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REVIEW

Escape responses of fish: a review of the diversity in motor control, kinematics and behaviour

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ABSTRACT

The study of fish escape responses has provided important insights into the accelerative motions and fast response times of these animals. In addition, the accessibility of the underlying neural circuits has made the escape response a fundamental model in neurobiology. Fish escape responses were originally viewed as highly stereotypic all-or-none behaviours. However, research on a wide variety of species has shown considerable taxon-specific and context-dependent variability in the kinematics and neural control of escape. In addition, escape-like motions have been reported: these resemble escape responses kinematically, but occur in situations that do not involve a response to a threatening stimulus. This Review focuses on the diversity of escape responses in fish by discussing recent work on: (1) the types of escape responses as defined by kinematic analysis (these include C- and S-starts, and single- versus double-bend responses); (2) the diversity of neuromuscular control; (3) the variability of escape responses in terms of behaviour and kinematics within the context of predator–prey interactions; and (4) the main escape-like motions observed in various species. Here, we aim to integrate recent knowledge on escape responses and highlight rich areas for research. Rapidly developing approaches for studying the kinematics of swimming motion both in the lab and within the natural environment provide new avenues for research on these critical and common behaviours.

KEY WORDS: Escape response, Fish, Kinematics, Mauthner cells, Swimming

Introduction

The past two decades have seen rapid developments in the ability to explore behaviour and its neural basis in a wide range of species, thanks to automated approaches to recording the movement of individual animals and groups (Dell et al., 2014; Neuswanger et al., 2016; Olsen and Westneat, 2015; Shamur et al., 2016). Accordingly, the analysis of animal movement and behaviour has become less labour intensive and more sophisticated, making use of machine learning and 'big data' (Hong et al., 2015; Valletta et al., 2017). By taking advantage of these techniques we can hope to achieve an integrative view of behaviour – one that links kinematics to motor control in multiple species – by deriving basic principles through species comparison.

One rich system for exploring behavioural diversity is the fish escape response (see Glossary) and related accelerative behaviours (collectively termed 'fast starts'; see Glossary). Early work on fish escape responses was based on kinematics (Webb, 1975, 1976; Webb,

1978a; Weihs, 1973) and neural control (Eaton et al., 1977; Eaton and Hackett, 1984), and it focused on a small number of species (mainly goldfish, trout and pike). As a result, fish escapes were seen as stereotyped responses (Webb, 1984a). This basic high-acceleration escape response was described as occurring in three stages: stage 1 (see Glossary), the 'preparatory' stage, in which the body bends rapidly with minimal translation of the centre of mass; stage 2 (see Glossary), the 'propulsive' stroke, when the fish accelerates away from its initial position; and stage 3, in which the fish either continues swimming or starts gliding (Weihs, 1973). The first two stages have been the focus of most literature on escape response kinematics (Webb, 1976, 1978a, 1982, 1986; Weihs and Webb, 1984), although later work showed that escape responses can consist of stage 1 only (i.e. single-bend responses as opposed to double-bend responses; Domenici and Blake, 1997). Stage 1 involves one of two distinct motor patterns: during the C-start, the body takes on the shape of a 'C', and in the S-start, the body bends into an 'S' shape.

Subsequent work on fish escape responses has addressed a broad range of species, and has demonstrated wide kinematic variability across species. More recent work has also revealed the use of escape-like motions (see Glossary) that resemble escape responses but that occur in the absence of a frightening stimulus (Canfield and Rose, 1993; Domenici et al., 2015; Wohl and Schuster, 2007). Escape response studies have developed to include a number of variables that add to the traditional 'locomotor-type' variables (e.g. speed and acceleration) to assess escape performance and its relevance in terms of vulnerability to predators (Domenici, 2010a; Walker et al., 2005). Escape traits that are relevant for successfully avoiding predation include the escape latency (see Glossary), the distance at which the prey react to the approaching predator and the directionality (see Glossary), in addition to locomotor traits. All of these traits may be affected by the behavioural context, such as whether the prey is: (i) part of a school, (ii) engaged in feeding or (iii) near a refuge (Domenici, 2010a,b). In addition, dissection of the neural circuits driving escape has provided detailed understanding of the escape circuit and variations in its structure and use; although Mauthner (M) cells are the primary reticulospinal neuron responsible for triggering fast escape responses, escapes controlled by other reticulospinal neurons can also occur (Korn and Faber, 2005; Liu and Fetcho, 1999). The escape response of fish has provided not only a prime example of simple sensorimotor circuits and their evolutionary diversity, but also allows us to begin to understand a broad repertoire of high-acceleration behaviours performed by a large number of fish species.

Here, we review the diversity of escape and related behaviours and their neural underpinnings. We aim to synthesize current findings and provide a foundation for future work on accelerative behaviours in fish. Understanding the diversity in the motor control and kinematic output of high-acceleration movements is fundamental for furthering our knowledge of how fish swim. Even more broadly, it can provide a window into how organisms evolve and coordinate suites of responses in a number of behavioural contexts.

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Glossary

Directionality
Escape responses can be divided into away and towards responses, when the head of the fish moves away from or towards the position of the threat, respectively. Directionality can be measured as the percentage of away responses out of the total number of trials.

Escape angle
The angle between (a) the line corresponding to the fish's orientation at the time of the stimulation and (b) the line corresponding to the fish swimming trajectory at the end of the escape response.

Escape latency
The time interval between the onset of the threatening stimulus and the first visible reaction by the fish.

Escape response
An accelerative motion performed as a response to a sudden threat. All escape responses are fast-starts, although not all fast starts are escape responses.

Escape trajectory
The angular sum of the stimulus angle and the escape angle.

Escape-like motion
Any accelerative motion that resembles an escape response from a kinematic perspective, but that is not triggered by a frightening, predator-like stimulus.

Fast start
An accelerative motion from resting or swimming, that can be observed during various behavioural contexts, including predator–prey encounters (i.e. predator strikes, escape responses) and social interactions.

Freezing
A startle response involving cessation of any pre-startle movement and a period when the fish is alert but unmoving.

Mauthner cells (M-cells)
Two giant neurons in the hindbrain of most fish species. They are known to control stage 1 of the escape response (although non-M-cell-mediated escapes also occur), and they have been shown to participate in some post-feeding turns away from the water surface.

Predator strike
An accelerative motion (fast start) towards an evasive prey item, often performed in line with the original postural axis of the predator.

Responsiveness
The proportion of escape responses out of the total number of stimulations.

Stage 1
The first body bend during a fast start. From a kinematic perspective, it starts at the onset of the response and it ends when the head stops turning or changes the direction of the turn.

Stage 2
The second body bend during a fast start. From a kinematic perspective, it starts at the end of stage 1 and it ends when the head stops turning or changes the direction of the turn.

Startle response
A response to a sudden threatening stimulus. It can involve locomotion (i.e. escape response), motion of only part of the body (i.e. head retraction) or freezing.

Stage 1 turning angle
The angle between the anterior midline of the fish at the start of the escape response and the end of stage 1.

Stage 1 turning radius
The radius of the approximate circle determined by the path of the centre of mass during stage 1.

Stimulus angle
The angle between (a) the line joining the stimulus and the fish centre of mass and (b) the line corresponding to the fish's orientation, at the time of the stimulation.

Turning rate
The angular velocity of the anterior midline of the fish.

Escape kinematics: diversity of escape responses

In the past couple of decades, multiple types of escape response (e.g. C-start, S-start, single bend, double bend) have been examined in depth (Domenici and Batty, 1997; Fleuren et al., 2018; Hale, 2002; Lefrançois et al., 2005; Spierts and Leeuwen, 1999; Tytell and Lauder, 2002). Consequently, the fast-start nomenclature has proliferated. In order to clarify the nomenclature, we propose a simple Venn diagram illustrating the current definitions of the fast-start behaviours discussed below (Fig. 1). As a response to a threat, fish typically show a startle response (see Glossary), which can consist of an escape response (a sudden acceleration), a head retraction or a freezing response (see Glossary). Of these, only escape responses involve locomotion and are considered fast starts; head retraction and freezing are startle responses but not fast starts. While escape responses can be considered a type of fast start, not all fast starts are escape responses: fast starts can also be predator strikes (see Glossary) or other accelerative motions. Finally, predators not only use strikes to capture their prey, prey capture can also be aided by suction feeding (Fig. 1; Norton and Brainerd, 1993). The kinematics of the main escape response variants and other accelerative behaviours, along with the behavioural contexts within which they are used and what is known about their neural control, are outlined below and illustrated in Fig. 2.

Stage 1 kinematics: C-starts and S-starts

The two most common stage 1 kinematic patterns are the C-start and S-start. These are different behaviours with distinct motor programs (e.g. Hale, 2002; Liu and Hale, 2017). To discern a true S-start from a C-start it is critical to use electromyography or other physiological approaches to determine whether the pattern of bending in stage 1 is actively generated, as water resistance can cause passive caudal bending and result in an S-like bend from a C-start motor pattern. Behavioural studies need to recognize this caveat to the interpretation of kinematic data sets. Unfortunately, electromyograms (EMGs) can be impractical for a variety of reasons; therefore, many escape response studies are based on video analysis alone. In addition, although electromyography can reveal the pattern of muscle activation, it cannot identify the underlying neural mechanisms.
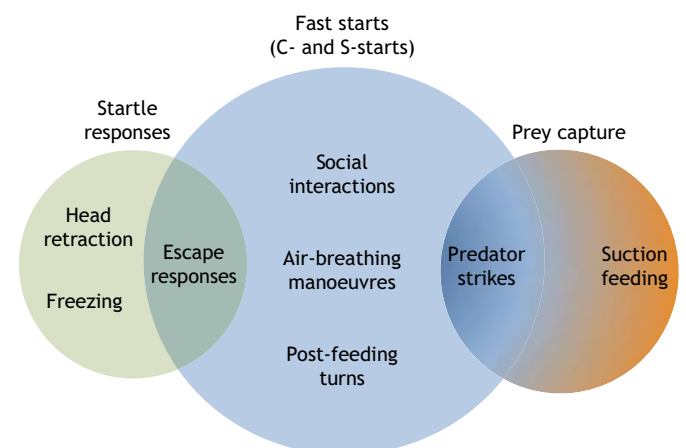

Fig. 1. Definitions of fast starts and other predator–prey motions. Venn diagram illustrating the relationship between various fast starts (i.e. escape responses, predator strikes and other accelerative motions) and other behaviours (i.e. startle responses and prey capture) related to predator–prey encounters. The color gradient between 'predator strike' and 'suction feeding' indicates that these two behaviours are not fully separated but form a continuum between two extremes (Norton and Brainerd, 1993). Further details can be found in the main text.
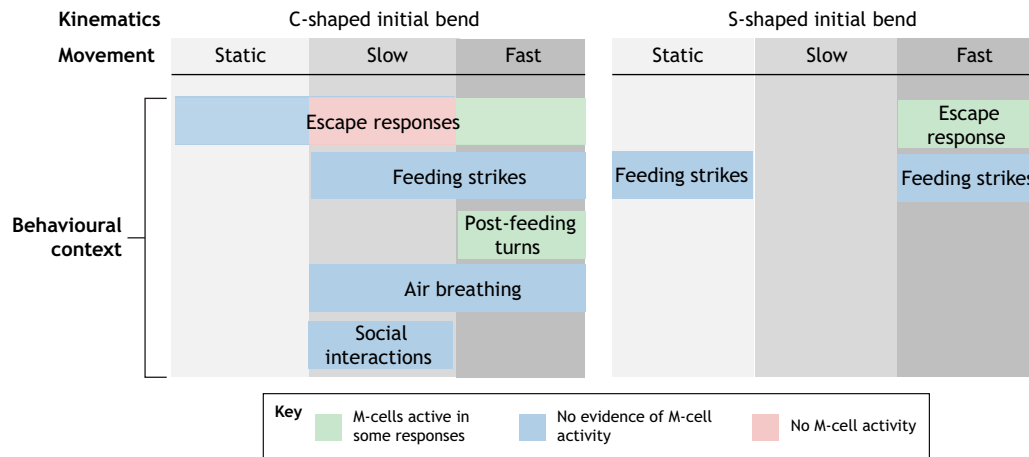
Fig. 2. The behavioural context of fast starts. Diagram illustrating various types of accelerative behaviours in relation to their kinematics, movement pattern of the initial bend (fast, slow or a static bend lasting a few seconds), behavioural context and neural control. Latency to respond to a stimulus, a key indicator of Mauthner cell (M-cell) activity, is difficult to quantify and thus has not been assessed in many behaviours, therefore categorisation is based on the kinematics of movement. Green areas indicate that the involvement of M-cells has been ascertained for some fast starts in this category. Pink areas indicate behaviours shown to occur without M-cell activity (Bhattacharyya et al., 2017). Blue areas indicate no evidence for M-cell activity. For C-shaped escape responses, fast, slow and static patterns occur (fast and slow responses, Domenici and Batty, 1997; static, Turesson et al., 2009). For S-shaped escape responses, only fast responses have been recorded (Schriefer and Hale, 2004). For C-shaped feeding strikes, slow and fast bends have been observed (Wohl and Schuster, 2007). For S-shaped feeding strikes, both fast (Schriefer and Hale, 2004) and static (Webb and Skadsen, 1980) patterns have been observed. Fast C-shaped bends were observed in post-feeding turns (Canfield and Rose, 1993), although their kinematics were not analyzed quantitatively. Air-breathing motions show a wide range of turning rates (Domenici et al., 2015). C-starts observed in social interactions are slow (Fernald, 1975). M-cell involvement is proven only for fast C-start escape responses (Eaton et al., 1981) and post-feeding turns (Canfield and Rose, 1993). See main text for further details.

C-starts

In the current literature, the most prevalent and best-known escape response is the C-start (Fig. 3), which is initiated with a 'C'-shaped bend that reorients the body (Eaton et al., 1977, 1981; Eaton and Hackett, 1984). The 'C' shape of the C-start movement during stage 1 is a coarse descriptor, meant to represent movements that include a whole-body bend to the left or right. The curvature of the bend and angular movement differ among startles (Domenici and Blake, 1991; Eaton and Emberley, 1991; Eaton et al., 1984). For example, an individual fish can perform C-bends of very different curvatures (Hale, 2002). Stage 1 turning angle (see Glossary) in a C-start is related to the final escape trajectory (Domenici and Blake, 1993b; Foreman and Eaton, 1993) and propulsion (Tytell and Lauder, 2008; Wakeling, 2006) of the escape. Stage 1 of a C-start may also play a role in the rapid local movement of the head or tail away from a threat (Catania, 2009). C-starts can also be observed in non-escape behaviours, including air breathing and even predator strikes (discussed below). Much slower 'C'-shaped body bends and turns are common in fish and are used in a range of other contexts, including in routine swimming and manoeuvring (Schrank et al., 1999; Webb and Fairchild, 2001).

S-starts

A second major type of escape response, the S-start, is initiated with an S-shaped bend of the trunk and tail during stage 1 (Fig. 3). Physiologically classified S-start escape responses are triggered by stimulation near the tail, and the overall movement is forward and away from the caudal stimulus. There are two subcomponents to stage 1 kinematics of the S-start: first, an 'S' shape is produced with an actively generated rostral bend to one side of the body and caudal bend to the other (Fig. 3). Second, the tail returns to the opposite side so that there is one bend, often focused near the tail (Hale, 2002; Liu et al., 2012). S-shaped movements are used in the predator strikes of pike (Harper and Blake, 1991; Schriefer and Hale, 2004). These strikes, however, show a kinematic pattern that differs from

the S-start typical of escape responses, in that the S bend forms well in advance of the accelerative movement and is of higher amplitude (Schriefer and Hale, 2004). In addition, the anterior region of the body does not change orientation appreciably, which is different to S-start escapes where there is angular head movement in stage 1.

Other startle responses

Beyond the C-start and S-start, there are other less common startle responses that involve rapid body motion during stage 1 but not swimming per se, so they are not classified as escape responses. For very elongated fish (e.g. eels and lamprey), withdrawal responses (i.e. head retraction) rapidly pull the head back from a head-directed stimulus, typically into a refuge (Bierman et al., 2004; Currie and Carlsen, 1985, 1987; Eaton et al., 1977; Meyers et al., 1998). The withdrawal responses of larval lamprey have been extensively studied at kinematic and physiological levels in response to head-directed stimuli. Unlike the C-start or S-start, head retractions can involve one or multiple bends along the body during stage 1, and those bends generally occur in the location of bends existing on the body prior to the response (Currie and Carlsen, 1985, 1987).

Slow and fast escapes

Stage 1 kinematics (e.g. turning rates; see Glossary) may vary as a result of the behavioural context and stimulus strength. The turning rate during stage 1 has been used to characterise escape response type, i.e. slow versus fast escapes, which are driven by different neural circuits (see below, Bhattacharyya et al., 2017; Domenici and Batty, 1997; Domenici et al., 2004). Various species (herring, cod, dogfish; Fig. 3) can show a slow or a fast rate of turning when escaping, although it should be noted that even the slow turns are much faster than turns observed during routine manoeuvring (Domenici and Batty, 1997; Domenici et al., 2004; Meager et al., 2006). Slow and fast escape responses can be related to the timing of the response (i.e. escape latency), whereby short latency responses show the highest turning rates, while long latency responses may
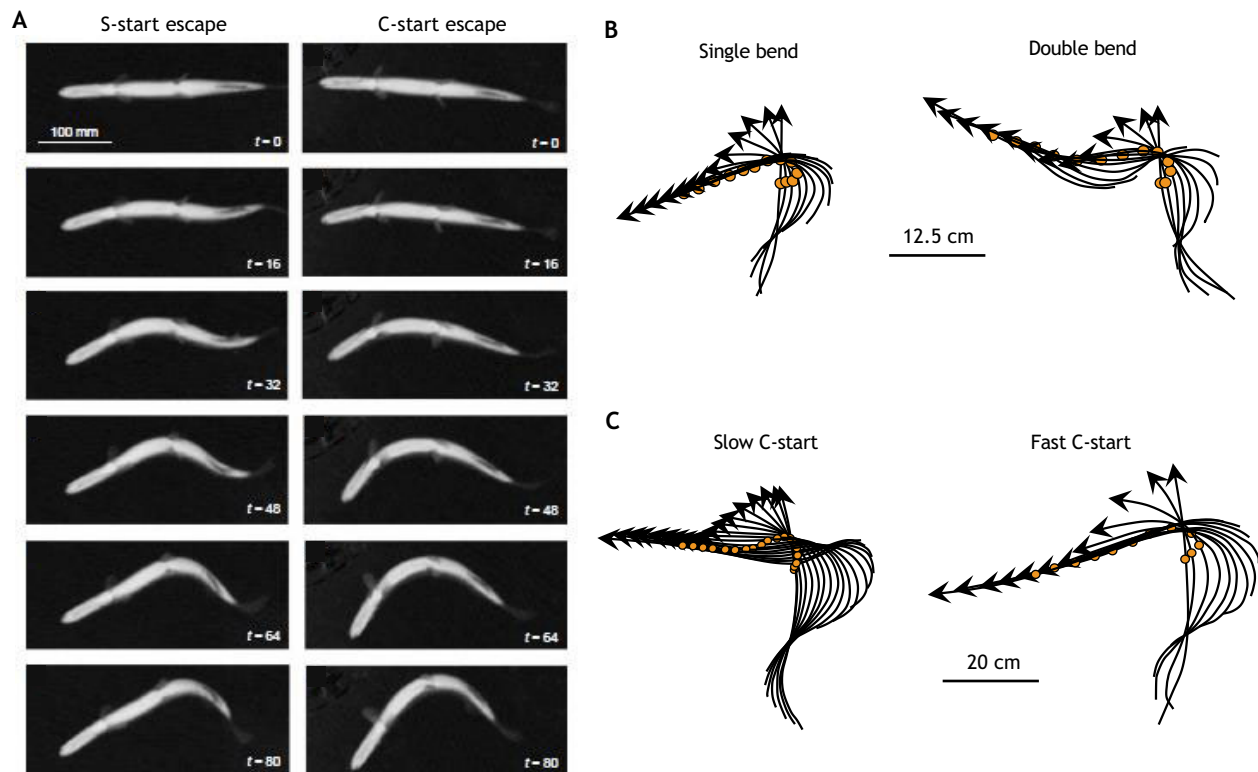
Fig. 3. Movement patterns associated with various types of escape response. (A) The initial motion of an S-start (top) and a C-start (right) of a muskellunge (*Esox masquinongy*) recorded from below (Hale, 2002). Time (in ms) is marked on the bottom right corner of each frame. An S-shape and a C-shape are formed after 32 ms in the S- and C-start, respectively (from Hale, 2002). (B) Single-bend (left) and double-bend (right) escape responses in the grey mullet (*Liza aurata*). The curved arrows represent the midlines (with the head at the tip of the arrow) along the body and the circles represent the centre of mass of the fish (when stretched straight) at 10 ms frame intervals. The single-bend response shows no reversal of turning direction of the head, and the tail straightens as the fish goes into a glide. In the double-bend response, a reversal in the direction of turning of the head occurs (at frame six) and the fish return flip is completed thereafter (reproduced with permission from Lefrançois et al., 2005). (C) Slow (left) and fast (right) responses in dogfish (*Squalus acanthias*). The curved arrows represent the midline (with the head at the tip of the arrow), and the circles represent the centre of mass of the fish (when stretched straight), at 40 ms intervals. Note the higher number of frames (i.e. the longer time) taken by fish on the left to achieve a similar turning angle to that of the fish shown on the right (from Domenici et al., 2004).

involve either fast or slow turning rates, as shown in herring (Domenici and Batty, 1994, 1997). One of the factors determining the occurrence of fast versus slow responses is the distance from the mechanical stimulus triggering the startle, with fast responses triggered by stimuli closer than those triggering slow responses (Domenici and Batty, 1997). In addition, the proportion of slow responses is higher when fish are part of a school, possibly because of the low perceived risk of predation in a group (Domenici and Batty, 1994, 1997). Recent work based on visual stimulation of larval zebrafish supports the idea that stronger stimulation can yield stronger responses (Bhattacharyya et al., 2017). Using fast and slow looming visual stimuli, larval zebrafish were more likely to respond to a slow stimulus with a longer latency and more variable, slower kinematics (i.e. a longer stage 1 duration and lower tail-beat frequency) than fish stimulated with fast looming stimuli (Bhattacharyya et al., 2017). In an ecological context, collectively, this work suggests that different escape responses (i.e. slow and fast) may be related to the strength of the threat perceived, and that resultant motor output may not necessarily yield a continuum in the response strength, but rather it may be characterized by responses with different strengths and neural controls.

Presence or absence of stage 2: single-bend versus double-bend responses

So far we have discussed the different escape types based on stage 1 kinematics. Other well-known variants of escape responses are based

on the presence or absence of stage 2: these are single-bend (escape responses that only show stage 1) and double-bend responses (escapes with both stage 1 and 2) (Domenici and Blake, 1997) (Fig. 3). These types of responses were initially observed from a kinematic perspective (Domenici and Blake, 1991). Subsequently, electromyographic studies confirmed that escape responses lacking stage 2 and the corresponding contralateral muscle contraction could occur (Foreman and Eaton, 1993). Single- and double-bend escape responses have been observed in various species, including angelfish (Domenici and Blake, 1991), knifefish (Kasapi et al., 1993), Japanese amberjacks (Noda et al., 2014), carp (Spierts and Leeuwen, 1999), European seabass (Lefrançois and Domenici, 2006), grey mullet (Lefrançois et al., 2005), catfish (Yan et al., 2015), brown trout (Tudorache et al., 2008) and killifish (Fleuren et al., 2018).

Double-bend escape responses produce higher speed than single-bend responses do, as a result of the additional muscular contraction and body bend (Domenici and Blake, 1991; Fleuren et al., 2018). In some escape responses, fish can accelerate in the final direction of the escape during stage 1, indicating that stage 1 can serve a propulsive role, in addition to its preparatory role for stage 2 (Fleuren et al., 2018). Because propulsive forces can be generated in stage 1 (Borazjani et al., 2012; Fleuren et al., 2018; Tytell and Lauder, 2008), locomotion can occur in single-bend responses.

The occurrence of single- and double-bend responses contributes to the variability of escape responses. Although the different energetic costs of single- versus double-bend responses have not

been investigated, it is likely that double-bend responses, because of their higher speed, require more energy than single-bend responses. For example, the occurrence of single-bend responses increases in hypoxia (Domenici et al., 2007b) and when fish are starved (Yan et al., 2015).

Posture prior to escaping

Many benthic species (e.g. blennies, gobies and sculpins) lie on the sea bottom while bent into a C-shape (P.D., personal observations). Such a posture can be maintained for a relatively long time (the order of minutes) and is not necessarily related to preparing an escape response. It is unlikely to involve any muscular contraction (which is different to the case of the S-posture observed in predatory fish in the water column, Webb and Skadsen, 1980), since the bottom may provide sufficient resistance for the body to remain bent. Nevertheless, the posture of certain benthic species can be modulated by a threatening stimulus, and this may affect how fast they escape. Black gobies react to a weak stimulus by slowly bending their bodies into a static C-shape, thereby increasing postural curvature (Turesson et al., 2009). When gobies are startled using a strong mechanical stimulus, their locomotor performance (i.e. distance covered within a fixed time) increases with postural curvature. Turesson and colleagues (Turesson et al., 2009) suggest that this is due to a large tail sweep directed backwards in individuals that adopt a highly bent C-posture prior to escaping. Given that other benthic species such as blennies and sculpins typically adopt a bent posture on sand or among rocks, it would be worthwhile to investigate the effect of posture on propulsive performance on these other species as well as on their escape success when attacked by a real predator. Interestingly, some predatory fish species may hold a static S-posture without significant forward motion prior to striking (Hoogland et al., 1956). This results in higher speed compared with attacks from a straight posture (Webb and Skadsen, 1980).

Neuromuscular control of escape responses

As our understanding of escape response variation broadens, new questions emerge on how neural circuits drive such a diverse behavioural repertoire. Developments in technology provide opportunities not only to better understand accelerative behaviours in fish, but also to develop these systems as general models for sensorimotor integration and motor control. The vast majority of studies on neural circuits that drive fast escape responses have investigated the short-latency C-start initiated by activity in the pair of reticulospinal M-cells and their downstream circuit (Fig. 4). However, recent investigations of S-starts are identifying novel complexities in the functions of these cells and the neural control of movement.

The neural control of short-latency C-starts has been widely studied to understand fundamental features of the nervous system. The large size of the neurons in the key startle circuit, particularly the fast-escape-dedicated M-cells, makes them accessible for studying basic neural properties (Zottoli and Faber, 2000). The basic startle circuit is simple, with relatively few neurons and synapses, which has facilitated the examination of circuit structure and function (Faber et al., 1989; Fetcho and Faber, 1988; Fetcho, 1991; Furukawa and Furshpan, 1963; Hackett and Faber, 1983). The M-cells have been described in a wide diversity of aquatic species, including lampreys, tadpoles and an array of osteichthyan fishes (Bierman et al., 2009; Rovainen, 1978) and are represented in early-stage chondrichthyan fishes (Bone, 1977; Stefanelli, 1980). M-cells receive multimodal sensory input; startles can be initiated by a number of different types of sensory stimuli including mechanosensory, auditory and visual cues (Eaton et al., 1991; Eaton

and Hackett, 1984; Kohashi and Oda, 2008). It should be noted that short-latency fast escapes can also be generated without M-cell activity in response to a subset of stimuli, particularly stimuli directed at the head (Liu and Fetcho, 1999). It is only after the M-cells and two other types of startle neurons, MiD2cm and MiD3cm, are ablated that the short-latency response is lost altogether (Liu and Fetcho, 1999).

Fast escape responses

The neural control of C-starts was originally described in goldfish (Eaton et al., 1991, 1981; Fetcho, 1991), in response to head-directed stimuli. As a result of the stimulation, typically only the M-cell on the side of the body closest to the stimulation fires, and it only produces one action potential, with local inhibition preventing the activation of the opposite M-cell and multiple spikes. M-cell activity is transmitted down the axon, which crosses the left–right midline, extending along the length of the spinal cord and exciting interneurons and motor neurons. Local commissural neurons are a critical component of these spinal neuron populations; these inhibit the activity of spinal neurons contralaterally (Fetcho and Faber, 1988; Liao and Fetcho, 2008; Satou et al., 2009). This M-cell-driven activation pattern results in a bend away from the stimulus that takes the general shape of a 'C'. EMG recordings from C-starts of diverse taxa show variability in the bilaterality of muscle activity in stage 1 (Tytell and Lauder, 2002; Westneat et al., 1998) and diversity in M-cell axon caps (Bierman et al., 2009; Rovainen, 1978) – structures at the base of the axon that include key inhibitory and excitatory inputs to the cell – that indicate inter-specific differences in the C-start circuit that have yet to be addressed. For example, there is no clear idea of how wide-scale bilateral muscle activity is achieved (e.g. Westneat et al., 1998), as it is not consistent with the models of the startle circuit. In addition, it is unclear how the less-studied, simple forms of the axon cap relate to circuit function.

The short-latency fast S-start and the withdrawal startle response can also both employ M-cells, but the underlying mechanisms differ among the startle types. During S-starts and withdrawals, M-cells fire bilaterally and nearly simultaneously. In the S-start, this results in regionalized muscle activity that drives bending rostrally on one side of the body and caudally on the other (Liu et al., 2012; Liu and Hale, 2014, 2017); this bilateral activity is possible because of the exceptionally short delay between action potentials, which prevents bilateral inhibition (Liu and Hale, 2017). M-cell-driven S-starts are initiated only through stimulation of the tail (Fig. 4). In the caudal spinal cord, stimulation triggers rapid activity of local circuits that inhibit local motor neuron activity and affect the ability of the M-cell action potentials to cause caudal bending (Liu and Hale, 2017; Fig. 4). Thus, the action potential of one M-cell may cause rostral bending on one side of the body, whereas the action potential of the other M-cell causes caudal bending on the other (Liu and Hale, 2017). While determining the circuit basis for S-starts, Liu and Hale (2017) also found that tail stimulation could generate C-starts driven by either unilateral or bilateral M-cell activation. In the case of bilateral activation, the resultant behaviour, S-start or C-start, depended on the overlay of local caudal spinal cord activity onto M-cell descending activation (Fig. 4). In lampreys, M-cells generally fire bilaterally (including in response to head-directed stimulation) to generate a withdrawal response; lampreys appear to lack direct inhibition between the M-cells (Bierman et al., 2009; Rovainen, 1978; Zottoli, 1978). As described above, bending tends to occur at the sites of pre-existing bends along the body (Currie and Carlsen, 1987).

The expression of single- or double-bend (Domenici and Blake, 1997) escape responses raises new questions about the specification of
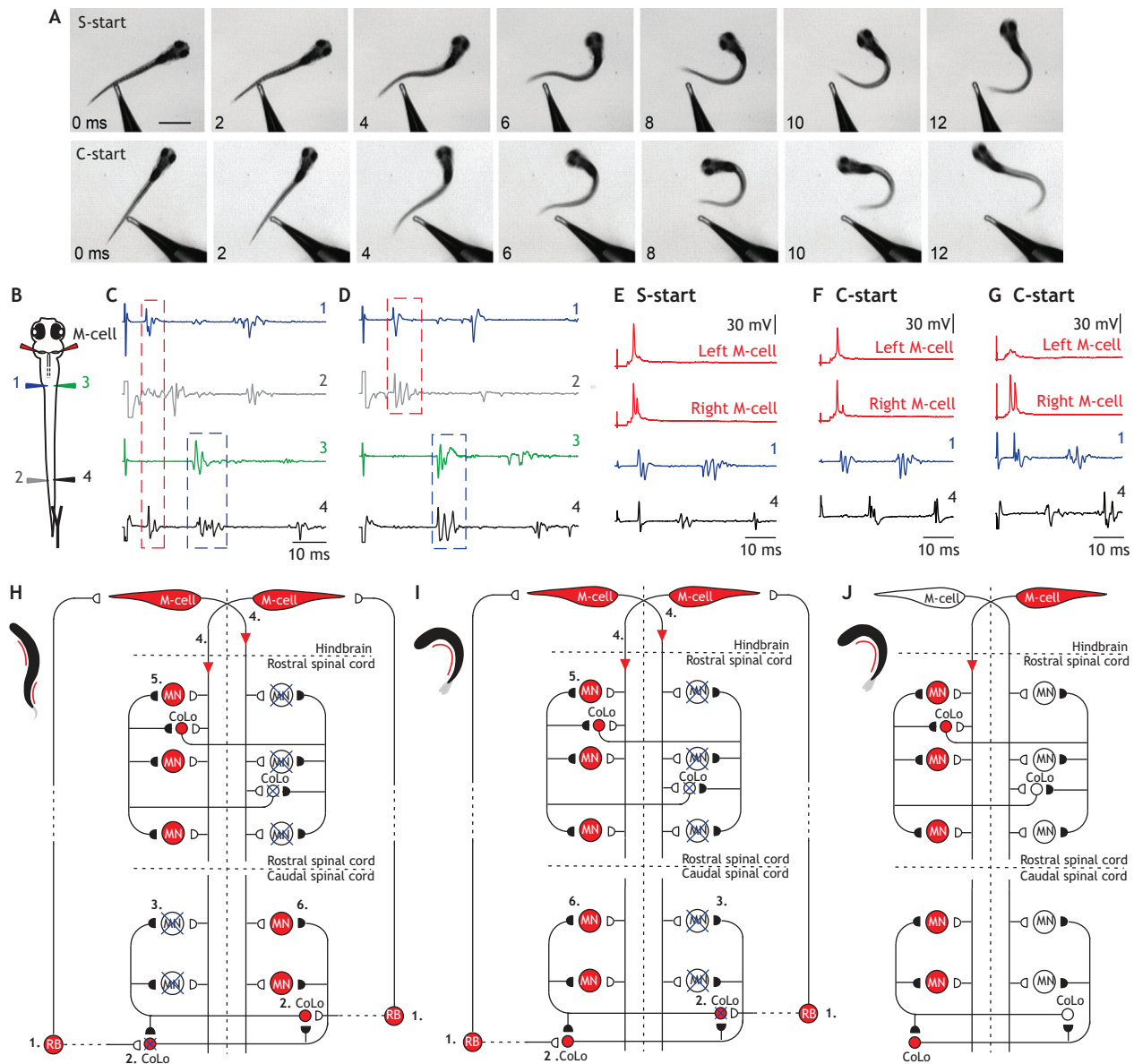
Fig. 4. Motor control of M-cell-generated S-start and C-start in larval zebrafish. (A) Caudal stimulation can generate both S- and C-start kinematic patterns. Reproduced from Liu et al. (2012). Scale bar: 1 mm. (B) Recording positions for M-cells and ventral root recordings shown in C–G. Arrowheads show locations of recordings and colours correspond to colours of associated responses. Y on the tail indicates location of the stimulating electrode. (C,D) Exemplar recordings from ventral roots (motor neurons) in the trunk and tail on the left and right sides of the body for the S-start (C) and the C-start (D). There are different patterns of ventral root activation for S-starts and C-starts. In stage 1 (activity in red dashed box), S-starts include activity rostrally on one side of the body and caudally on the other, whereas C-starts show unilateral activity along the length of the trunk and tail. Stage 2 (activity in blue dashed box) was similar between S-starts and C-starts (courtesy of Y. C. Liu). (E–G) Exemplar whole-cell patch recordings of M-cell neural activity of an S-start (E) and two C-starts, all stimulated at the tail. The lower two traces of each column show ventral root recordings that can differentiate S-start and C-start motor patterns and are used to ascertain whether the M-cell response would generate an S-start or C-start. Bilateral M-cell activity, shown in red, could generate either an S-start (E) or a C-start (F). (G) Activity of a single M-cell could only generate a C-start. Image modified from Liu and Hale (2017). (H–J) Models for the M-cell-initiated startle circuits. Red cells are activated whereas white cells are inhibited. Red arrowheads represent M-cell spikes. Red lines on the fish silhouette represent motor activity. Excitatory spinal interneurons involved in the startle response are not represented in these diagrams. (H) An S-start motor pattern is generated as follows: a stimulus to the tail causes Rohon Beard sensory neurons (RBs) in the caudal spinal cord to be activated (1), which in turn activates commissural local interneurons (CoLos) on both sides of the cord (2). CoLos in the ipsilateral caudal spinal cord inhibit motor neurons (MN) and their counterparts on the contralateral side (3). Sensory information from RBs is also relayed to the M-cells to fire the ipsilateral and contralateral M-cells within short latencies of each other (4). In the rostral spinal cord, the ipsilateral M-cell activates CoLos and motor neuron on the contralateral side, causing motor output on the contralateral side and inhibiting motor output that would be otherwise generated by the contralateral M-cell (5). In the caudal spinal cord, inhibition from CoLos reduces the likelihood of motor neuron activity on the contralateral side, thus the descending M-cell spikes are more likely to fire motor neurons on the ipsilateral side (6). This causes bilateral motor activity on opposite sides of the rostral and caudal trunk. (I) An alternative C-start can be elicited when motor neurons in the caudal cord are inhibited on the opposite side as rostral motor activity, allowing motor activity in the caudal trunk and tail to match with that in the rostral trunk (2). The ipsilateral M-cell fires slightly before the contralateral and causes motor activity on the rostral contralateral side (4). In the caudal spinal cord, motor neurons on the contralateral side are more likely to fire due to inhibition from CoLos to motor neurons on the ipsilateral side (6), thus causing unilateral motor activity on the contralateral side. (J) The fundamental model of an M-cell-generated response is that one M-cell fires and activates motor neurons contralaterally while inhibiting them ipsilaterally through CoLos. Image modified from Liu and Hale (2017).

stage 2. While the neural control of stage 1 has been studied in depth for fast responses, and stage 3 is likely controlled by fast rhythmic swim circuits, the transition between these very different movements is not well understood. The kinematics of stage 2 may be specified during stage 1; the control of stage 2 may, in fact, determine the end of stage 1, with the onset of stage 2 counter-bending (Foreman and Eaton, 1993). Comparing single- and double-bend responses initiated with M-cell activity would provide insight into the neurophysiological control of stage 2, with a focus on discerning how stage 2 is initiated and controlled. This is a key requirement for understanding this system.

Slow escape responses
'Slow' escapes (in terms of latency and kinematics) are observed in various fish species (Domenici and Batty, 1997; Domenici et al., 2004), and are likely to be driven by different circuits from fast responses (Bhattacharyya et al., 2017). In terms of latency, Kohashi and Oda (2008) demonstrated that the reticulospinal neuron MiD3cm has high activity during escape responses with long escape latency, when the M-cell is inactive, and lower activity during short-latency responses when the M-cell is active. Although it is not known whether MiD3cm alone can trigger a long-latency escape, this work suggests that some cells, including MiD3cm, may play different and important roles in both short-latency and longer-latency responses. In addition, recent work has shown that spiral fibre neurons, a group of excitatory neurons that project onto the M-cells (Bartelmez, 1915; Bodian, 1937; Nakajima, 1974; Scott et al., 1994), also play a role in regulating escape latency, since bilateral ablations of these neurons largely eliminate short-latency escapes (Lacoste et al., 2015). In terms of kinematics, M-cell escapes show significantly faster kinematics (i.e. shorter stage 1 duration and faster stage 1 tail angular velocity) than non-M-cell escapes in responses of larval zebrafish to looming visual stimuli (Bhattacharyya et al., 2017).

Future directions in the neuromuscular control of escape responses
Expanding the examination of neural control beyond stage 1 of fast responses will provide a range of opportunities to investigate fundamental features of sensorimotor circuits and lead to a deeper understanding of escape behaviour. Comparisons beyond fish and other vertebrates will help us to identify themes and variations on how similar behavioural responses are controlled. In fruit flies (*Drosophila melanogaster*), which are also a model for escape and for which features of the escape control are similar to those of fish (Hale et al., 2016), a formidable genetic toolkit is providing new access to escape circuits and associated behaviours. For example, transgenic approaches (including optogenetic activation) demonstrate that a specific neuron drives the freezing response to visual looming stimuli (Zacarias et al., 2018). Examining the neural basis of more subtle variability of the kinematics of escape and related behaviours, including the variety of escape-like motions discussed below, is an exciting direction in the future of the field.

Escape performance variability within the context of predator–prey interactions
The study of escape responses has made a lot of progress towards an integrative approach over the past two decades, from a focus on propulsive performance (i.e. speed and acceleration) (Harper and Blake, 1990; Webb, 1976, 1978a; Weihs, 1973) to a wider, more ecologically relevant perspective in which many alternative variables are measured [e.g. responsiveness (see Glossary), timing and direction of the response; reviewed by Domenici, 2010a,b]. Therefore, there are many escape response variables, and their relative importance is likely to vary across contexts (Fuiman et al.,

2006; Nair et al., 2017; Scharf et al., 2003; Walker et al., 2005). In addition, escape response variables show a range of performance levels that are affected by context and vary both within and across species (Domenici, 2010a) (Table 1). Such variability may fall along a continuum, as an expression of the flexibility in a basic motor program, although there is some evidence that, at least for some traits, the variability is due to alternative neural 'types' of escape response, related to different neuronal commands (Kohashi and Oda, 2008; Liu and Fetcho, 1999; Liu and Hale, 2017). From an ecological perspective, for some escape traits (such as for reaction distance, Ydenberg and Dill, 1986), the strength of the response is modulated by the level of threat.

Responsiveness and reaction distance
The first and foremost variable that determines escape success is whether or not the prey responds to the threatening stimulus (Fuiman et al., 2006). The proportion of fish that respond to a given threat can be scored as 'responsiveness' (Domenici, 2010a,b). Responsiveness is largely determined by the strength of the threat and by environmental conditions such as water clarity (for visual stimuli) and oxygen level (Domenici et al., 2007b; Meager et al., 2006). Furthermore, reaction distance (i.e. the distance at which a prey reacts to an approaching predator) or flight initiation distance (FID) (Cooper and Blumstein, 2015) is related to the approach speed of the predator and the predator's frontal profile (Dill, 1974; Domenici, 2002; Webb, 1984b, 1986). Slowly approaching predators with narrow frontal profiles may be able to catch their prey before they can react (Webb, 1984b). For example, the narrow profile of the sailfish's bill has been suggested to prevent early evasive behaviour by their prey when the bill is inserted into the school of prey (Domenici et al., 2014). At a theoretical level, reaction distance is expected to largely depend on both the level of threat (i.e. risk of predation) and the potential loss of opportunity (e.g. feeding) (Ydenberg and Dill, 1986). Accordingly, reaction distance decreases when prey are near a refuge, as a result of the lower perceived risk of predation (Dill, 1990), and when fish are foraging (Krause and Godin, 1996). In addition, reaction distance is affected by the relative orientation of the prey to the predator, with the shorter reaction distance occurring when the prey is attacked posteriorly (Kimura and Kawabata, 2018). Predator success (i.e. number of strikes per capture event) is inversely related to the prey's apparent looming threshold (ALT; the threshold looming rate of the approaching predator that triggers a response in the prey; Dill, 1974), suggesting that prey that react when the predator is closer (i.e. those with a high ALT), are captured more easily (Webb and Zhang, 1993). Similarly, differences in reaction distance among four prey species were suggested to be a determinant of interspecific differences in vulnerability to predation (Scharf et al., 2003), and reaction distance is a significant factor in determining survival in *Poecilia reticulata* attacked by predators (Walker et al., 2005).

Escape latency
Prey react to a threat with a delay (i.e. escape latency) as a result of sensory and neural processing (Dill, 1974; Eaton and Hackett, 1984; Turesson and Domenici, 2007). Unless invasive techniques such as neural recording are used, behavioural latencies can only be measured by using sudden rather than looming stimuli. Escape latency has been measured using sudden visual (Batty, 1989) and mechano-acoustic stimuli (Blaxter et al., 1981; Domenici and Batty, 1994; Eaton and Hackett, 1984). Latency to a visual stimulus was found to be longer than the latency to a mechano-acoustic one (Batty, 1989). Accordingly, visual stimuli trigger the M-cells

Table 1. Indicative performance levels for escape response variables of adult fishes

Variable type	Variable	Size effect	Performance (indicative range)
Escape behaviour	Responsiveness	= [1]	0–100% *,[2]
	Latency	= [3]	5–150 ms [4,5]
	Apparent looming threshold	↑ ‡,[1]	0.1–5 rad s⁻¹ [1,6]
	Directionality	Not tested	60–90% [7]
	Escape trajectories	= [8]	90–180 deg [9]
Escape kinematics (manoeuvrability)	Turning radius (cm)	↑ §,[10]	0.5–14.1 cm [10]
	Turning radius (length)	= [10]	0.05–0.4 lengths [10]
	Turning angles	= [10]	0–180 deg [5,11]
	Stage 1 turning rate (average)	↓ [10]	500–8000 deg s⁻¹ [10]
Escape kinematics (distance–time variables)	Fast start duration	↑ [12]	30–200 ms [13]
	Distance covered during fast start	↑ [12]	2–20 cm [12,14]
	Speed within fast start (m s⁻¹)	↑ ¶,[12]	1.5–2.8 m s⁻¹ [12]
	Speed within fast start (length s⁻¹)	↓ ¶,[12]	3–30 length s⁻¹ [13]
	Acceleration	= [10,15]	20–150 m s⁻² [13]

The arrows represent a size-related increase or decrease in the trait measured; = indicates no size effect. Indicative values are for a range of sizes spanning approximately 5–50 cm.

*Responsiveness varies as a result of stimulus strength.

‡Apparent looming threshold (i.e. the rate of change in the angle subtended by the predator's image as seen by the prey; Dill, 1974) was found to decrease with prey size in the sculpin *Leptocottus armatus* (i.e. reaction distance increases with prey size).

§Turning radius increases with size (turning radii measured in cm are larger in large fish, although when measured in lengths, they are relatively constant). This implies a decrease in manoeuvrability in large fish (see main text).

¶Speed (in m s⁻¹) was measured in fish with lengths of 9.6–38.7 cm (Webb, 1976).

[1]Paglianti and Domenici, 2006; [2]Blaxter et al., 1981; [3]Turesson and Domenici, 2007; [4]Domenici, 2010a; [5]Eaton and Hackett, 1984; [6]Domenici, 2002; [7]Domenici et al., 2011a; [8]Domenici and Blake, 1993b; [9]Domenici et al., 2011b; [10]Domenici, 2001; [11]Domenici and Blake, 1991; [12]Webb, 1976; [13]Domenici and Blake, 1997; [14]Domenici and Blake, 1993a; [15]Vogel, 2008.

through a longer pathway than mechano-acoustic stimuli (Mirjany and Faber, 2011), i.e. from the optic nerve to the M-cell via the optic tectum (Temizer et al., 2015; Zottoli et al., 1987). Minimum behavioural latency to a mechanical stimulus ranges from 5 to 20 ms, although longer latencies (80–120 ms) can also occur when the threat level is lower (e.g. being further away from the stimulus or being part of a school; Domenici and Batty, 1997). Latency may increase when fish are performing other activities such as feeding (Bohórquez-Herrera et al., 2013), possibly because of limits in the rate of neural processing of multiple sources of information. In addition, escape latency can be modulated by perceived risk of predation, as it is reduced when prey anticipate a predator (via sight or smell) (Ramasamy et al., 2015). In terms of the contribution of escape latency to survival, individuals with the shortest escape latencies are known to have higher chances of survival (Katzir and Camhi, 1993; McCormick et al., 2018)

Directionality and escape trajectories

Directionality has been defined as the proportion of escape responses in which the head (or the C bend in C-starts) moves away from the stimulus (Blaxter et al., 1981; Domenici et al., 2011a). Thus, directionality can be calculated for a given treatment, such as exposure to a given temperature or oxygen level (Lefrançois et al., 2005; Preuss and Faber, 2003), although it could be also measured for a given population or a given individual. While directionality is a very simple trait to measure, it is relevant from both neurophysiological and ecological perspectives. At the neurophysiological level, the proportion of 'away' responses can be used as a proxy of the neurosensory ability to detect the direction of the stimulus. Specifically, in M-cell responses triggered with a mechano-acoustic stimulus, particle displacement (i.e. one of the two components of sound in water, the other being pressure change; Canfield and Eaton, 1990) was suggested to determine the firing of the M-cell on the side of the stimulation, which ultimately activates axial muscle contralaterally and produces a bend away from the stimulus (Canfield and Eaton, 1990). In addition, recent work using

cell ablation techniques has shown that spiral fibre neurons contribute to the directionality of the escape response (Lacoste et al., 2015). Furthermore, any malfunction of the sensory system for the detection of the threatening stimulus is likely to negatively affect directionality. For example, a well-functioning and intact lateral line is essential for directionality in response to mechano-acoustic stimuli, since removal of the entire lateral line (with cobalt chloride or gentamicin) significantly reduces the proportion of away responses (Mirjany et al., 2011).

Away responses make up the majority of the escape responses under control conditions (87% in Eaton et al., 1981; 77% in Domenici and Blake, 1993a,b; 77% in Mirjany et al., 2011), while factors that limit neurosensory capacities – such as hypoxia (Lefrançois et al., 2005) and rapid cooling (Preuss and Faber, 2003) – can decrease directionality. In addition, other factors such as the surroundings (e.g. obstructions), can affect directionality (Mirjany et al., 2011). From an ecological perspective, in open field situations, escape directions away from a threat increase escape success (Walker et al., 2005). However, a certain amount of variability in the response may be useful from an evolutionary standpoint, since predators can have various attack strategies. For example, tentacle snakes take advantage of the away responses of fish by stimulating them with their body on one side of the prey and catching them with the mouth positioned on the other side (Catania, 2009). In these cases, fish performing 'towards' responses may indeed avoid being captured. The orientation of the threat can affect directionality (Domenici and Blake, 1993b; Nair et al., 2017). When a robot predator approaches laterally, zebrafish escape away from the threat; if the predator approach is rostral or caudal, prey escape away or towards the threat with equal probability (Nair et al., 2017).

Although an optimal trajectory relative to the approaching danger can be calculated on the basis of the relative speed of predators and prey (Domenici, 2002; Weihs and Webb, 1984), escape trajectories (measured relative to the stimulus) in fish show a large degree of variation (Domenici et al., 2011b). This is in line with the principle of unpredictability in prey motion, also called 'protean behaviour'

(Humphries and Driver, 1970). The unpredictability of the escape path is in contrast to the predictable strike direction of a predator, and it is a fundamental feature of the fast escapes (Korn and Faber, 2005). Recent work shows that optimal escape trajectories can be observed when the predator is approaching at an intermediate speed (Soto et al., 2015). Furthermore, multiple factors influence prey trajectories, including: (i) sensory constraints (i.e. angular limits in the visual fields), (ii) the need for high speed to distance the prey from the threat (Domenici et al., 2011b; Soto et al., 2015) and (iii) the presence of a shelter (Shi et al., 2017). Recently, the variability of escape trajectories was found to be reduced when fish were startled while swimming in a flow, such that the escape trajectories were in line with the flow direction, possibly to minimise destabilisation that would occur if fish escaped at an angle to the flow (Anwar et al., 2016).

Propulsive performance
It has been suggested that speed (Katzir and Camhi, 1993; Walker et al., 2005) and acceleration (Walker et al., 2005) are among the variables that significantly affect prey capture in the case of a predator strike. Most work has measured propulsive performance based on high-speed video (typically >250 Hz) measurements of the displacement of the centre of the mass (CM) of the fish when stretched straight (as first proposed by Webb, 1976), although the motion of other points, e.g. the physical centre of mass (Fleuren et al., 2018; Weihs, 1973) and the tip of the head (Eaton et al., 1981) have also been considered. In addition to inter-specific variability due to morphological and physiological differences (Domenici and Blake, 1997), propulsive performance can vary within a given species as a result of the behavioural context. For example, escape locomotion can be affected by prior exposure to predators in two ways: (i) by affecting morphology as a result of long-term exposure to predators and (ii) by affecting motivation, for example as a result of short-term exposure to predator cues, which increases the perceived risk of predation. In terms of morphology, fish populations exposed to predators typically have a larger tail and/or larger body depth and they show higher propulsive performance in fast starts (Domenici et al., 2008; Langerhans and Reznick, 2010). Although in some cases morphological differences are genetically based, phenotypic plasticity has also been demonstrated (Langerhans and Reznick, 2010). For example, crucian carp exposed to predators develop a deep body within a few months (Brönmark and Miner, 1992; Brönmark and Pettersson, 1994), and show increased propulsive performance (e.g. speed) during escapes (Domenici et al., 2008). With respect to locomotion, fish exposed for five minutes to the sight and/or odour of a predator display a higher propulsive performance (e.g. speed) when startled, highlighting the flexibility and context dependency of escape responses in relation to the level of threat (Ramasamy et al., 2015).

Manoeuvrability
Manoeuvrability in escape responses has been assessed mainly by considering the turning radius (see Glossary) and the rate of turning. Turning radius is an important factor to take into account in predator–prey interactions (Webb, 1976) as prey can have much tighter turns than their predators and can use turning to their advantage (Domenici, 2001; Weihs and Webb, 1984). Turning radius increases with fish size (Table 1) and therefore manoeuvrability is lower in large fish compared with small fish. Turning radius is commonly measured based on the path of the CM during stage 1, and tends to be a relatively constant proportion of the body length (about 10–15% of body length) for generalist species. However, it is tighter for manoeuvring specialists (e.g. angelfish, 6%) and much larger for

cruising specialists with a rigid body (e.g. tuna, 40%) (Domenici, 2001). Although the role of turning radius in escaping predation has not been evaluated experimentally, Webb (1976) suggested that it should be a key variable in determining the outcome of predator–prey encounters. Turning rate during stage 1, a measure of agility (Webb, 1994), can be affected by threat level (e.g. distance from the stimulus, Domenici and Batty, 1997), and is one of the main factors affecting the escape success of guppies evading their natural predator, the pike cichlid (Walker et al., 2005). Turning angles during stage 1 can vary from nearly 0 deg to about 180 deg, and are largely dependent on stimulus direction (Eaton and Emberley, 1991; Domenici and Blake, 1993a,b). Maximum turning angles are a measure of manoeuvrability and tend to be smaller in species with a rigid body (i.e. tuna) compared with more flexible ones (Domenici, 2001). Having a large range of turning angles allows fish to achieve a large range of trajectories independent of how they are orientated relative to the attacking predator (Domenici et al., 2011a,b).

Escape traits and their contribution to escape success
Many variables tested have been found to affect escape success significantly, at least in a given species and/or context. The first determinant is clearly whether the prey responds to an attack. An unresponsive prey is likely to be captured, as suggested by Fuiman et al. (2006). However, even the effects of such a simple trait are not always as straightforward as expected. When attacked by tentacle snakes, unresponsive prey are likely to survive the attack (Catania 2009). How far from a predator a fish responds to the attack (i.e. its reaction distance) also affects vulnerability (Walker et al., 2005; Scharf et al., 2003). Clearly, letting the predator get too close is a dangerous behaviour that can lead to capture. From a fitness perspective, when a prey is captured, it loses all potential future fitness. However, this does not mean that escape distance is maximised. As pointed out by previous work (summarised in Cooper and Bloomstein, 2015), prey do not necessarily escape as soon as a predator is detected, because reaction distance is the result of a compromise between the perceived risk of predation and the cost of abandoning other activities that presumably increase fitness (e.g. feeding, courting, mating). Engagement in other activities (i.e. feeding) affects other escape traits, such as escape latency (Bohórquez-Herrera et al., 2013), an aspect of performance that is known to affect survival in the field (McCormick et al., 2018).

The direction of the initial body bend (i.e. directionality) is related to the final trajectories of the fish relative to the threat (Domenici and Blake, 1993a,b). Escape trajectories are highly variable (Domenici et al., 2011a), but, as mentioned above, escaping away from a predator leads to higher survival (Walker et al., 2005). However, as in other traits (e.g. responsiveness), the relationship between escape trajectories and survival is likely to be context dependent and species specific (see Catania, 2009). Manoeuvrability is also a potential determinant of escape success. While no previous experimental work has investigated the role of turning radius, theoretical work predicts that it should be a relevant trait for survival (Webb, 1976). Prey agility, measured as turning rate, significantly affects survival (Walker et al., 2005). Finally, locomotion – measured as speed (Katzir and Camhi, 1993; Walker et al., 2005) and acceleration (Walker et al., 2005) – is a significant factor affecting survival of predator attacks, although, like other escape traits, locomotion can be modulated by the perceived risk of predation (Ramasamy et al., 2015).

Clearly, more work is needed in order to investigate the relative importance of these traits in different predator–prey pairs and in ecologically relevant contexts, including in field situations. This would allow us to determine the most relevant selective pressures

(e.g. on sensory channels or locomotion) in various contexts. This would be aided by field techniques such as accelerometry, which could be used to detect prey escape responses and predator strikes (Noda et al., 2014; Broell et al., 2013).

While previous work clearly shows that escape performance can vary substantially depending on the behavioural context, ecologically relevant issues regarding escape performance are the variability of performance level among individuals and the repeatability of escape performance within individuals (Box 1). The assessment of repeatability is particularly relevant from an ecological and evolutionary point of view, because it is an indicator of the extent to which escape performance traits can be shaped by selection (Hitchcock et al., 2015); trait repeatability has been suggested to set the upper limit for trait heritability (Dochtermann et al., 2015). In addition, studying the effects of various environmental stressors on the diversity of escape responses may be fundamental to our understanding of escape responses in the context of climate change (Box 2).

Escape-like motions

Recent progress has been made on accelerative swimming motions that resemble escape responses from a kinematic point of view, yet are not triggered by frightening stimuli. This suggests that a motor output similar to that of an escape response may be generated even if no startling stimulus is present. These escape-like motions are relevant from both an ecological and a physiological point of view, because they highlight the diversity and context-dependency of the fast-start system. Although, in most cases, the neural control is unknown, in post-feeding turns (Canfield and Rose, 1993) the kinematic similarities with escape responses are supported by recording of M-cell activity. Thus, M-cells can be activated in the absence of a typical startling stimulus. In some escape-like motions, such as those used for attacking prey (Wohl and Schuster, 2007), a stimulus (the prey) is present. However, in these cases the reaction is towards the stimulus, unlike an escape response which tends to be directed away from the stimulus. It would be interesting to investigate the neural mechanisms

> **Box 2. Environmental effects on escape responses**
> Climate change stressors such as hypoxia, temperature and ocean acidification can affect fish escape performance. Burst performance (i.e. speed) tends to increase with higher temperature, and this effect can be ascribed mainly to the effect of temperature on muscle performance and power output (Wakeling, 2006; Wilson et al., 2010). This effect can be modulated by the thermal history of the individual (Wilson et al., 2010). In addition, temperature affects escape latency (Preuss and Faber, 2003; Webb, 1978b) and directionality (Preuss and Faber, 2003), by acting on neural processing time. Using laboratory-staged predator–prey encounters, temperature was found to affect escape success in various ways, either increasing (Grigaltchik et al., 2012) or decreasing it (Allan et al., 2015); this possibly results from differential effects of temperature on each pair of predator and prey. Because escape swimming is fuelled anaerobically, hypoxia was originally hypothesised to have no effect on single fast start events (Beamish, 1978). However, certain escape components, such as responsiveness and directionality, are related to brain and sensory functions, and are negatively affected by hypoxia (as is escape speed at very low oxygen saturations) (Domenici et al., 2007b). Recent work has shown that ocean acidification can negatively affect directionality, responsiveness and locomotor performance (Allan et al., 2014) as well as escape performance in predator–prey interactions (Allan et al., 2013). These effects were ascribed to the effect of acidification on neurotransmitter function (Nilsson et al., 2012). However, transgenerational acclimation can reduce these negative effects of acidification (Allan et al., 2014) and work on multiple stressors (temperature and acidification) shows that temperature is the main factor in modulating escape success in predator–prey encounters (Allan et al., 2017). Overall, these results suggest that the effects of climate change on escape responses may occur through decreased muscle performance and/or as a result of interference with brain and sensory functions. Because the effects of these stressors are likely to be highly taxon specific (e.g. they may affect fish but not their avian or marine mammal predators), they may have profound ecological repercussions on a number of predator–prey relationships (Domenici et al., 2007a).

that are involved in producing accelerations that are directed away from or towards the stimulus in different contexts.

Escape-like motions include a number of behaviours for which a fast motion may be necessary (Fig. 2). Fernald (1975) measured the rates of body turns in cichlids (*Astatotilapia burtoni*) during agonistic displays to conspecifics. Such agonistic turns are likely to correspond to slow C-starts, because of their slow turning rate (200–2000 deg s^{-1} in 7 cm fish, compared with 4000 deg s^{-1} in fast C-starts of similar-sized fish; Domenici, 2001). Fast motions in social contexts have also been observed in many other species, such as digging and quivering in salmonids (Esteve, 2005). Although some of these motions do not involve swimming per se, it would be interesting for comparative purposes to measure their kinematics and investigate their neural control.

Other escape-like motions have been observed in the context of feeding rather than escape. Archerfish (*Toxotes jaculatrix*) and fruit-catching fish (*Brycoguate malensis*) strike using a predictive start towards prey or food items as they land on the water surface (Krupczynski and Schuster, 2008; Wohl and Schuster, 2007). The strike of archerfish is kinematically equivalent to an escape response (Fig. 5A,B), despite the fact that archerfish are not escaping from a threat, but are darting towards prey. The archerfish strike shows a wide range of turning rates (387–4631 deg s^{-1}) that overlap with those of escapes. In fact, both archerfish and fruit-catching fish are not necessarily facing the food item as it falls towards the water surface, and therefore they may need to turn (using a C-start) to reach the prey before competitors. The scale-eating cichlid fish *Perissodus*
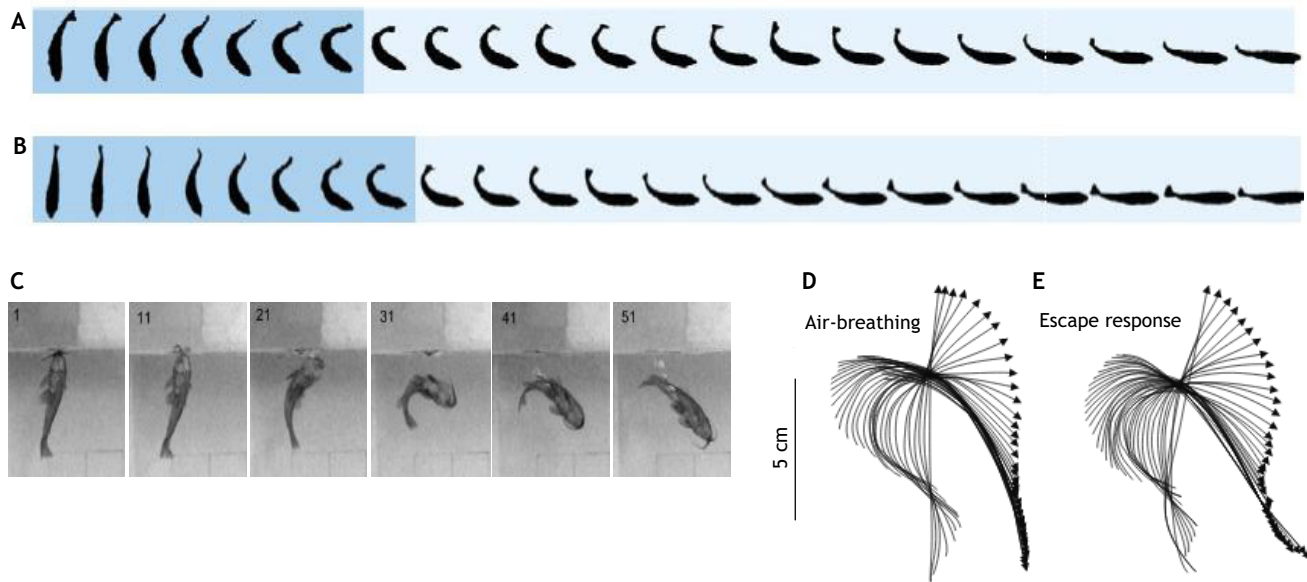
> **Box 1. Intraspecific variability and repeatability of escape performance**
> One way to assess the variability of escape performance is to measure the degree of stereotypy through the coefficient of variation (CV) of a given trait. Stereotypical traits tend to have a low CV (i.e. between 0 and 20%), whereas most escape response traits show a CV >20% (Domenici, 2010b). However, Wainwright and colleagues argue that there should not be an absolute threshold for a trait to be considered stereotypic, and a given trait should be assessed by comparing it with the CVs of other performance traits in the same species (Wainwright et al., 2008). Marras et al. (2011) compared the CV of escape response traits in European seabass with the published CVs of other swimming performance traits in the same species. The CVs of these other traits were all between 15 and 18%, whereas the CVs of escape response traits ranged from 23 to 41%, suggesting that escape response traits have a comparatively low degree of stereotypy. Similarly high CVs (>20%) in escape traits were found in tropical damselfish (Jornod and Roche, 2015). Despite this variability among individuals, most escape response traits show a high degree of repeatability within each individual in various species, including European seabass (Marras et al., 2011), bluegill sunfish (Hitchcock et al., 2015), tropical damselfish (Jornod and Roche, 2015) and red drum larvae (Fuiman and Cowan, 2003). High repeatability in escape response traits indicates that these traits are likely to reliably represent the expected performance level of each individual, which is subject to natural selection.

Fig. 5. Examples of escape-like motions. Comparison of (A) an archerfish strike at prey on the surface with (B) an archer fish escape C-start. Video at 500 frames s^{-1}, every second frame is shown. Stage 1 (dark blue background) and stage 2 (light blue background) are shown (from Wohl and Schuster, 2007). (C) An air-breathing motion by the catfish *Hoplosternum littorale*. High-speed video recording at 240 fps (every 10 frames are shown). (D,E) Tracings of the mid-line of *Hoplosternum littorale* (D, air breathing; E, escape response) with arrowheads indicating the position of the snout while the other end of the arrow represents the tail. Each line is separated in time by 4.17 ms (i.e. frame-by-frame at 240 fps). Reproduced from Domenici et al., 2015.

microlepis attacks prey and bites off their scales; it does so by exhibiting a fast body flexion to one side of its prey. This body flexion shows some similarities in kinematics with escape responses, suggesting that these two behaviours may share similar neural controls (Takeuchi et al., 2012). Interestingly, escape-like strikes are not limited to these species, but can be learned by other species. Goldfish conditioned to respond to a sound associated with food turn towards the sound with a tail flip response that is similar to an escape response, although no neural recording nor kinematic measures have been reported (Moulton and Dixon, 1967). Recently, Penrod and colleagues trained sculpin to respond to a mechanical stimulus to which they previously reacted with an escape response (Penrod et al., 2018). After training, sculpin learned to recognise the stimulus as a food item, and they turned towards it using a C-start, with kinematics comparable to those of an escape response. Similarly, work on goldfish shows that these fish may occasionally strike an object in the tank, while executing 'voluntary' C-bends that show turning rates (1390–3390 deg s^{-1}) that overlap with their C-start escape responses (1170–4380 deg s^{-1}) (Canfield, 2007). Canfield suggests that the item in the tank may have acquire a food-related salience for the goldfish that triggers an innate 'prey strike' motion.

Other studies have shown that fish may execute escape-like motions to minimise their vulnerability in anticipation of danger. Goldfish turn quickly away from the water surface after having captured a prey item (Canfield and Rose, 1993). While no quantitative kinematic analysis was carried out, this escape-like motion is likely to show a fast turning rate, since neural recordings show that it is triggered by the M-cells; however, the use of a slow turning rate cannot be excluded. Because this M-cell-initiated flexion occurs during the terminal phase of a predatory event, Canfield and Rose (1993) suggest that the fast removal of the prey from the water surface may minimise the vulnerability to surface predators. Similarly, catfish (*Hoplosternum littorale*) follow air gulping at the surface with a turn (spanning from slow to fast

turning rates, similar to those observed in escape responses) which re-directs the fish towards the bottom, possibly to minimise time at the surface and exposure to avian predators (Domenici et al., 2015) (Fig. 5C–E). Domenici et al. (2015) suggest that the contact with the surface may act as a triggering mechanism, since catfish possess very sensitive barbels (Caprio, 1975). Although escaping from potential danger is a plausible explanation for such fast motions, there are other possible explanations. Because these motions are accompanied by the expulsion of air bubbles from the anus, it is possible that the fast C-bend may facilitate air expulsion as a result of a quick reduction in the space of the body cavity (Domenici et al., 2015).

Lastly, fast accelerative motions have also been observed in some fish species when they are infected by parasites (Lafferty and Morris, 1996). According to these authors, parasites modify the behaviour of the infected fish (i.e. their intermediate hosts) by inducing these accelerative motions, which make the fish more conspicuous and therefore more susceptible to predation by the final host, i.e. birds. Since the kinematics and neural control of these accelerative motions is still unknown, it would be interesting to compare them to 'true' escape responses from a kinematic perspective, and to investigate their neural control along with the potential interference of the parasites at the neural level.

Overall, these findings show that C-starts and other similar fast motions occur not only in response to a startling, predator-like stimulus, but are observed in a variety of other contexts including: (i) leaving areas of potential danger, (ii) catching a prey item before competitors and (iii) agonistic displays. Their kinematic patterns (slow or fast turning rates, static C-bends) are specified in Fig. 2. While most behaviours are of the fast type, it is possible that further work may show a wider variety of kinematic patterns.

This work suggests that motions similar to those triggered by a typical frightening stimulus, such as an approaching object or a sudden mechanical disturbance, can occur in many fish species. In

some escape-like motions, such as those used for attacking prey (Wohl and Schuster, 2007), a stimulus (i.e. the prey) is present. However, in these cases the reaction is towards the stimulation, unlike an escape response, which tends to be directed away from the stimulus. Future work on the kinematics and neural control of escape-like motions could be instrumental in elucidating the bases of fish swimming motions for which high speed and acceleration may be fundamental for survival, feeding or intraspecific interactions. Previous work has suggested that similarities between the kinematics of 'true' escape responses and that of escape-like motions implies the possibility of a common neural control, i.e. the M-cell (Wohl and Schuster, 2007; Takeuchi et al., 2012; Domenici et al., 2015; Canfield, 2007). Thus far, the only escape-like behaviour that was shown to involve the M-cell, is the post-feeding turn observed in goldfish (Canfield and Rose, 1993). There is no evidence of M-cell involvement for any of the other escape-like motions observed (Fig. 2).

Conclusions and future directions

Although originally considered to be an all-or-none stereotypic behaviour, the escape response (and other escape-like motions) of fish is now known to encompass a large diversity of kinematic patterns and be used in a wide range of behavioural contexts. The study of escape responses is highly integrative, involving neurobiology, biomechanics, behaviour and ecology; this allows the evaluation of the various components of escape responses – such as their timing and propulsive performance−and their associated variability in terms of neural control and kinematic output, as well as their ecological relevance in terms of survival. Thus, escape responses can be considered as a fully integrated model of a behaviour that is fundamental for survival. Furthermore, studying the diversity of escape responses at various levels of experimental complexity, from the laboratory to the field, will be of particular value.

Work on these behaviours would benefit from greater integration of behavioural and physiological approaches. Development of recording devices to study muscle activity and neurophysiology in free-swimming fish would be of particular value, allowing the advanced kinematic data to more readily be linked to motor control. A lot of past work on escape behaviour has been based on video analysis in the laboratory; however, the use of modern field techniques such as accelerometry (Noda et al., 2014) promises to add an ecological dimension to this work and to work on predator–prey interactions in general. Such techniques may allow us to assess propulsive performance and detect specific patterns of fast start (e.g. strike versus escape) (Broell et al., 2013) in the field. When assessing the fitness values of escape responses within an ecological context, we will need to take all of the relevant information into account, and consider comprehensive models of escape behaviour (Murphy et al., 2008) that promote integration among various fields of investigation. Such an integrative approach will not only provide a more nuanced understanding of these fundamental behaviours but also will prove fundamental for assessing the role of escape responses in the outcome of predator–prey interactions in various contexts, and particularly in shaping fish communities in the light of climate change and anthropogenic disturbances.

Competing interests
The authors declare no competing or financial interests.

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