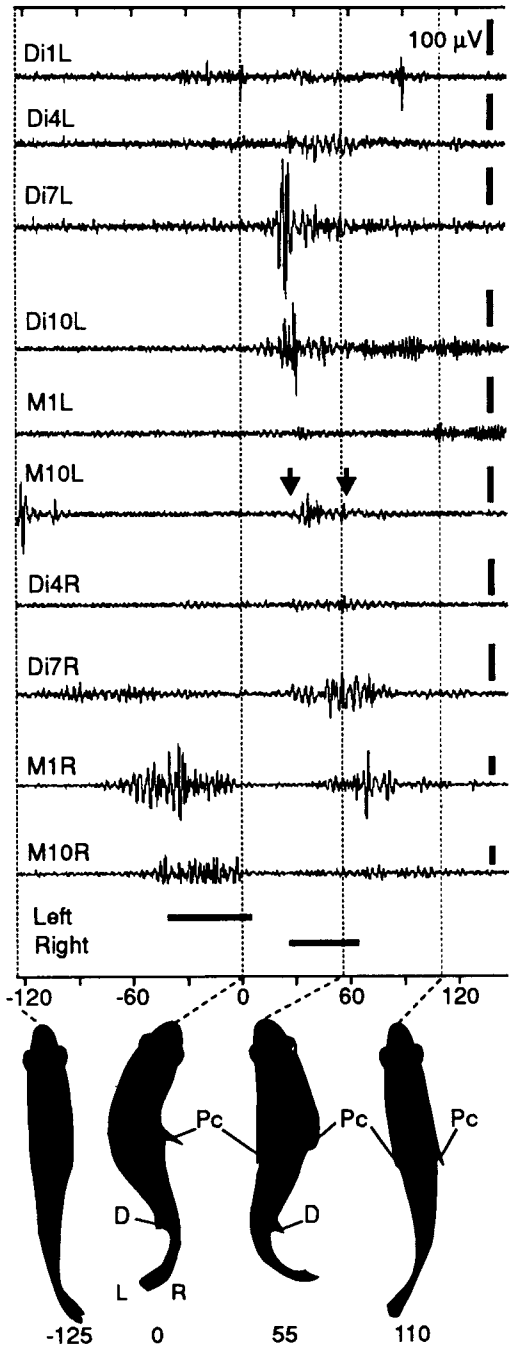
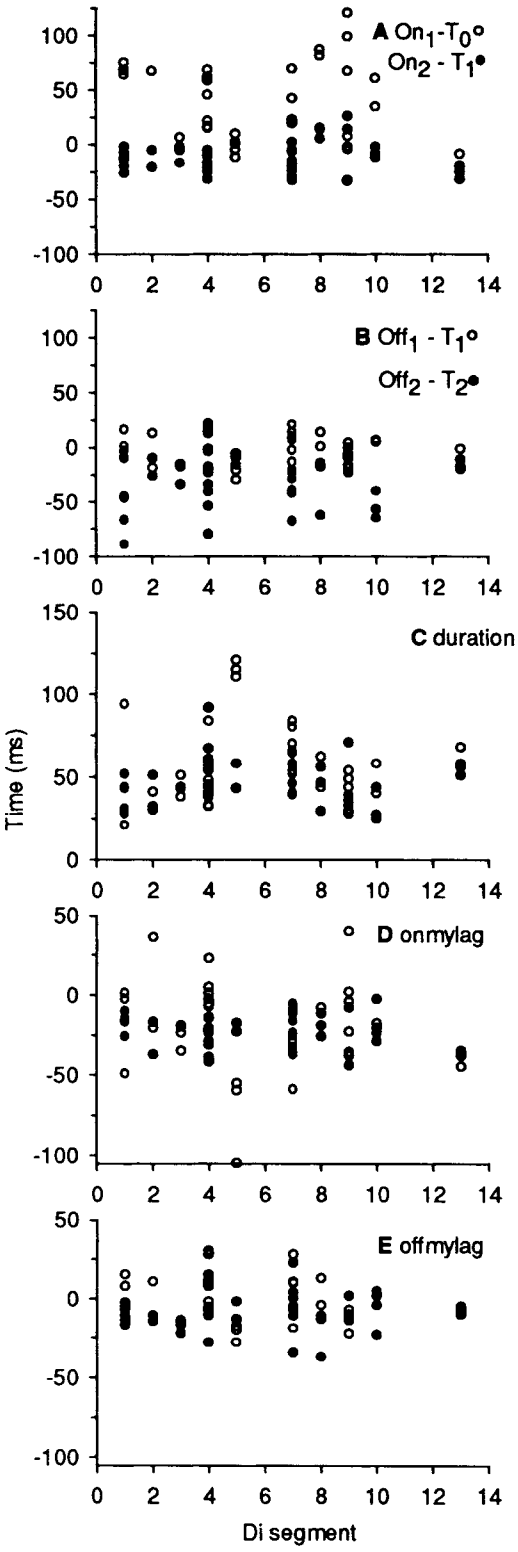


Fig. 4. *Lepomis macrochirus*. EMGs and fish position for kick and glide swimming. Abbreviations are as in Fig. 2. Arrows indicate ON_1 and OFF_1 of the red myomeric muscle which tends to have diminished amplitude as the faster white myomeric muscle is recruited intensively (Jayne and Lauder, '94). Zero, 55 and 110 ms correspond to T_0, T_1, and T_2, respectively. The left side of the fish is the primary side for this example. Note the large amount of Di activity on the left side as the tail is swept from right to left (0–55 ms).



36 ms (range 17–74, SD = 13 ms), respectively. The kick and glide episodes are often sufficiently fast so that the red myomeric EMGs during a kick have diminished amplitude compared to that observed at slower speeds, and this has been observed previously for the kick and glide swimming of *Lepomis macrochirus* when the white myomeric muscle is recruited at moderate to high intensities (Jayne and Lauder, '94).

As indicated in Figure 4, the amplitudes and durations of muscle activity could vary considerably between the primary and secondary sides for a single episode of kick and glide swimming. However, the EMGs and kinematics of kick and glide swimming are extremely variable, and, for the pooled data, no consistent differences are evident between the EMG variables from the primary vs. the secondary sides.

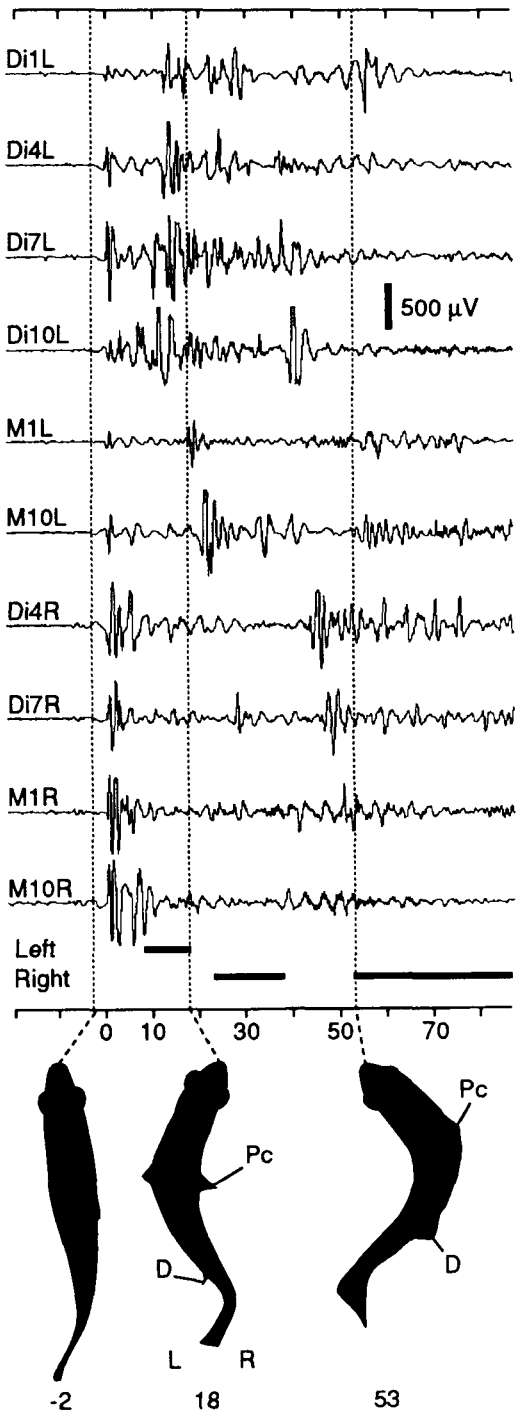
C-start

Figure 6 shows the EMGs and body position during a C-start, and Figure 7 illustrates the variation in EMG variables among longitudinal locations and between the primary and secondary sides. Within our measurement error (±1 ms) all of the onsets of Di and red myomeric muscle activity are synchronous along the entire primary side of the fish. Consequently, the mean values of ON_1–T_0 (Fig. 7A) and $ONMYLAG_1$ (Fig. 7D) are 0 ms, and there is no variance for these quantities.

During stage 1 (defined by EMG rather than kinematic events, as in Jayne and Lauder ['93]), EMGs on the primary side have very small mean durations for both the Di muscles (mean = 10 ms, range 3–16, SD = 4 ms, N = 10) and for the red myomeric muscle (mean = 12 ms, range 7–16, SD = 3, N = 10). Furthermore, nearly the entire portion of these stage 1 EMGs is within the time interval (T_0–T_1) when the body is swept laterally towards the primary side. For the Di and

Fig. 5. EMG variables vs the longitudinal position of dorsal inclinator for the kick and glide behavior of four individuals of *Lepomis macrochirus*. The open and closed circles represent data from the primary and secondary sides, respectively. **A:** Di onset relative to the time of maximum lateral displacement towards the contralateral side. **B:** Di offset relative to the time of maximum lateral displacement towards the ipsilateral side. **C:** Duration of dorsal inclinator activity. The time lags between EMG onsets (**D**) and offsets (**E**) of the Di muscle relative to the ipsilateral red myomeric muscle at the corresponding longitudinal location. None of the quantities shown in the figure was significantly correlated with longitudinal position.

red myomeric muscle of the primary side, mean values of $\%DUR_1$ are 98% (range 94–100%, SD = 2%) and 99% (range 95–100%, SD = 2%), respectively.

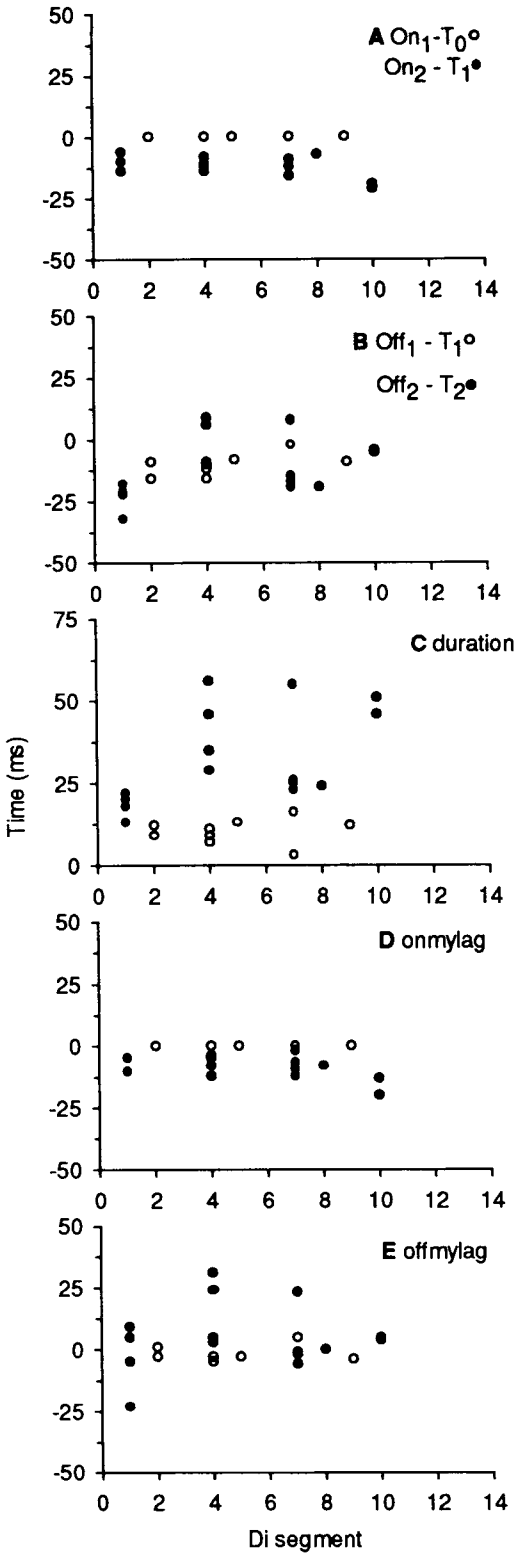


High amplitude activity of the Di muscles on the primary side often occurs during and before lateral movement of the body towards the primary side. However, bending of the soft portion of the dorsal fin towards the secondary side (Fig. 6) (8–18 ms) suggests that the fin is not sufficiently stiff to resist the forces imposed by the water during the lateral movement of the fish. Offset of the primary side Di activity slightly precedes the time of maximum lateral displacement towards the primary side (Fig. 6, Di4R, Di7R; Fig. 7B) as indicated by a mean value for OFF_1–T_0 of −11 ms (range −17 to −2 ms, SD = 4 ms). The offset of Di activity on the primary side is also nearly synchronous with that of the ipsilateral red myomeric muscle (mean $OFFMYLAG_1$ = −2 ms, range −6 to 5 ms, SD = 3 ms).

Both kinematic and EMG events during stage 2 of the C-start are slower than those of stage 1. For example, lateral displacement towards the primary side during stage 1 often occurs within approximately 15–20 ms, whereas lateral displacement from the primary to secondary side resulting from the stage 2 EMG is often approximately twice as long (Fig. 6). For the Di and red myomeric muscles on the secondary side the mean values of EMG duration are 33 ms (range 13–56 ms, SD = 14 ms) and 19 ms (range 6–28 ms, SD = 7 ms), respectively.

After correcting for multiple comparisons, none of the EMG variables for either the primary or secondary sides is correlated significantly with longitudinal position. However, three EMG variables of the Di muscles on the secondary side have correlations with longitudinal position with P values between 0.02 and 0.06. ON_2–T_1 (Fig. 7A) and $ONMYLAG_2$ (Fig. 7D) tend to decrease posteriorly, and duration (Fig. 7C) tends to increase posteriorly. The anterior Di muscles on the secondary side generally have a very brief, high frequency spike that is coincident with the onset of the stage 1 EMG of the primary side, and, after a delay approximat-

Fig. 6. *Lepomis macrochirus*. EMGs and fish position for a C-start. Abbreviations are as in Fig. 2. For this example, the stage 1 EMG occurred on the right (primary) side of the fish, and the onset of the stage 1 EMG was used to standardize the elapsed time to 0 ms (T_0). For the body of the fish near the posterior base of the soft dorsal fin, maximum lateral displacement towards the primary side occurred at 18 ms (T_1), and maximum lateral displacement towards the secondary side occurred at 53 ms (T_2).



ing 10 ms, a high amplitude stage 2 EMG is evident. This pattern of muscle activity during stage 2 of the C-start has been well documented previously for the myomeric muscle (Jayne and Lauder, '93). In contrast to the anterior Di muscles, the posterior Di muscles on the secondary side (Fig. 6, Di10L) often lack a distinct interval of no activity between the onset of the stage 1 EMG (on the contralateral side) and the onset of the stage 2 EMG, and this observation combined with the weak negative correlation between ON_2–T_1 indicates that posterior activity of the Di muscles often precedes that of the anterior sites on the secondary side.

For the secondary side, Di activity overlaps considerably with the timing of lateral displacement from the primary to the secondary side, and the mean value of $\%DUR_2$ is 56% (range 19–76%, SD = 17%). The onset of Di activity precedes the beginning of lateral displacement towards the primary side with a mean value for ON_2–T_1 of −12 ms (range −21 to −6 ms, SD = 4 ms), and the offset of Di activity precedes maximum displacement towards the secondary side with a mean value for OFF_2–T_2 of −11 ms (range −32 to 9 ms, SD = 12). Consequently, nearly all of the Di activity not occurring during lateral displacement towards the secondary side precedes rather than follows this kinematic event. During lateral displacement towards the secondary side, the soft dorsal fin often bends towards the primary side (Fig. 6, 24–38 ms); however, the pattern of activity of the Di muscles on the secondary side is consistent with resisting this passive bending of the fin towards the primary side.

Fig. 7. EMG variables vs. the longitudinal position of dorsal inclinators for the C-starts of three individuals of *Lepomis macrochirus*. The open and closed symbols represent data from the primary and secondary sides, respectively. **A:** Di onset relative to the time of maximum lateral displacement towards the contralateral side. **B:** Di offset relative to the time of maximum lateral displacement towards the ipsilateral side. **C:** Duration of dorsal inclinator activity. The time lags between EMG onsets (**D**) and offsets (**E**) of the Di muscle relative to the ipsilateral red myomeric muscle at the corresponding longitudinal location. For the secondary side, three variables having nearly significant correlations with longitudinal location were (A) onset relative to T_1 ($Y = -8.39 - 0.684 * X$, $r^2 = 0.26$, $P = 0.052$) and (C) duration ($Y = 20.9 + 2.29 * X$, $r^2 = 0.26$, $P = 0.054$) and (D) the lag between onset of activity of the Di and red myomeric muscle ($Y = -4.15 - 0.839 * X$, $r^2 = 0.28$, $P = 0.025$). Note the differences in activity patterns between the dorsal inclinators of the primary and secondary sides.

Both the onset and offset of Di activity on the secondary side are very similar to those of the ipsilateral red myomeric muscle. The mean values of $ONMYLAG_2$ (Fig. 7D) and $OFFMYLAG_2$ (Fig. 7E) are −8 ms (range −20 to −2 ms, SD = 5 ms) and 5 ms (range −23 to 31 ms, SD = 13 ms), respectively.

Braking behavior

Figure 8 shows EMGs and body position during a feeding episode, and Figure 9 illustrates the variation in EMG variables among longitudinal locations and between the primary and secondary sides. Initially fish accelerate from a standstill toward the prey. During this acceleration phase, the timing of Di activity relative to red myomeric muscle and relative lateral displacement resembles that of the three other swimming behaviors described previously. Activity of the Di muscles overlaps considerably with that of the ipsilateral red myomeric muscle and with the time interval of lateral displacement towards the side of the active muscle. Furthermore, during the acceleration phase of the feeding event, there is often a distinct pattern of posterior propagation of Di muscle activity (Fig. 8, left side muscles from −440 to −370 ms).

For the sequence shown in Figure 8, the fish begins to decelerate near the prey more than 100 ms prior to stopping completely (at 0 ms), and a large burst of left side Di activity is evident from −100 to 10 ms in this particular sequence. During and slightly after this prolonged activity of the Di on the primary side, the soft dorsal fin bends conspicuously towards the primary side (Fig. 8, −6 to 70 ms). Unlike the acceleration phase, activity of the Di muscles on the primary side during the braking phase is associated most closely with red myomeric activity on the contralateral rather than the ipsilateral side (Fig. 8, M10R). Activity of the red myomeric muscle on the secondary side generally flexes the posterior region of the fish such that the region of the body near the soft dorsal fin is maximally displaced towards the primary side, whereas the caudal fin is displaced laterally towards the contralateral side (Fig. 8, silhouette at 25 ms).

During the early stages of braking, both pectoral fins generally are protracted simultaneously, and because of the protraction of the pectoral fins, highly variable amounts of deceleration could occur before the median fins become important for contributing to braking. Furthermore, as the fish glides towards the prey item, more than one episode of pectoral and median fin movements could contribute to decelerating the fish, and such is the case for the sequence in Figure 8 between −200 and −250 ms. However, for the following pooled data (Fig. 9) we only quantified the EMGs from the Di muscles which are most closely associated with the time at which the fish stops.

For the pooled data (N = 29) from the Di muscles of primary side (Fig. 9A,B), the mean values of onset (ON_1–T_s) and offset (OFF_1–T_s) relative to the time of stopping are −135 ms (range −266 to −48 ms, SD = 51 ms) and 7 ms (range −171 to 81, SD = 51 ms), respectively, and EMG duration has a mean value of 142 ms (range 61–257, SD = 57). For the pooled data (N = 17) from the red myomeric muscle of the secondary side, the mean value of EMG duration is 139 ms (range 70–230, SD = 51). The lag times between the onset (Fig. 9D, ON_1MY_2LAG) and offset (Fig. 9E, OFF_1MY_2LAG) of the Di muscles of the primary side relative to those of the red myomeric muscle of the secondary side have mean values of 18 ms (range −139 to 170 ms, SD = 65 ms) and 17 ms (−138 to 76 ms, SD = 45 ms). Thus, the EMGs from the primary side Di muscles and red myomeric muscle of the secondary side have nearly identical average durations and times of activity.

Some activity of the Di muscles of the secondary side occurs near the time of stopping, and Figure 9 summarizes the observations of the timing of this activity relative to stopping as well as relative to the contralateral myomeres. For example, the mean values of ON_2–T_s and OFF_2–T_s from the Di muscle of the secondary side are −55 ms (range −201 to 0 ms, SD = 68 ms) and 47 ms (range −77 to 183, SD = 68). As suggested by a comparing the mean values of the timing of Di activity relative to Ts for the primary and secondary sides, there is occasionally some simultaneous activity of the Di muscles from contralateral sides. However, inspection of EMGs from contralateral sites with identical longitudinal locations within individual sequences generally shows that such bilateral activity is minimal (Fig. 8, Di7L vs. Di7R near 0 ms). Furthermore, the tendency for more posterior locations on the primary side to have later times of onset (Figs. 8, 9A) tends to increase the apparent overlap for pooled data compared to the direct observations from contralateral sites with identical longitudinal location.

For many feeding sequences, the fish momentarily swim backwards after coming to a

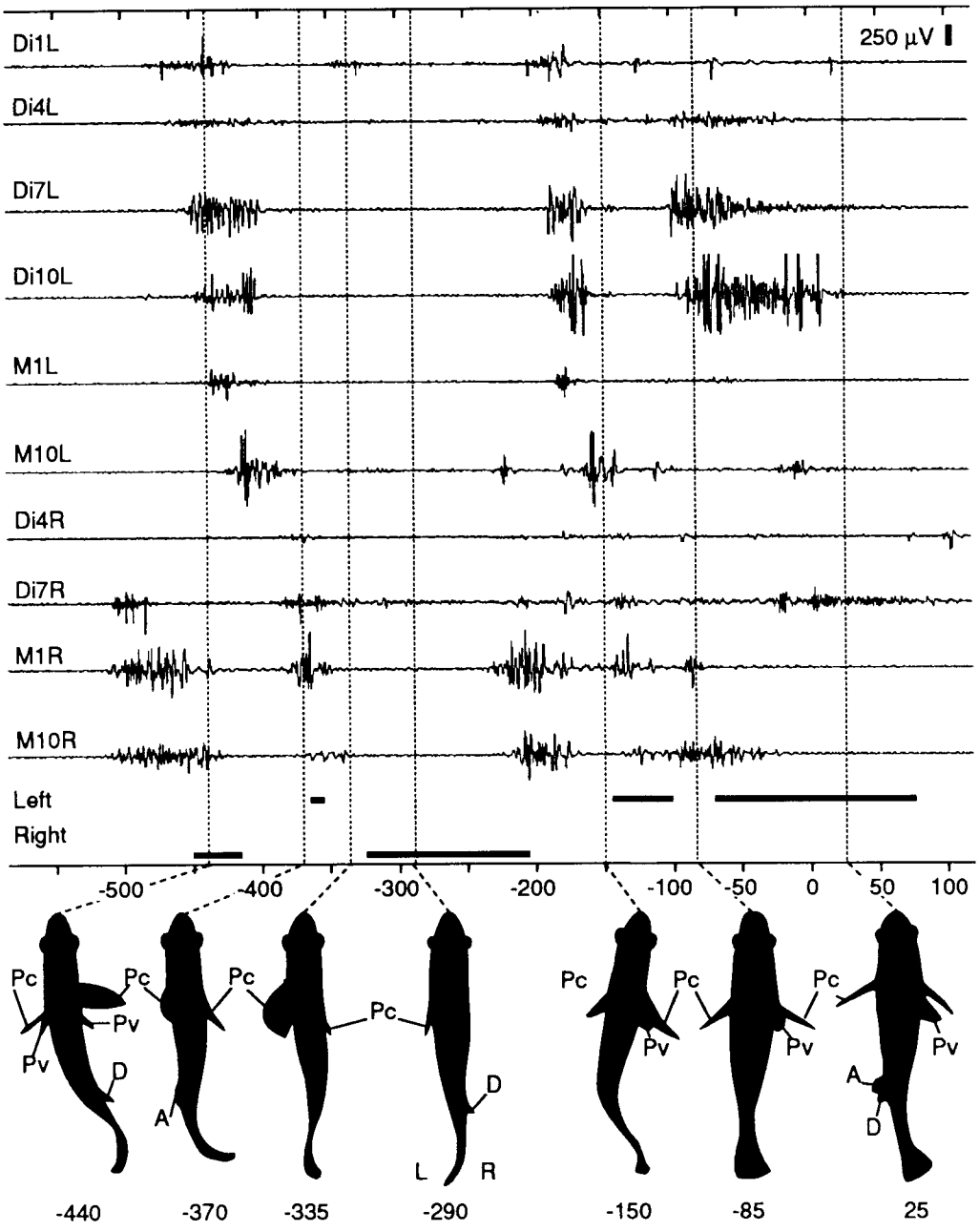
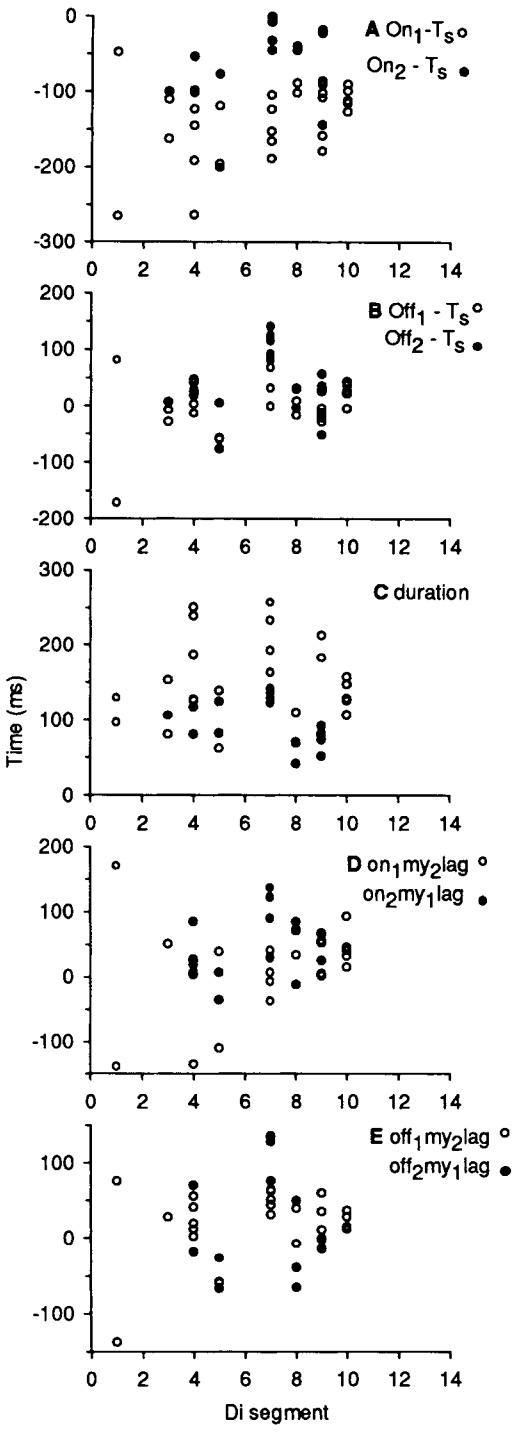


Fig. 8. *Lepomis macrochirus*. EMGs and fish position for braking during prey capture. Abbreviations are as in Fig. 2, and A indicates the anal fin. The fish came to a complete stop at 0 ms (T_s), and −85 ms is the time just before the fish begins to assume an S-shaped posture with the median and caudal fins pointing towards opposite sides (T_i). The fish accelerates forward from a standstill from approximately −500 ms to 320 ms, and then it glides forward with a relatively straight body from approximately −300 ms to −200 ms. For the region of the body at the posterior base of the soft dorsal fin, maximal displacement to the right occurred at −440 ms and −335 ms, and maximal displacement to the left occurred at −370 ms. Note that Di activity on the left side is generally propagated posteriorly, and during braking the posterior Di muscles of the left (primary) side has very pronounced activity.



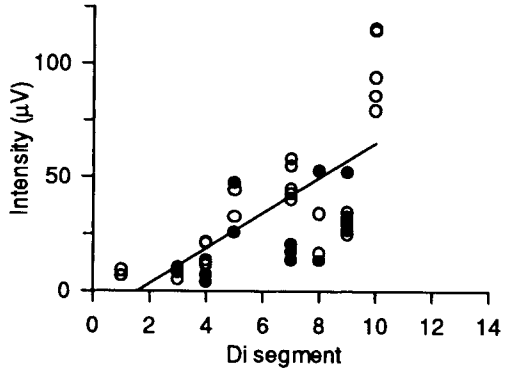


Fig. 10. *Lepomis macrochirus.* Intensity of EMG bursts (rectified integrated area divided by burst duration) from the dorsal inclinators vs. longitudinal location for braking during prey capture. Open and closed symbols indicate data from the primary and secondary sides, respectively. For the primary side, the intensity of Di activity increased posteriorly ($Y = -11.9 + 7.72 * X$, $r^2 = 0.49, P < 0.001$).

complete stop. Thus, some of the observed activity of the Di muscles on the secondary side appears to be directly correlated with backward swimming or at least in preparation for such movements. However, kinematic events after the fish stop are highly variable, and these diverse motions complicate generalizations for the muscle activity of the secondary side during and slightly after braking.

For the sequence that Figure 8 illustrates, the most posterior Di muscle on the primary side has the highest amplitude activity. Similarly, the pooled data from the Di muscles of the primary side have a highly significant posterior increase in the intensity of activity (Fig. 10).

In summary, the accelerating and decelerating phases of feeding sequences have nearly opposite patterns of activation of the Di muscles. During the acceleration phase, activ-

Fig. 9. EMG variables vs. the longitudinal position of dorsal inclinators for the braking of three individuals of *Lepomis macrochirus.* The open and closed symbols represent data from the primary and secondary sides, respectively. Di onset (**A**) and offset (**B**) relative to the time of stopping (T_s). **C:** Duration of dorsal inclinator activity. The time lags between EMG onsets (**D**) and offsets (**E**) of the Di muscle relative to the contralateral red myomeric muscle at the corresponding longitudinal location. For the primary side, Di onset relative to T_s (A) nearly had a significant posterior increase ($Y = -178 + 6.57 * X$, $r^2 = 0.13, P = 0.052$).

ity of the Di muscles probably helps prevent the soft dorsal fin from bending towards the contralateral side as the body is swept through the water towards the side having Di activity, whereas during the braking phase, prolonged Di activity is consistent with actively bending the soft dorsal fin laterally towards the side of Di activity as the body forms a fairly rigid S-shaped posture.

DISCUSSION

Comparisons among behaviors

Of the four behaviors that we studied, dorsal inclinator activity and the function of the soft dorsal fin are quite similar for the three propulsive behaviors. For steady swimming, kick and glide swimming, and the C-start, Di activity occurs mainly when the body of the fish is being swept laterally towards the side of the fish that has muscle activity, and this pattern of activity is consistent with stiffening the fin to oppose lateral bending of the fin away from the side of the fish having Di muscle activity. For the two faster propulsive behaviors (kick and glide and C-start), the resistive forces of the water appear sufficiently large to bend the soft dorsal fin laterally despite activity of the Di muscles. In contrast to the three propulsive behaviors, activity of the Di muscle during braking appears to actively flex the soft dorsal fin toward the side having muscle activity in a fashion consistent with providing a large drag force that could help decelerate the fish.

Besides the distinction of the Di muscles being used either to oppose bending or to actively bend the soft dorsal fin, it is useful to compare several of the EMG variables among the behaviors in order to compare and contrast motor patterns. The two variables that are most easily compared among all four behaviors are the intensity and duration of Di muscle activity (Fig. 11). For Di activity on the primary side during the three propulsive behaviors, the rank order of steady swimming, kick and glide swimming, and the C-start is the same based on mean values of increasing intensity (Fig. 11A) and of decreased duration (Fig. 11B). For the C-start, mean values of the intensity and duration are approximately ten times greater and one-tenth the respective values of steady swimming. During braking the mean intensity of Di activity on the primary side (Fig. 11A) is intermediate to the mean values of the kick and glide and C-start, whereas the mean duration of Di activity (Fig. 11B) during braking (142 ms) is greater than the mean value

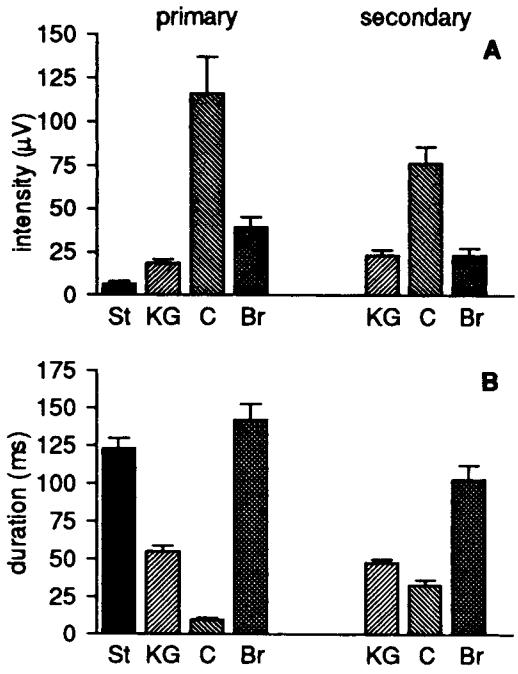


Fig. 11. *Lepomis macrochirus*. Mean values ± SE of intensity (**A**) and EMG duration (**B**) for data pooled from all longitudinal locations for both the primary and secondary sides for steady swimming (St), kick and glide swimming (KG), C-starts (C), and braking during prey capture (Br).

of any propulsive behavior. Thus, for the three propulsive behaviors, the intensity of muscle activity varies inversely with EMG duration, whereas the braking behavior has EMGs with both relatively high intensity and very long duration.

For the secondary side, EMG variables were only determined for kick and glide, C-start, and braking (Fig. 11). The mean duration of Di activity on the secondary side during braking (103 ms) is more than twice that of both kick and glide (48 ms) and the C-start (33 ms). For the secondary side, the mean intensity of Di activity for the C-start has a value approximately three times greater than those of both the kick and glide and braking. Hence, the rapid time course of muscle activity during the kick and glide swimming approaches that of the secondary side during the C-start; however, the intensity of activity on the secondary side during the C-start is generally considerably greater than that of the kick and glide (Fig. 11A). Within a single behavior, the greatest relative differences between primary and secondary sides are for the C-start.

Additional EMG variables could only be compared meaningfully among the three propulsive behaviors because different events were used to standardize the data for the braking behavior. Despite the much shorter time course of events during kick and glide swimming compared to steady swimming, these two behaviors have very similar mean times for the primary side onset (Fig. 12A) and offset (Fig. 12B) of Di activity relative to maximum lateral displacement. In addition, mean values of Di onset time relative to lateral displacement (Fig. 12A) for the secondary side are very similar for both the kick and glide swimming and C-start. Previous studies of myomeric muscle activity in *Lepomis macrochirus* have also found that kick and glide swimming (Jayne and Lauder, '94) and stage 2 of the C-start (Jayne and Lauder, '93) have a similar pattern in which muscle activity is propagated posteriorly in contrast to the standing pattern of muscle activity during stage 1 of the C-start. Consequently, muscle activity of both the Di and myomeric muscle suggests that stage 2 of the C-start is effectively indistinguishable from episodes of rapid kick and glide swimming.

For all three propulsive behaviors, the onset and offset of Di activity generally precedes or is nearly synchronous with that of the ipsilateral red myomeric muscle. The greatest mean values of the timing differences between Di and ipsilateral red myomeric activity are for steady swimming (Fig. 12C,D), and these values generally decrease with increased speed of the propulsive behaviors.

Comparisons of myomeric and dorsal inclinator motor patterns

For diverse species of bony fishes (Blight, '76; Grillner and Kashin, '76; Williams et al., '89; van Leeuwen et al., '90; Rome et al., '93; Jayne and Lauder, '95a) and other vertebrates (Grillner, '74; Kahn et al., '82; Wallén and Williams, '84; Jayne, '88; Frolich and Biewener, '92) that swim using lateral undulations of the vertebral column, there are three general features of the axial (myomeric) motor pattern: 1) there is posterior propagation of activity; 2) at a given longitudinal location, left and right side muscle activity does not overlap (i.e., unilateral); and 3) activity alternates between the left and right sides. With the exception of stage 1 of C-starts, both steady and certain unsteady swimming behaviors of fishes usually activate the myomeric musculature in the manner given above.

Muscle activity that we have found for the Di muscles does not conform simply to the patterns of the myomeric muscles. Individual sequences could be found in which activity of Di muscles propagates posteriorly (Fig. 8). However, no behavior has pooled values of times of Di onset (Figs. 3A, 5A, 7A, 9A) and offset (Figs. 3B, 5B, 7B, 9B) that are significantly correlated with longitudinal position. Hence, *Lepomis macrochirus* are capable of posteriorly propagating activity of the Di muscles under certain circumstances, but this is not a motor pattern that is used predictably for the behaviors that we analyzed.

When the timing of activity for Di muscles could be compared directly for contralateral sites at the same longitudinal location, high amplitude portions of EMGs usually do not overlap temporally for opposite sides. However, in contrast to our recordings from the red myomeric muscle that is lateral to the soft dorsal fin, we did observe periods during which the Di muscles have some bilateral activity (Figs. 4, 8).

Alternating left and right side muscle activity is primarily an expectation for steady (rhythmic) locomotion. We were able to readily observe alternating activation of the red myomeric muscle during steady swimming; however, low levels (if any) of recruitment of the Di muscles occur during steady swimming. Occasionally we did observe low levels of Di activity that alternated between the left and right sides, but more commonly we observed activity of the Di muscles from only one side during several successive cycles of steady swimming. Thus, there is no apparent obligate pattern of alternating activation of the Di muscles even when the red myomeric muscle is being activated with such a pattern during steady swimming.

A striking feature of the cumulative observations of Di activity for all four behaviors is the extent to which activity of the Di muscles apparently can be decoupled from that of the myomeric musculature. For example, during steady swimming the Di muscle may or may not be activated on one or both sides while the red myomeric muscle is being used in an alternating fashion. Furthermore, when the Di muscles are activated during propulsive behaviors, they are generally used at times that are closely associated with activity of ipsilateral red myomeric fibers, whereas during braking the Di muscle activity is closely associated with that of the contralateral red myomeric activity (when present). Presum-

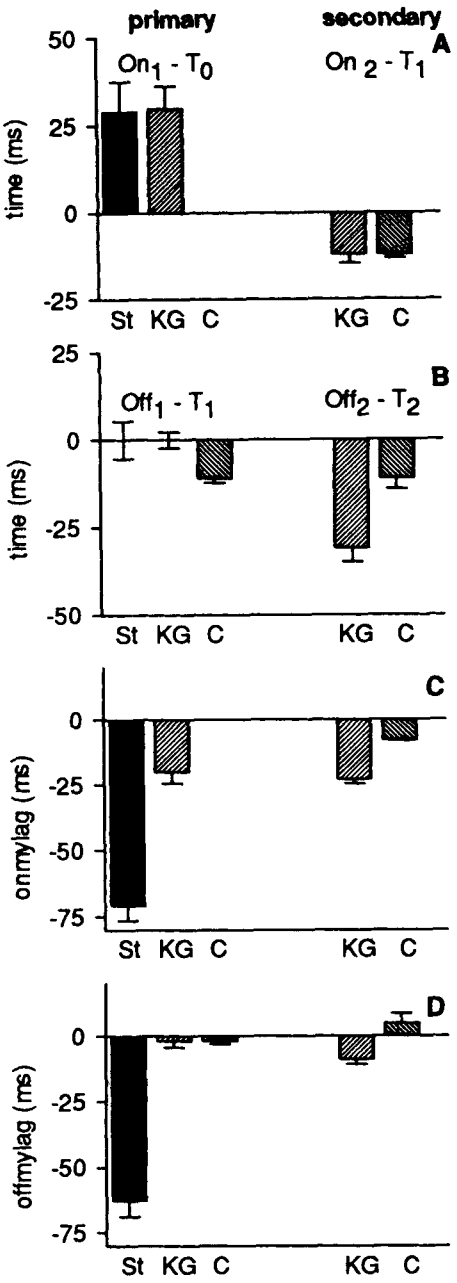


Fig. 12. *Lepomis macrochirus*. Mean values ± SE of EMG timing variables for data pooled from all longitudinal locations for both the primary and secondary sides for steady swimming (St), kick and glide swimming (KG) and C-starts (C). **A:** Di onset relative to the time of maximum lateral displacement towards the contralateral side. **B:** Di offset relative to the time of maximum lateral displacement towards the ipsilateral side. The time lags between EMG onsets (**C**) and offsets (**D**) of the Di muscles relative to the ipsilateral red myomeric muscle at the corresponding longitudinal location. Note that in panels A and C all values for the primary side during the C-start are zero.

ably, this capacity to decouple Di and myomeric activity adds tremendously to the diversity of how the median fins may be moved relative to the structures more closely associated with the vertebral column.

Mechanisms of modulating stiffness

Both the median and appendicular fins of teleost fishes are remarkable for the extent to which muscle activity can modify shape and function. A detailed anatomical study of fin structure by Geerlink and Videler ('87) suggests that the osteology of the spines and rays of fins differs fundamentally and has significant consequences for how these two structures function. Median fin spines in teleosts consist of a single skeletal element that extends distally into the webbing of the fin. The articulation between the base of the median fin spines and the underlying pterygiophores is such that very little lateral movement of the spine is possible under biologically meaningful loads (Geerlink and Videler, '87). In contrast, the soft rays of the fins consist of paired skeletal elements which are bound to each other by a complex wrapping of connective tissue. The base of the left and right skeletal elements of the median fin rays have processes to which the dorsal inclinator muscles attach, and the base of these skeletal elements of the rays can also be pivoted laterally relative to their site of attachment to the underlying pterygiophore. Pulling ventrally on the base of a single skeletal element of a fin ray curls the entire fin ray such that is becomes concave towards the side under tension (Geerlink and Videler, '87). Beside curling towards one side, it also appears that movements at the base of the fin can also alter the extent to which the entire fin ray is oriented laterally. The generalized skeletal anatomy of both fin rays and spines also allows these structures to be erected or depressed relative to the dorsal surface of the body of the fish.

Several anatomical features besides the articulations with pterygiophores are probably important for determining how the soft dorsal fin moves in *Lepomis macrochirus*. In *L. macrochirus*, a substantial amount of webbing connects the most posterior spine to the most anterior ray of the dorsal fin (Fig. 1). Although dorsal inclinator muscles are present lateral to most of the dorsal fin spines in *L. macrochirus*, these muscles generally have reduced size compared to their homologues that insert onto the fin rays of the soft dorsal fin. The most anterior fin ray is attached to a spine anteriorly and a ray posteriorly, inter-

mediate fin rays are surrounded immediately only by other rays, and the most posterior ray is attached to another ray anteriorly, but it has a long free posterior margin. Consequently, activity of a dorsal fin inclinator, erector, or depressor can potentially affect ray and spine movements within the fin at locations distant from the muscle itself.

Some of our experimental observations are particularly interesting in light of the longitudinal variation in the dorsal fin structures. During steady swimming there was often no detectable activity even though the dorsal fin was never completely depressed during steady swimming. The soft dorsal fin always had a substantial surface area that was readily visible in the lateral view. Thus, at lowest speeds of steady swimming, it appears that only the passive mechanical properties of the skeletal, connective, and relaxed muscle tissues are opposing the lateral forces imposed by the water upon the fin as it is oscillated laterally by alternating flexions of the body.

During faster steady swimming, some Di activity is present, but anterior sites often have slight activity compared to the more intense activity of the posterior sites (Fig. 2, left side Di activity). The lack of anterior Di activity cannot be attributed simply to faulty recording electrodes because later sequences involving other behaviors often had EMGs with amplitudes sufficiently high so that onset and offset times could be determined readily for the same anterior sites. In addition to these observations for steady speed swimming, during the braking behavior there is a highly significant posterior increase in the intensity of Di activity (Fig. 10). Perhaps the anterior mechanical linkage to the spines of the dorsal fin significantly helps to minimize lateral flexion of the anterior soft dorsal fin during intermediate speed steady swimming, whereas some Di activity is needed to adequately resist the bending forces of the water acting on the posterior soft dorsal fin. During braking when the fin is actively flexed towards the side having muscle activity, it is also possible that intense Di activity maximally flexes the posterior rays, and their webbed connections combined with lesser amounts of Di activity may maximally flex the anterior soft dorsal fin. In addition, the mechanical linkage of the anterior soft fin ray to the fin spine may be an important constraint to the maximal extent of lateral flexion of the soft dorsal fin.

The rapid propulsive behaviors of kick and glide swimming and the C-start were particularly interesting because despite a pattern of Di activity that should oppose lateral bending of the soft dorsal fin, the fin was still bent in a direction that was consistent with the resistive forces of the water being the primary cause of lateral bending. Many species of fishes that are maneuvering specialists have a deep-bodied shape (Webb, '84). The deep-bodied morphology presumably has the advantage of being better able to withstand the resistive forces generated by the water; however, the surface area of such a rigid structure cannot be readily modulated. Thus, it would also be interesting to determine whether certain maneuvering specialists may also have a combinations of dorsal fin morphology, Di muscle fiber type, and motor patterns which are better able to withstand the considerable forces imposed by water during these rapid movements.

We examined behaviors with a nearly tenfold difference in the duration of tail movements from one side to the opposite side. Because most biological tissues such as tendon and muscle are viscoelastic (Fung, '81), large differences in the rates of movement could substantially affect the relative importance of the passive mechanical properties for determining movement. The time course taken for the Di muscle to develop tension is another important consideration for interpreting the correlation between activity of the Di muscles and movement, but we presently lack contractile measurements for the Di muscles. For example, even if the Di muscles are activated in an unilateral fashion, the lag time for complete relaxation could result in substantial production of opposing forces of the contralateral Di muscles acting on a single fin ray. We also observed a number of sequences with some bilateral activity of the Di muscle. Thus, bilateral production of tension at the base of single fin rays may be a mechanism of stiffening the fin in addition to the use of unilateral Di muscle activity on the side towards which the body is being swept laterally.

In this first study of the in vivo patterns of Di muscle use in a teleost fish, we have documented considerable diversity in motor pattern, and there are probably several advantages to having a locomotor surface such as the dorsal fin in which muscle activity can be used to control surface area, orientation, and stiffness. For example, a compliant dorsal fin can be strongly flexed by Di activity in order to provide a braking surface that is nearly perpendicular to the longitudinal axis of the fish. However, the advantages of having a compliant fin in which function is modulated

by muscle activity should be considered in light of the inability of the dorsal fin to oppose bending induced by rapid movements through the water. For example, during C-starts bending of the soft dorsal fin would appear to produce drag forces that would oppose forward movement of the fish. Whether such a compliant locomotor surface is a net advantage for rapid accelerations could be tested experimentally by ablating the soft portion of the dorsal fin. Future comparative studies should clarify tradeoffs of having stiff (e.g., tuna) vs. compliant (e.g., generalized teleosts) median fins and using rigid skeletal elements vs. muscle activity to provide stiffness as well as which designs and functions are effective for propulsive versus braking movements.

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