

Strikes and startles of northern pike (*Esox lucius*): a comparison of muscle activity and kinematics between S-start behaviors

Julie E. Schrieffer¹ and Melina E. Hale^{1,2,3,*}

¹Department of Organismal Biology and Anatomy, ²Committee on Neurobiology and ³Committee on Computational Neurobiology, University of Chicago, Chicago, IL 60637, USA

*Author for correspondence (e-mail: mhale@uchicago.edu)

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Summary

S-starts are a major class of fast-start behaviors that serve diverse locomotor functions in fishes, playing roles in both feeding strike and escape startle events. While movement patterns are similar during strike and startle, their motor control mechanisms have not been compared. To investigate heterogeneity in **S**-start responses and to test the hypothesis that **S**-starts are generated by the same patterns of muscle activity regardless of the behavioral context in which they function, we examined kinematic and muscle activity patterns of northern pike (*Esox lucius*) performing feeding and escape **S**-starts. Movements were recorded with high-speed video (250 Hz). Muscle activity was recorded from seven electrodes, one in the left adductor mandibulae and bilaterally in the anterior, midbody and posterior epaxial white muscle. Although **S**-shaped movements are produced in both feeding and escape, kinematics and electromyogram (EMG) patterns differ. Stage 1 (pre-propulsive movement) is significantly slower and more variable during feeding strikes and involves caudal bending with less rostral movement than recorded for startle behaviors. Correspondingly, there is strong caudal muscle activity prior to rostral activity

during strikes, whereas in startles caudal muscle activity had near simultaneous onset with contralateral rostral activity. Onset of jaw muscle activity occurred significantly after the onset of axial muscle activity during feeding strikes. By contrast, during startles, jaw activity onset was nearly simultaneous with the onset of axial muscle activity. Stage 2 kinematics generally did not differ between the strike and startle; however, EMGs indicate that stage 2 movements are generated by different patterns of muscle activity for the two behaviors. Although strikes and startles are similar in their propulsive performance, they appear to be initiated and driven by fundamentally different motor control mechanisms. We suggest that **S**-start startle behavior is mediated by a simple system of descending reticulospinal input to spinal neurons while the **S**-start strike involves a more complex neural circuit, allowing greater modulation of stage 1 movements while maintaining high stage 2 performance.

Key words: *Esox lucius*, pike, strike, startle, prey capture, fast-start, S-start.

Introduction

Fast-starts are swimming movements that involve a short burst of high-acceleration activity. Fast-starts have been identified in several behavioral contexts including escapes (e.g. Weihs, 1973; Webb, 1976), feeding strikes (e.g. Webb and Skadsen, 1980; Rand and Lauder, 1981), post-feeding turns (Canfield and Rose, 1993) and social interactions (Fernald, 1975). Because of its importance in feeding and escape, fast-start behavior is closely linked to survival and has been found to evolve quickly with changes in predator pressure (O'Steen et al., 2002).

The focal fast-start behavior for research has been the **C**-start escape response. **C**-start behavior generally includes a **C**-shaped bend away from the stimulus direction (stage 1) followed by a propulsive tail stroke (stage 2) and often subsequent swimming (stage 3) (Weihs, 1973). **C**-starts have been examined in a wide range of species (reviewed by

Domenici and Blake, 1997), through ontogeny (e.g. Taylor and McPhail, 1985; Fuiman, 1994; Hale, 1996, 1999) and within ecological (O'Steen et al., 2002) and evolutionary (e.g. Zottoli, 1978; Hale et al., 2002; O'Steen et al., 2002) contexts. Because **C**-start escape behavior is controlled by a small population of reticulospinal neurons and because of the simplicity and accessibility of its neural circuits (e.g. Faber et al., 1989; Fetcho, 1991; Zottoli and Faber, 2000; Eaton et al., 2001), it has become a model system for examining the neural control of movement.

While the **C**-start has been studied from diverse perspectives, a second type of fast-start behavior called the **S**-start (Hoogland et al., 1956; Webb, 1976) has been a focus of research on muscle dynamics (Frith and Blake, 1995; Johnston et al., 1995; Spierts and Van Leeuwen, 1999) and kinematics (Harper and Blake, 1990, 1991) but has not been studied across

a wide range of taxa nor has its neural basis been established. However, the fact that the behavior has been identified in taxa as phylogenetically distant and ecologically distinct as pike (i.e. Hoogland et al., 1956; Webb and Skadsen, 1980) and carp (Spierts and Van Leeuwen, 1999) suggests the behavior may be used by a broad array of species. S-start behavior has been shown to occur in both feeding strikes and escape startles (reviewed by Domenici and Blake, 1997). During the S-start startle response, the fish forms an 'S' shape with a bend in the tail contralateral to the major rostral body bend. Recent electromyography data on S-start escape behavior in the Esocidae species muskellunge (*Esox masquinongy*) have demonstrated that the S-start startle is generated through a qualitatively different pattern of muscle activity than the C-start (Hale, 2002). This result suggests that the S-start is an independent type of startle response from the C-start and is not generated by the same neural circuit.

The S-start type of fast-start behavior has been identified as functioning in feeding strikes in several esocid species (Webb and Skadsen, 1980; Rand and Lauder, 1981; Harper and Blake, 1991). Prior to the propulsive movement of the strike, the fish's body takes on an S shape with a major bend to one side rostrally and to the opposite side caudally. The S-start of the strike has been subdivided into two categories based on the length of time the S-bend is maintained (Webb and Skadsen, 1980). During type A strikes, the strike begins with the fish in a straight position and the S-bend occurs as part of the strike. By contrast, during the type B strike, the strike is initiated from an S-shaped position. Additional distinctions in S-start strikes have been made according to the acceleration profiles of the movement and the number of tail strokes following the S-bend prior to prey capture (Harper and Blake, 1991).

The role of the S-start fast-start in strike behavior is unique. While C-starts have been identified in post-feeding turns, in that context they probably function as a defensive maneuver away from the water surface (Canfield and Rose, 1993) where prey is available but the fish are also more vulnerable to predators. By contrast, during S-start strikes, the S-bend occurs prior to prey capture and thus is an integral part of the prey capture event.

The presence of two independent roles of the S-start – attack and escape – raises questions about the degree of shared *versus* independent neural control of these behaviors. We build upon previous studies on S-start kinematics (Webb and Skadsen, 1980; Rand and Lauder, 1981; Harper and Blake, 1991) by examining muscle activity patterns along with kinematics of S-start strike and startle in order to address the hypothesis that the S-start strikes and startles are generated by the same patterns of muscle activity and to examine how a simple movement pattern is controlled in very different behavioral contexts. Our first objective was to characterize the kinematics and muscle activity pattern of the S-start feeding strike in the northern pike (*Esox lucius*). The axial muscle activity of S-start feeding strikes had not been examined previously in any species. Our second objective was to compare the movement and motor pattern of the S-start strike

with that of the S-start startle response of the same species. For both strikes and startles, we recorded high-speed video and electromyograms from epaxial muscle in three positions on each side of the body and from the jaw adductor muscle on one side of the body to examine the coordination of S-start axial muscle activity and the relationship between jaw and axial activity.

Materials and methods

Northern pike (*Esox lucius* L. 1758) were obtained from the Jake Wolf Fish Hatchery, Illinois Department of Natural Resources, IL, USA. Four fish ranging from 22.8 cm to 24.5 cm total length (mean \pm s.d., 23.7 \pm 0.8 cm) and from 20.1 cm to 22.3 cm standard length (21.2 \pm 1.0 cm) were examined. The fish were maintained at the Field Museum of Natural History, Chicago, IL, USA in tanks at 20°C. Experiments were conducted at the Field Museum of Natural History and at the University of Chicago with IACUC approval from both institutions. While in the laboratory, fish were fed minnows on alternating days. Fish were not fed for 24 h prior to an experiment.

We chose to work on the northern pike because this species and other members of the Esocidae are considered acceleration specialists and have been models for strike and startle behaviors. Comparative work on kinematics of strikes and startles is available for many esocid species (e.g. Webb, 1976; Webb and Skadsen, 1980; Rand and Lauder, 1981; Harper and Blake, 1990, 1991; Frith and Blake, 1995; New et al., 2001; Hale, 2002).

Kinematics

Kinematics of strike and startle responses were recorded from ventral view in a 60 cm \times 60 cm tank. Startle responses were elicited by touching or pinching the tail with metal forceps. Fish were near the center of the tank when startles were elicited. As angular movements during the startle are in part determined by stimulus direction (Eaton and Emberley, 1991; Domenici and Blake, 1993), we used a caudal stimulus to minimize the difference in initial movement angles of strikes and startles and so as not to initiate C-start behavior, which tends to be generated by more rostral stimuli. Strike responses were obtained by introducing a free-swimming prey minnow (*Pimephales promelas*) into the filming tank. In choosing strikes to analyze, we only examined strikes in which the prey fish was not next to the tank wall and there was no contact between the pike and the walls of the tank during the movements analyzed. The minimum possible distance between the pike and the wall of the tank at the initiation of the response was approximately 9 cm. This is a conservative estimate as the tank wall was not always visible in the field of view and so the distance to the edge of the field of view was used instead. The maximum distance between the pike and prey upon initiation of the strike was 6 cm.

Fast-starts were recorded at 250 frames s⁻¹ with a Redlake PCI-1000S digital high-speed video camera. Images were

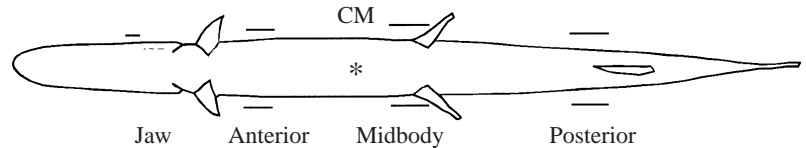


Fig. 1. Electrode placement. Northern pike (*Esox lucius*) were implanted with seven electrodes to measure white epaxial muscle activity: one in the left jaw and bilaterally in anterior, midbody and posterior positions in the middle of the epaxial white muscle. Bars represent approximate range in the positions of electrodes among the fish. The asterisk indicates the center of mass (CM).

viewed and digitized with NIH Image 1.62. We examined the initial non-propulsive movements and the first propulsive tail stroke for both strikes and startles. Kinematic parameters were determined from midline points reconstructed from digitized outlines of the fish as described by Hale (2002) using a midline analysis program designed by Jayne and Lauder (1995). The fish images were digitized along the axis from the tip of the snout to the caudal peduncle. We did not digitize the caudal fin because it was not always clear in the images and our primary concern was with the muscular part of the tail. We examined movement at 5% intervals along the body and at points corresponding to the longitudinal positions of the axial electrodes and the center of mass, which was determined for the longitudinal axis of the fish as described by Westneat et al. (1998; Fig. 1; Table 1). Velocity and acceleration were calculated with QuickSAND software written by J. A. Walker (Walker, 1998). Angles of head movement during stages 1 and 2 were measured with NIH Image version 1.62.

Electromyography

Electromyograms (EMGs) were recorded with fine-wire electrodes implanted in epaxial muscle. Electrodes were made from 0.05 mm-diameter double-stranded, insulated, stainless steel wire from the California Fine Wire Company as described by Hale (2002). Fish were anesthetized with 3-aminobenzoic acid ethyl ester (MS222) in water. Seven electrodes were used, three on each side of the body in the epaxial white muscle and a seventh in the jaw adductor on the left side of the body at approximately 0.5–1 cm in depth. Longitudinal positions (Fig. 1; Table 1) were chosen so that the EMGs would describe the distribution of muscle activity along the length of the body. We assumed that the jaw muscles were active bilaterally and that, at least for the broad-scale analysis of cranial activity in this research, the left jaw muscle reflected activity patterns on the right. After experiments, the study animals were euthanised with MS222. Measurements of total and standard length and

the longitudinal positions of the center of mass and electrodes were recorded (Table 1).

EMGs were amplified with Grass P 511 amplifiers (gain 5000 or 10 000). Data were stored directly to a computer at a sample rate of 5000 points s^{-1} channel $^{-1}$ using National Instruments' analog-to-digital acquisition system and custom LabView Virtual Instrument (VI) software (National Instruments Corporation, Austin, TX, USA). An additional channel collected a square wave signal that was simultaneously recorded by the video system onto the kinematic sequences to synchronize EMGs and behavior. The relative timing of EMG activity to movement as well as the EMG amplitudes and durations were analyzed with LabView software using custom VIs written by M. W. Westneat. In order to align the responses, the first activity of each response is set to zero and the onset and offset of subsequent EMG bursts are determined as time from that zero. In the case of strikes, which always involved activity in caudal muscle first, this results in no standard error for the onset of the first burst of caudal activity as caudal onset was always set to zero.

Statistics

Trials of S-start escape responses and strikes were measured for each of four fish. In most cases, three trials of each behavior were analyzed; however, for one fish only two strikes were analyzed and for another only two S-starts were analyzed. In order to combine trials of tail bending to the right and left, the data were standardized to the direction of head movement. We quantified variation between behaviors and among individuals using analysis of variance (ANOVA) with repeated measures in the program JMP (SAS Institute) to test for specific differences in kinematics and EMG variables. None of the variables showed significant inter-individual effects.

Results

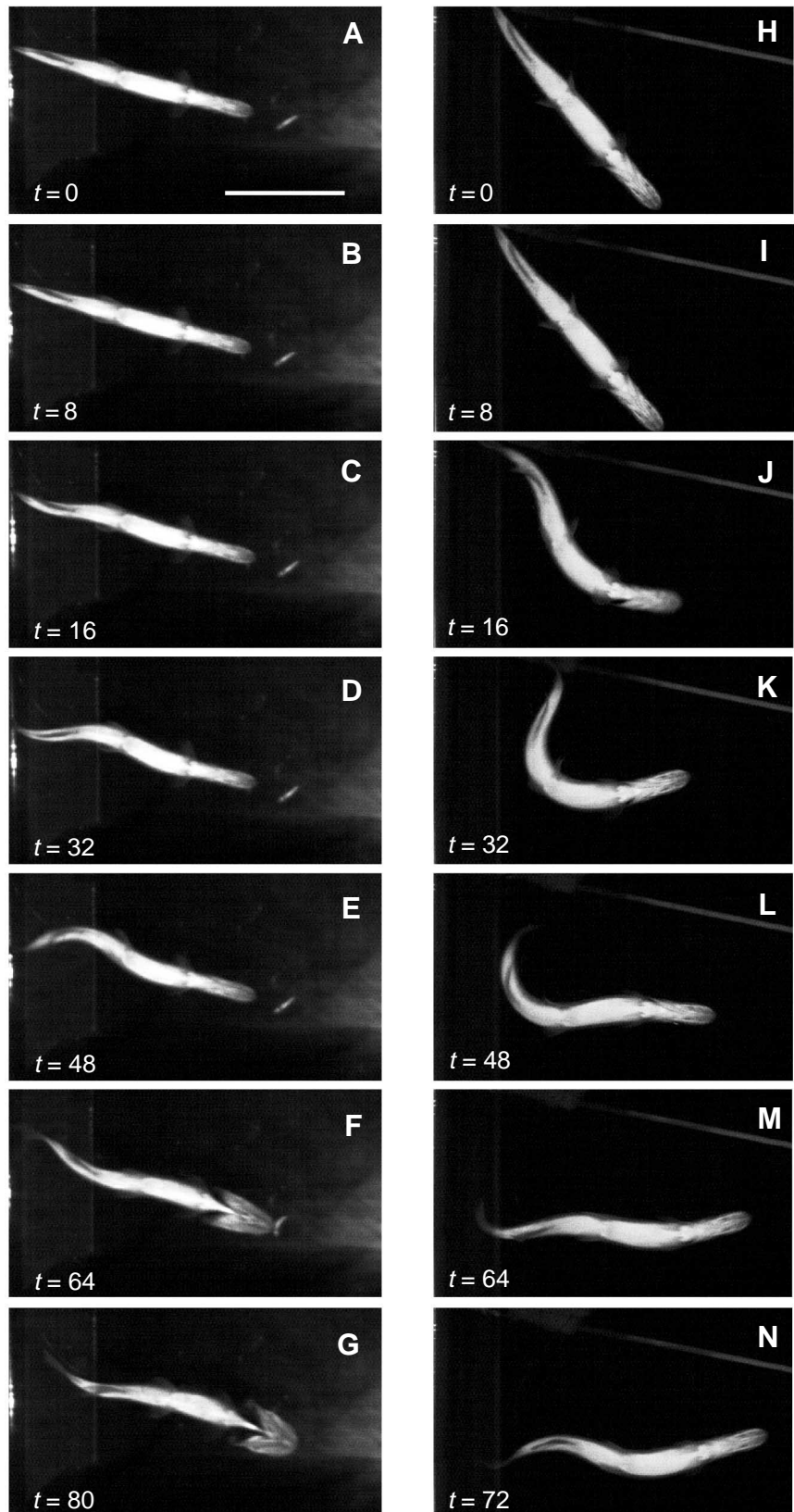
Kinematics

Analysis of high-speed video showed different patterns of movement for strikes and startles. Strikes were initiated by caudal bending into a shallow S shape with little or no rostral movement (Fig. 2A–C). The S-bend was followed by a stronger caudal bend at the end of stage 1 (Fig. 2E). We call this the L-bend as it is similar to the L-bend (or J-bend) of the startle; however, only infrequently did the movement have the magnitude to resemble an L shape. Because S- and L-bends are non-propulsive, we consider them both to be components of stage 1. This designation fits the general classification of

Table 1. Electrode and center of mass position as a percentage of standard body length (SL)

Landmark	Mean position (% SL)	Range (% SL)
Center of mass	47.78±1.6	45.8–50.0
Jaw electrode	17.26±0.7	16.0–18.0
Anterior electrodes	35.02±1.7	32.8–36.4
Midbody electrodes	55.4±2.0	52.2–58.3
Posterior electrodes	82.06±1.4	79.3–83.4

Fig. 2. Movements of a strike and a startle of the northern pike (*Esox lucius*). The feeding strike (A–G) is characterized by isolated caudal movement (C–E) followed by a forward lunge accompanied by the opening of the jaw (F,G). The startle response (H–N) is characterized by an initial S-shaped bend (J) followed by a stronger bend (L-bend; K) and a propulsive tail stroke (L–N) with no jaw opening. A comparison of the feeding strike and escape startle demonstrates that initial movement is restricted to the caudal region of the body during the feeding strike (C–E) while the startle involves significant rostral and caudal movement (I–K). Scale bar, 10 cm.



stage 1 as being the preparatory stage of the fast-start (Weihs, 1973). In stage 2, the propulsive stage of the strike, the fish accelerated toward its prey with a rostral to caudal wave of bending (Fig. 2F,G), with most bending occurring caudally.

The S-start startle involved generally similar kinematics stages. The movement pattern of the startle is characterized by an initial S-shaped bend with the tail bending in the opposite direction to the major body bend (Fig. 2J). The S-bend is followed by movement into a tight caudal L-bend (Fig. 2K). During stage 2 of the startle, a wave of bending is propagated from rostral to caudal along the entire length of the body (Fig. 2L–N).

One difference between strike and startle behaviors is the angle of head movement during stage 1 of the response (Fig. 3). The angle of head movement from initiation of the response through the S-bend was lower for the strike response than for the startle [$12.7 \pm 5.2^\circ$ (mean \pm S.E.M.) compared with $45.7 \pm 3.9^\circ$, respectively; $P < 0.0001$]. Similarly, change in head angle was significantly lower for the strike from the end of the S-bend to the L-bend at the end of stage 1 ($5.0 \pm 2.2^\circ$ compared with $12.8 \pm 1.5^\circ$; $P < 0.01$). There was no significant difference in the angular head movement between strikes and startles during stage 2 of the response ($4.0 \pm 2.2^\circ$ compared with $7.0 \pm 1.9^\circ$; $P = 0.31$).

Total duration of stages 1 and 2 was significantly greater ($P < 0.05$) for the strike (100.3 ± 10.3 ms) than for the startle (70.9 ± 6.2 ms) (Fig. 4). The difference in total duration was reflective of a longer duration stage 1 during the strike behavior (72.2 ± 9.7 ms for the strike compared with 42.7 ± 3.1 ms for the startle). Stage 1 duration was highly variable among strikes as reflected in the high

standard error (9.7 ms compared with 3.1 ms for the startle). Comparison of strike and startle within stage 1 shows that the difference in duration in stage 1 is a result of a longer initial

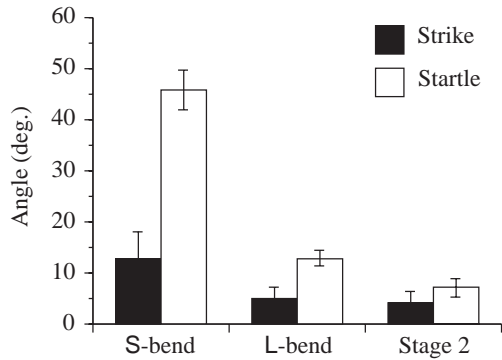


Fig. 3. The angle of head movement during behavioral stages of strike and startle responses. Values are means \pm S.E.M. The angles of head movement during the S-bend and from the maximum S-bend to the maximum L-bend are significantly greater for the startle than for the strike. There was no significant difference in the angle of head movement in stage 2 of strike and startle behaviors.

S-bend for strike behaviors (55.5 ± 9.1 ms for the strike compared with 23.7 ± 2.3 ms for the startle; $P < 0.005$). There was no significant difference ($P = 0.219$) in the duration of the L-bend between the strike (14.7 ± 2.0 ms) and the startle (19.0 ± 2.2 ms) or in the duration of stage 2 of strikes (36.5 ± 8.2 ms) and startles (29.5 ± 4.1 ms; $P = 0.064$).

The peak linear velocity of the center of mass in stage 2 (Fig. 5A) was not significantly different between strikes and startles ($P = 0.524$). Strikes had a mean velocity of 1.69 ± 0.20 m s⁻¹ while startles averaged 1.75 ± 0.24 m s⁻¹. Similarly, the peak linear acceleration of the center of mass in stage 2 (Fig. 5B) did not differ among fast-start types ($P = 0.383$). The peak acceleration during the strike was 54.61 ± 10.97 m s⁻² and during the startle was 80.20 ± 13.84 m s⁻².

Electromyography

S-start strikes and startles result from qualitatively different muscle activity patterns. Fig. 6 illustrates an example of strike and startle EMG responses. While the pattern of muscle activity for the startle was highly stereotyped, strike responses were considerably more variable, particularly in the onset of muscle activity. The strike example shown (Fig. 6A) was chosen because it illustrates the main features of the response summarized in Fig. 7 and statistically below.

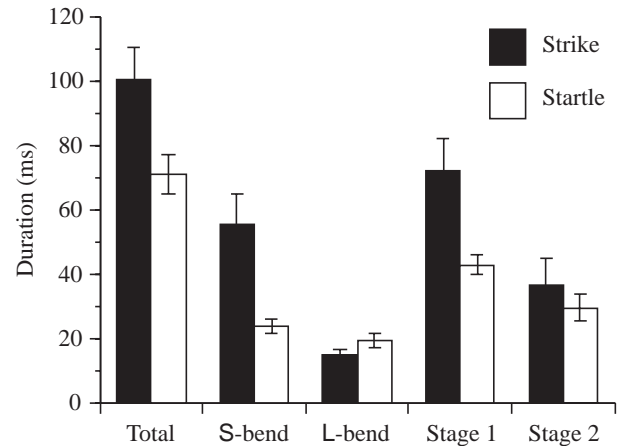
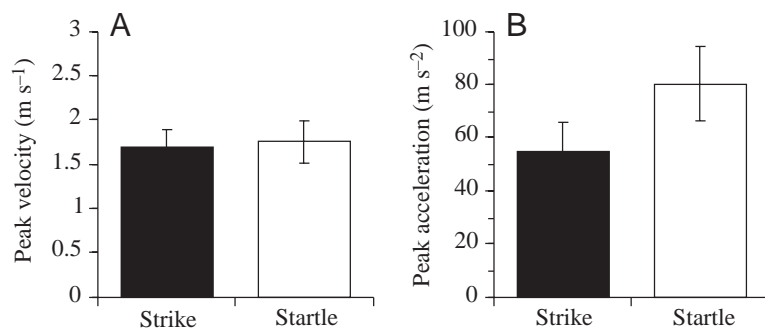


Fig. 4. Durations of kinematics stages of S-start behaviors for the northern pike (*Esox lucius*). Values are means \pm S.E.M. The durations of the combined stages 1 and 2 movements, the S-bend and stage 1 were significantly greater for strikes than for startles. By contrast, there was no significant difference in L-bend or stage 2 durations between strikes and startles.

The most obvious difference between strikes and startles is the relationship of the onset of jaw adduction to the onset of axial muscle activity, which was significantly delayed for the strike relative to the startle ($P < 0.0001$). During the startle response, jaw adductor activity occurred at the initiation of axial muscle activity, on average within 1 ms of axial muscle (0.64 ± 0.39 ms). During the strike, the onset of jaw adductor muscle activity was delayed relative to the first onset of axial muscle activity recorded, occurring on average 43.05 ± 6.04 ms after axial muscle onset. The onset times of adductor muscle activity had non-overlapping distributions when compared between strike and startle trials (Fig. 8). There was no significant difference in the duration of jaw adductor muscle activity (97.1 ± 20.43 ms for the startle and 118.7 ± 10.8 ms for the strike; $P = 0.22$), which was highly variable among trials. Mean amplitudes of the jaw adductor activity were not significantly different between strikes (0.356 ± 0.064 mV) and startles (0.328 ± 0.09 mV; $P = 0.81$).

The pattern of axial muscle activity also differs between fast-start types. The duration of the initial caudal muscle activity is considerably longer for strikes than startles (26.9 ± 2.2 ms versus 14.4 ± 2.2 ms, respectively; $P < 0.001$) and of lower mean amplitude (0.208 ± 0.07 mV versus 0.596 ± 0.074 mV, respectively; $P < 0.001$). The onset of the initial burst of rostral activity was delayed relative to initial caudal activity of the strike (Fig. 7). The onset

Fig. 5. Mean peak center of mass velocity (A) and acceleration (B) of S-start behaviors for the northern pike (*Esox lucius*). Values are means \pm S.E.M. Mean peak linear velocity and linear acceleration were measured during the propulsive movement in stage 2. Neither velocity nor acceleration was significantly different between strike and startle behaviors.

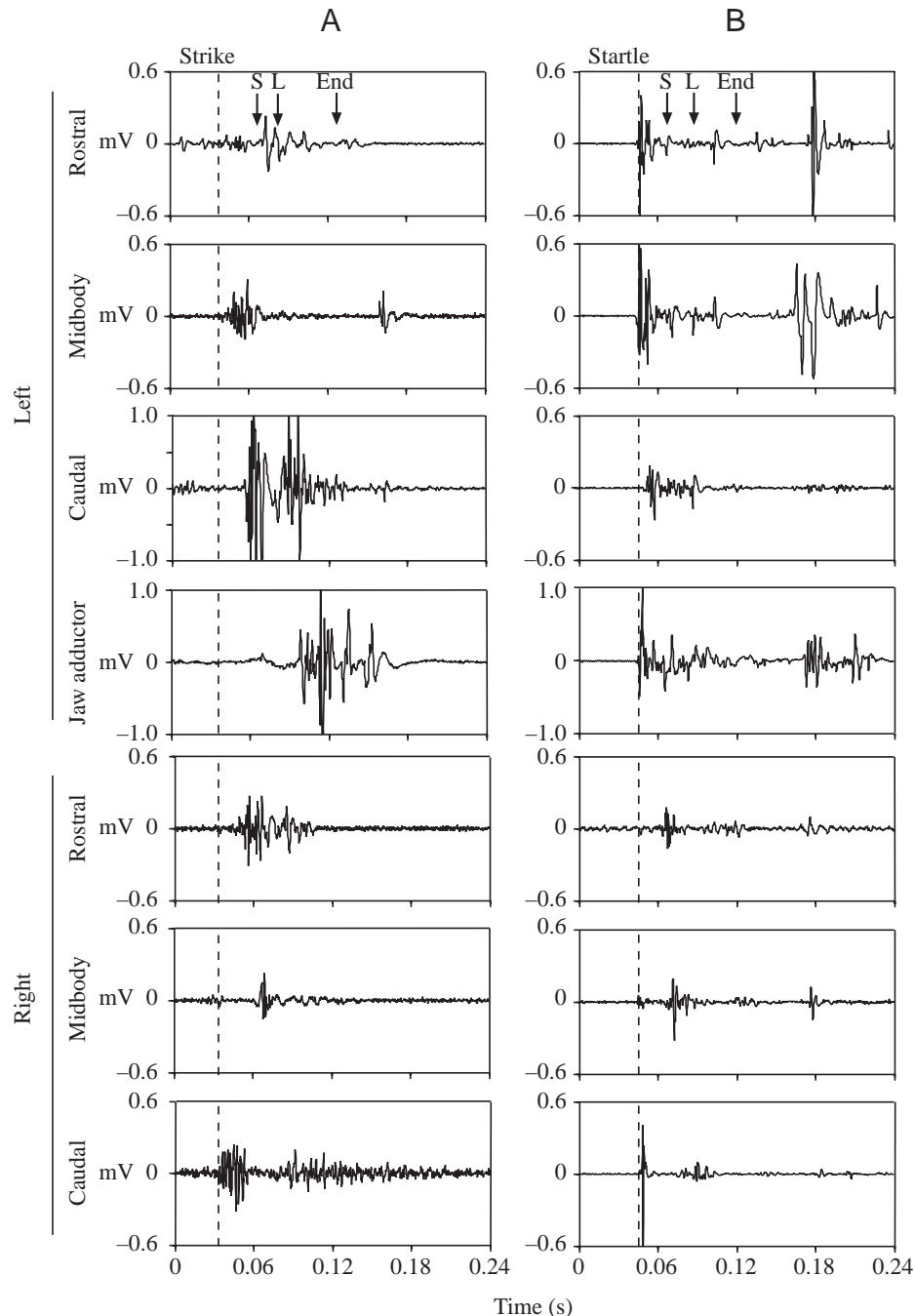


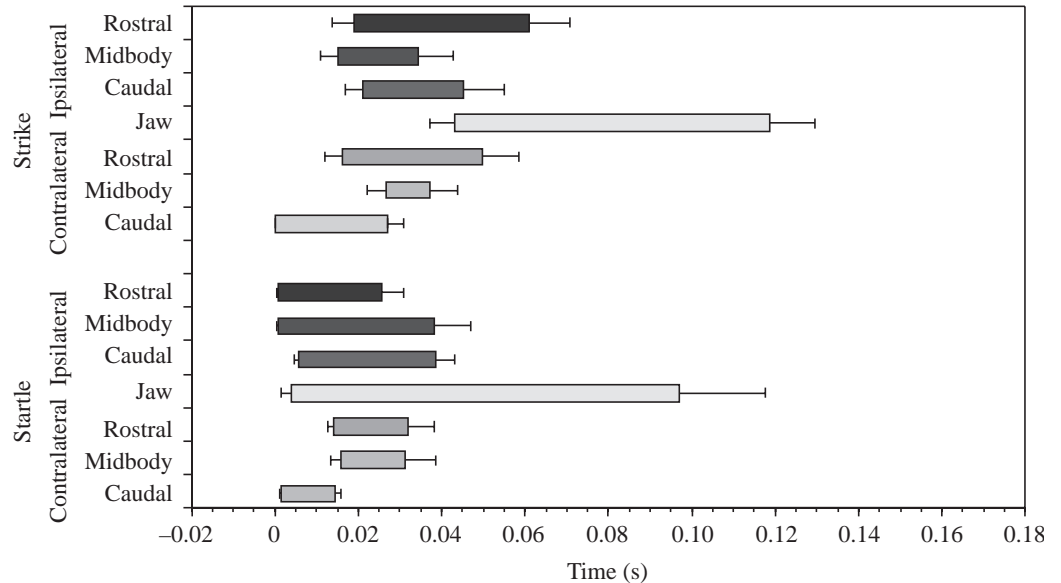
Fig. 6. Examples of electromyogram (EMG) patterns from S-start strike and startle behaviors. EMGs from rostral, midbody and caudal axial white muscle on both sides of the body and from left side jaw adductor muscle are shown. S, L and End indicate the end of the S-bend, L-bend and stage 2, respectively. The y-axis for jaw adductor EMGs of strikes and startles and for left caudal activity of the strike range from -1.0 mV to 1.0 mV while all other graphs range from -0.6 mV to 0.6 mV. Traces are aligned to first onset of activity with a vertical broken line. During the strike, caudal muscle activity (right side) occurs prior to more rostral activity; during the startle, there is near simultaneous activity of rostral and midbody muscle on one side of the body, in this case the left, with caudal muscle on the opposite side. During the strike, jaw muscle activity onset is considerably delayed from first onset of axial activity, while during the startle the jaw muscle is active from initiation of axial muscle activity.

corresponding activity for the startle, which occurred 1.0 ± 0.35 ms after the onset of initial activity ($P < 0.002$). The high variability in the onset times of both rostral and midbody ipsilateral activity during the strike is evident in high standard error values, both over 4 ms. There was no significant difference in either duration ($P = 0.83$) or mean amplitude ($P = 0.06$) of this activity. For the strike, the duration of midbody activity was 34.3 ± 8.6 ms and mean amplitude was 0.202 ± 0.056 mV, and for the startle the mean duration was 38.4 ± 8.6 ms and the amplitude was 0.372 ± 0.072 mV.

In contrast to the dramatic differences in stage 1 muscle activity patterns, contralateral muscle activity associated with stage 2, determined through comparison of EMGs from the contralateral rostral and midbody electrodes, was similar for strike and startle behaviors. With the exception of the amplitude of midbody activity ($P < 0.05$), there were no significant differences in onset times, durations or mean amplitudes of muscle activity between the strike and the startle behaviors. The anterior electrode onset occurred at 16.1 ± 4.2 ms after the initial burst of muscle activity for the strike and 14.1 ± 1.3 ms for the startle. The durations of strike and escape bursts were, respectively, 49.8 ± 8.7 ms and 31.9 ± 6.3 ms. EMG amplitudes were 0.298 ± 0.062 mV for the strike and 0.252 ± 0.05 mV for the startle. For the midbody

of rostral activity occurred, on average, 19.1 ± 5.46 ms after initial caudal activity for the strike; during the startle, initial rostral activity occurred 0.71 ± 0.28 ms following the first burst of activity in either jaw or more caudal axial muscle. The durations of rostral activity differed significantly between behaviors, being longer for the strike than for the startle (61.0 ± 9.9 ms versus 25.5 ± 5.3 ms, respectively; $P < 0.02$). The mean amplitude of the response was not significantly different: 0.252 ± 0.054 mV (strike) and 0.37 ± 0.112 mV (startle) ($P = 0.08$). Similar to the rostral activity, onset of midbody activity for the strike occurred an average of 15.0 ± 4.1 ms after the onset of initial activity. This was significantly after the

Fig. 7. Summary of the electromyographic recordings of S-start strike and startle muscle activity. The left margin of each bar is mean onset of activity and the right side is mean offset. Trials were aligned by setting the first onset of muscle activity to zero. Error bars represent the standard error of onset time (left) and duration (right). There is no standard error for initial caudal activity during the strike because this activity was, without exception, the first activity recorded for the strike. During the strike, initial caudal activity is followed by rostral and midbody activity on both sides



of the body. Jaw adductor muscle activity is delayed relative to axial activity. During the startle response, jaw muscle is coactive with contralateral caudal muscle on one side of the body and rostral and midbody ipsilateral muscle on the opposite side. The initial activity is immediately followed by ipsilateral caudal muscle and stage 2 contralateral activity.

electrode, onset occurred at 26.5 ± 4.5 ms for the strike and 15.3 ± 2.7 ms for the startle. The duration of midbody activity was 37.3 ± 6.6 ms for the strike and 30.4 ± 8.3 ms for the startle, and amplitude was 0.234 ± 0.04 mV for the strike and 0.146 ± 0.068 mV for the startle.

Despite similarity in their EMG patterns, the stage 2 contralateral activity appears to differ in function between strike and startle behaviors. During the startle, contralateral rostral and midbody EMG onsets are considerably delayed relative to the onset of rostral and midbody activity on the ipsilateral side ($P < 0.0001$; Figs 6, 7). By contrast, during the strike, rostral and midbody muscle onsets are not significantly different between the ipsilateral and contralateral electrodes [$P = 0.66$ (rostral); $P = 0.10$ (midbody)]. During the strike, the ipsilateral activity and contralateral activity appear to function together in stage 2. Instead of generating a wave of body bending as in startle behavior (Fig. 2L–N), the bilateral rostral activity during the strike is associated with minimal bending in the trunk during stage 2 (Fig. 2E,F) while the primary propulsive tail stroke is generated by caudal ipsilateral muscle (relative onset time 19.1 ± 4.0 ms).

Discussion

S-start strikes and startles have been grouped together and classified as the S-start type of fast-start behavior. The S-start strike occurs prior to prey capture as part of the primary locomotor movement of the feeding event and thus is used in a fundamentally different behavioral context from the S-start startle, in a directed attack as opposed to a reactive escape. We examined whether the same motor pattern functions in both strike and startle contexts or if the S-start behavioral classification could subsume several behaviors that differ in

their neuromotor control. Although this and other previous studies have described general similarities in kinematics among S-start responses (reviewed by Domenici and Blake, 1997), our examination of muscle activity demonstrates that stage 1 of S-start strikes and startles is generated by different patterns of axial and jaw muscle activity, suggesting that the neural control of these behaviors is different. By contrast, many aspects of stage 2 did not differ significantly between strikes and startles, including aspects of stage 2 kinematics and muscle activity, indicating that this part of the response may result from more similar neural commands.

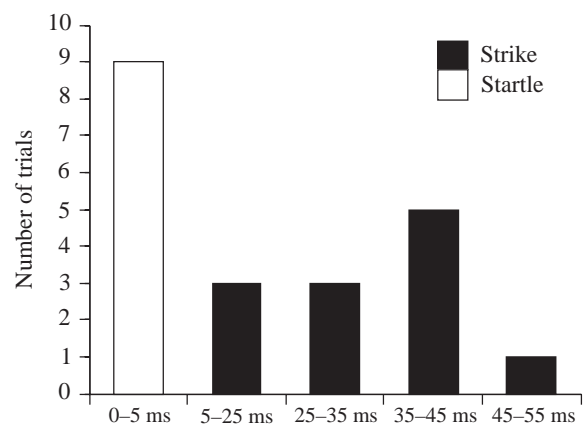


Fig. 8. Frequency distributions of adductor muscle electromyogram (EMG) onset times. There were non-overlapping distributions of adductor muscle onset time between strike and S-start escape behaviors. Onset of adductor muscle activity during the startle took place within 5 ms of the initiation of axial activity while during the strike the delay between axial and cranial activity was longer and more variable.

In previous work on strike behavior, Harper and Blake (1991) subdivided the strikes based on acceleration profiles that corresponded to tail strokes subsequent to the initial S-bend. In all of the trials examined, the northern pike accomplished prey capture by the end of stage 2, eliminating this type of variation. Webb and Skadsen (1980) subdivided the strike based on initial patterns of bending. They found that some strikes were initiated from a straight position and the S-bend was part of the propulsive movement, while in others the fish initiated the propulsive movement from an initial, non-propulsive, S-shaped bend. We did not see the diversity of responses described in these previous studies. The strikes we recorded were variable but did not fall into distinct categories and so we did not subdivide the responses. In several trials, axial movement preceded the activity of the white muscle recorded during strike behavior. We hypothesize that red axial muscle activity may be driving this bending. Further investigations of the role of red muscle in strike behavior and the coordination of red and white muscle would clarify these observations.

Initiation of the fast-start response

Major differences in the initiation of strikes and startles were found in kinematics and muscle activity patterns of stage 1. During strike behavior, the initial bending was for the most part restricted to the caudal region of the body, with little angular movement observed rostrally during either the S-bend or the L-bend. The movement pattern was reflected in the muscle activity pattern in which the onset of rostral and midbody muscle activity was delayed relative to caudal muscle activity. The angular movement during startle behavior was much higher; more than four times the angular movement of the strike for the S-bend. During the startle, the onset of activity among electrode positions was much closer, with the rostral and midbody activity occurring early in the behavior, on average 1 ms after caudal activity.

We suggest that minimizing head movement during stage 1 may have advantages for the feeding strike that are not relevant to the escape startle. First, minimizing rostral movement decreases the chance of detection by the prey fish as the tail movement is less likely to generate disturbance felt in front of the predator. Such tactics have been suggested for muskellunge predatory behavior. New et al. (2001) found that when positioning its body for the strike, the muskellunge appeared to minimize axial movements, relying instead on fin-based locomotion, and proposed that minimizing axial movement will decrease the chance of predator detection. Second, maintaining a relatively constant head position facing the prey may aid in accurately targeting the propulsive movements of stage 2. New et al. (2001) demonstrated that visual orientation prior to the strike provides important sensory information for successful prey capture.

The timing of S-start behaviors also differed between strikes and startles. The duration of the S-bend of the strike was significantly longer and considerably more variable than the S-bend of the startle response. This difference was due to a longer

S-bend during the strike than startle, on average 55.5 ms for the strike as opposed to 20.9 ms for the startle. During the startle, minimizing latency to respond and generating a rapid movement from the onset of the stimulus is advantageous for a successful escape. By contrast, during strikes, increasing the duration of initial movements may allow for fine-tuning of the behavior to increase the likelihood of a successful feeding event. This is critical for feeding as prey movement may be unpredictable and the relative locations of predator and prey may change rapidly with prey fish movement prior to the strike. In addition, early fast movements may alert the prey to the presence of the attacking predator and allow more time for escape (reviewed by Domenici and Blake, 1997).

Coordination of jaws and axis

The relative onset of jaw adductor muscle activity also differed markedly between the strike and startle. The adductor muscle did not contract during the early movements of the strike; mean onset was 43 ms after initial activity of axial muscle. This allowed the jaws to remain open as the pike approached the prey, closing only after the prey entered the pike's mouth. In contrast to the strike during the S-start, startle behavior jaw adductor muscle was active nearly simultaneously with axial muscle, on average 3 ms after first initiation of axial activity. Yasargil and Diamond (1968) and Diamond (1971) found the same pattern of activity during the Mauthner cell initiated C-start behavior. In addition, they described concurrent bilateral adduction of the opercula and movement of the eyes. Other than those initial descriptions and the one here, the coordination between cranial and axial motor control during startle behaviors has not been investigated. The function of this activity is also unclear. In mammals, the startle response generally involves a bilateral protective move, drawing in extremities and causing contraction of jaw and other cranial muscles (e.g. Caesar et al., 1989). The cranial response in fishes may also serve this function, protecting the head from attack. Alternative functions are also possible. For example, cranial muscle activity and closing of the jaws and, at least during the C-start, shutting the opercula and eyes may streamline the head, reducing drag during propulsion. Despite differences in the timing of jaw adduction, the durations and amplitudes of jaw movement did not differ between strike and startle behaviors. We suggest that jaw muscle is maximally active during both behaviors, thus generating similar patterns of contraction.

As with the axial muscle activity, the differences in timing of jaw activity during S-start startles and strikes suggest there are differences in how jaw and axial muscle activities are coordinated, although mechanisms for these differences are unclear. Our study was limited to one cranial muscle; further study of the coordination of cranial activity in the strike and startle, following the work of Diamond (1971), would provide additional insight into variation in the cranial portions of the response.

Stage 2 propulsion

Despite major differences in the initial movements of the

strike and startle, stage 2 is remarkably similar between the two behaviors. The angle of head movement in stage 2 and the duration of that movement were not significantly different between response types. We measured performance of the startle and strike kinematics by determining the peak linear velocity and acceleration of the center of mass in stage 2. As with movement angle and duration, we found no significant differences between strikes and startles.

To assess muscle activity in stage 2, we examined EMGs from rostral and midbody muscle on the opposite side of the body to the initial rostral activity. We found that there was no significant difference in onset times, durations or rostral electrode amplitude of stage 2 EMGs. Although EMG parameters are similar for the contralateral rostral and midbody muscle in strikes and startles, we suggest that this activity is used in very different ways. During the strike, rostral and midbody muscle onset times do not differ between the ipsilateral and contralateral sides. We suggest that this bilateral activity functions to stiffen the body in stage 2. Bilateral activity has been suggested previously as a mechanism for increasing body stiffness during the C-start (Diamond, 1971; Foreman and Eaton, 1993; Westneat et al., 1998; Hale et al., 2002; Tytell and Lauder, 2002). During the propulsive movement of the strike, this activity might prevent rostral bending to improve prey targeting.

Another possible role of bilateral rostral activity may be in cranial movement during the strike. Thys (1997) has shown muscle activity in the rostral epaxial muscle of the largemouth bass (*Micropterus salmoides*) during strike behavior and suggests that these muscles are used to raise the neurocranium when the mouth opens. More detailed examination of regional activity of rostral myomeres, as performed by Thys (1997), may clarify the role of bilateral rostral muscle activity in the strike behavior.

Categorizing fast-start responses

We conclude that the term S-start subsumes a range of behaviors that share several general characteristics of muscle activity and movement patterns but that differ in their neural control in fundamental ways. The S-start startle of northern pike demonstrates the same pattern of muscle activity as that described previously for the muskellunge (Hale, 2002): near simultaneous rostral muscle activity on one side of the body and caudal muscle activity on the opposite side of the body. The strike is similar to the startle in that it involves regional activity along the length of the body during initial non-propulsive movements. However, in contrast to the startle, during the strike caudal muscle is active prior to contralateral rostral activity and the duration of that activity is longer and more variable. While it is possible that the two S-start behaviors may involve the same or overlapping populations of cells in the hindbrain and spinal cords, those cells must be coordinated by independent mechanisms. We suggest that, like the Mauthner-elicited C-start startle behavior, the S-start startle involves a simple neural circuit with relatively few cells. By contrast, we suggest that there is greater processing of

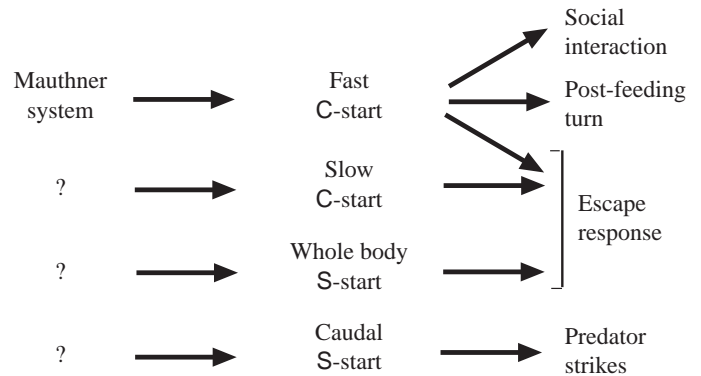


Fig. 9. Diagram of motor control and function of fast-start behaviors, modified from fig. 5 of Domenici and Blake (1997). The designations of whole-body S-start *versus* caudal S-start reflect the differences in rostral bending during the initial movements of strike and startle behaviors. This work confirms the role of an independent S-start behavior that functions as a startle and demonstrates differences in the motor control of strike and startle behaviors. While there are indications that these behaviors are controlled by different, but possibly overlapping, neural circuits, neural mechanisms have yet to be identified.

sensory cues during the initial movements of the strike and thus a more complicated neural circuit is employed.

It is highly unlikely that the Mauthner cell could function during the S-start startle or strikes. As discussed by Hale (2002), the Mauthner cell has been shown to elicit strong muscle contraction along the full length of the spinal cord and to override conflicting motor patterns to generate a startle response (Jayne and Lauder, 1993; Svoboda and Fetcho, 1996). That such strong neural activity could be inhibited to generate the regional EMG pattern that characterizes the S-start behaviors is unlikely. Thus, while Mauthner cell-elicited behaviors can occur in post-feeding turns (Canfield and Rose, 1993), as yet they have not been identified as part of the high-acceleration prey capture portion of the feeding strike.

Domenici and Blake (1997), in their figure 5, provide a useful summary diagram of the fast-start types, their roles in behavior and neural control. The diagram illustrates how little is known about the S-start type of fast-start. While the neural basis of S-starts has yet to be studied, our data begin to refine classifications of S-start behaviors. Fig. 9 adds to Domenici and Blake's diagram to incorporate recent data on S-start behaviors. In addition to confirming that S-starts are an independent behavior from the C-start that functions in escape (see also Hale, 2002), we suggest that the S-start strikes and startles should be subdivided based on differences in muscle activity of initial movements and the implications of those differences for the motor control in stage 1.

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