ZOOLOGY

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Alternative forms of axial startle behaviors in fishes☆

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ABSTRACT

For most aquatic vertebrates, axial movements play key roles in the performance of startle responses. In fishes, these axis-based startle behaviors fall into three distinct categories – the C-start, withdrawal, and S-start – defined by patterns of body bending and underlying motor control. Startle behaviors have been widely studied due to their importance for predator evasion. In addition, the neural circuits that control startles are relatively accessible, compared to other vertebrate circuits, and have provided opportunities to understand basic nervous system function. The C-start neural circuit has long been a model in systems neuroscience and considerable work on neural control of withdrawal response has been conducted in the larval lamprey. The S-start response has only recently been explored from a physiological perspective and we focus here on reviewing S-start motor control and movement in the context of the other two responses. Axial elongation has previously been associated with startle behavior in comparisons of C-starts and withdrawal, with extremely elongate animals performing withdrawals. We suggest that the S-start tends to occur with moderate body elongation, complementing the C-start in animals with this body form. As many larval fishes are moderately elongate, we suggest that the S-start may be common in larvae but may be secondarily lost with body shape change through development.

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1. Introduction

For most vertebrates, movement of the anteroposterior body axis contributes to locomotion through generating force, stabilizing the body, and/or facilitating limb movement. Locomotion that relies on axial movement as a major source of thrust production is an ancestral characteristic of vertebrates, and the majority of aquatic vertebrates use axial movement in at least some locomotor contexts. Axial movement is particularly common during high-speed swimming and when an animal is accelerating rapidly. For example, many fishes use paired fins during slow steady swimming or maneuvering, but switch to axial bending, and the use of larger myomeric axial muscles for force production, as speeds increase above the level that can be sustained by paired fins. At the high end of speed and acceleration, startles are for the most part axis-powered behaviors in aquatic vertebrates. These responses to threatening stimuli most often involve fast burst swimming initiated with a rapid re-orientation of the body that is accomplished by axial bending.

Axial startle responses have provided a behavioral window into the neural control of axial movement and the fundamental principles of movement systems. Several factors that allow such escape behaviors to be effective also benefit the study of their motor control: (i) Rapid response times necessitate simple neural circuits; fewer components and connections make their study more tractable. (ii) Major kinematic features of the escape behavior are relatively consistent and readily elicited, and thus more easily identified and quantified. (iii) Startles are performed by a wide phylogenetic and morphological diversity of species and occur through a wide range of life history stages. These characteristics provide many opportunities for exploring structure–function relationships comparatively, through development, and through evolution, making the startle response an excellent model for examining neural control of behavior and of axial motor control more specifically.

Here we review the axial startle responses of aquatic vertebrates, their motor patterns, and aspects of their underlying neural control. We discuss possible evolutionary trends in startle behavior and neural circuitry. Two types of axial startle response have been studied in depth in fishes: the C-start and the withdrawal response (Fig. 1). The specific goal of this paper is to put the relatively less explored S-start startle system (Fig. 1) into the context of those better-understood behaviors.

2. Startle kinematics

Axial startle kinematics have been documented in a wide phylogenetic range of fishes and aquatic amphibians (e.g., Eaton et al., 1977; Webb, 1978; Hale et al., 2002; Ward and Azizi, 2004). Despite species-specific variation in patterns of movement, commonalities
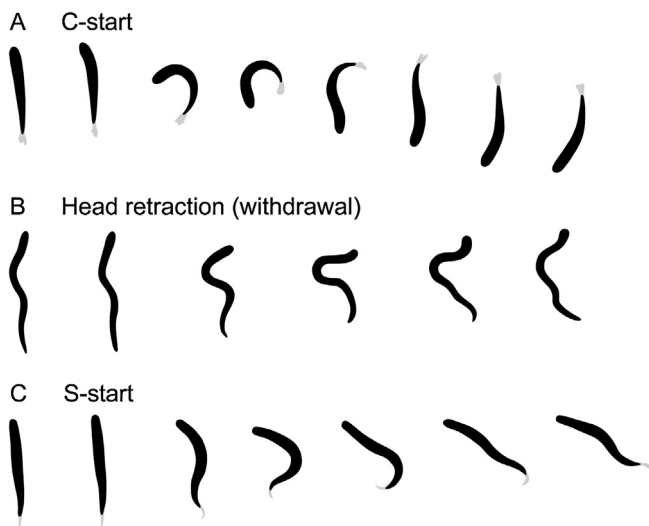
Fig. 1. The C-start, withdrawal, and S-start startle responses. Silhouettes of the body from a dorsal or ventral view are in black; caudal fins, where visible, are in gray. (A) C-start of chinook salmon (*Oncorhynchus tshawytscha*), modified from Hale (1996). (B) Withdrawal (head retraction) of larval lamprey (*Petromyzon marinus*), modified from Currie and Carlsen (1987). (C) S-start of northern pike (*Esox lucius*), modified from Schriefer and Hale (2004).

in the response among taxa allow for broad categorization of startles. While the majority of species have been studied in the context of C-start behavior, it is now clear that at least some perform multiple distinct types of startle, a change in our fundamental understanding of startle control.

C-starts have been described in a wide range of species and throughout ontogeny in fishes (Table 1). The C-start is described by its axial movement patterns as having three kinematic stages (Weihs, 1973). During stage 1, the body bends into a "C" shape with the head rotating away from the stimulus at high angular velocity and acceleration, so that by the end of this phase, the head may have turned more than 180° from the starting orientation. In this phase, the animal forms the C-bend with little displacement of the center of mass. During stage 2, the animal generates an anterior to posterior wave of axial bending, turns in the opposite direction from the initial C-bend, and moves forward and away from the stimulus. A more variable period of fast-burst swimming, stage 3, often follows stage 2. As with other startles, the C-start is a rapid behavior. Stages 1 and 2 of the C-start can be completed in less than 20 ms in larval zebrafish, and commonly within several hundreds of milliseconds in adult fish and amphibians. Latency between stimulus and response, fundamentally related to the success of a fast-start (O'Steen et al., 2002; Walker et al., 2005), has been shown to be very short. However, the timing of the stimulus and the perception of stimulation are difficult to quantify and most studies have focused on motor output and behavior.

Although C-starts share fundamental features among species, kinematics between species and even between startles of an individual animal can vary significantly. By trial, species, or developmental stage, the major kinematic variables of each startle stage vary: latency to initiation, duration and timing, maximum and average head rotation angle, maximum and average velocity and acceleration, and distances translated (e.g., Harper and Blake, 1990; Domenici and Blake, 1997; Hale, 1999; Wilson and Franklin, 2000; Azizi and Landberg, 2002; Marras et al., 2011). The kinematic stages themselves can also vary. The C-start is defined by movement in stage 1 but need not include stages 2 and 3. Stage 3 is often absent and while stage 2 is generally present, C-starts can lack that stage as well, as exemplified by carp (*Cyprinus carpio*; Spierts and Van Leeuwen, 1999) and knifefish (*Xenomystus nigri*; Kasapi et al., 1993).

Operationally, it is useful to describe C-start stages with kinematics rather than by underlying motor pattern (nerve or muscle activity recording), as motor pattern data are only available for a small number of the existing studies and cannot be obtained in some experimental contexts. However, the combination of physiology and behavior is key to establishing links from behavior to neural control and can help to tease apart variability due to passive effects and active control. The C-start stage 1 bend often does not truly take the shape of a "C" (Jayne and Lauder, 1996). In some cases the "C" is more "O"-shaped as the head and tail cross during stage 1. These responses have not generally been classified separately as there is no evidence that they represent discretely different motor control strategies. In a more common variation on the C-start, the caudal body region bends in the opposite direction forming an "S" shape during stage 1. Sometimes the contralateral caudal bending is limited to the caudal fin and appears to be due to passive resistance of the water. In other cases, there may be more involvement of the tail and thus the source of the bending is more ambiguous.

S-starts have been described as a distinct kinematic pattern from C-starts in several species including northern pike (*Esox lucius*; Harper and Blake, 1990; Schriefer and Hale, 2004), muskellunge (*Esox masquinongy*; Hale, 2002), carp (*Cyprinus carpio*; Spierts and Van Leeuwen, 1999), rainbow trout (*Oncorhynchus mykiss*; Webb, 1976; Harper and Blake, 1990), and larval zebrafish (*Danio rerio*; Liu et al., 2012) (Table 1). The first movements of stage 1 form the S-bend, with curvature to one side of the body in the trunk region and a second smaller bend of the tail to the opposite side. The S-bend is followed rapidly by reversal of the tail toward the direction of rostral bending so that an "L"- or "C"-shaped bend is formed by the end of stage 1 (Fig. 2). After stage 1, a wave of axial bending, analogous to stage 2 of the C-start, occurs and is often followed by swimming that is consistent with stage 3.

Like the C-start, the S-start is a high-performance response. Key kinematic parameters – angular head velocity, angular head acceleration, and timing of response initiation – are comparable between C- and S-starts. Beyond axial bending patterns, the main difference between these two responses is head rotation angles, where the S-start generally involves small head rotation angles compared to the C-start (e.g., Frith and Blake, 1995; Domenici and Blake, 1997; Spierts and Van Leeuwen, 1999; Hale, 2002). Angular displacement of the head is related to the orientation of the stimulus; in muskellunge, northern pike, and larval zebrafish, the S-start tends to result from caudal stimulation while the C-start is much more likely to occur in response to more rostral stimulation.

Other studies that relate stimulus position to orientation of the startle response have found similar trends in head rotation angles. Responses elicited by head stimulation often result in greater head angles in stage 1 than do tail-elicited responses (e.g., Eaton et al., 1984; Foreman and Eaton, 1993; Liu and Fetcho, 1999; Spierts and Van Leeuwen, 1999; Budick and O'Malley, 2000). Such differences are hypothesized to reflect strategies for escape. For a threatening stimulus approaching from the head, a large stage 1 turn may help to orient stage 2 swimming away from the predator. Likewise, the low head angle response to a perceived threat at the tail may result in a small angular movement so that swimming continues in a direction close to the initial orientation of the fish and, again, away from the potential predator. From the data reported, it is unclear whether differences in turn angle in these studies result from alternative forms of startle or represent variation in the C-start response, but it seems likely that both are factors.

Head withdrawal, or head retraction, responses have been described in a range of species (Table 1). Ward and Azizi (2004) conducted a broad phylogenetic survey (nine species of fishes and amphibians) of the withdrawal response and showed that there was a positive correlation between species that performed withdrawals and axial elongation; elongate species with more vertebrae