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Are fish less responsive to a flow stimulus when swimming?

Karla E. Feitl, Victoria Ngo and Matthew J. McHenry*

Department of Ecology and Evolutionary Biology, 321 Steinhaus Hall, University of California, Irvine, CA 92697-2525, USA

*Author for correspondence (mmchenry@uci.edu)

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SUMMARY

Fish use the lateral line system to sense the water flow created by a predator's strike. Despite its potential importance to the survival of a diversity of species, it is unclear whether this ability becomes compromised when a fish swims. Therefore, the present study compared the behavioral responsiveness of swimming and motionless zebrafish (*Danio rerio*) larvae when exposed to the flow of a suction-feeding predator. This flow was generated with an impulse chamber, which is a device that we developed to generate a repeatable stimulus with a computer-controlled servo motor. Using high-speed video recordings, we found that about three-quarters (0.76, *N*=121) of motionless larvae responded to the stimulus with an escape response. These larvae were 66% more likely to respond to flow directed perpendicular than flow running parallel to the body. Swimming larvae exhibited a 0.40 response probability and were therefore nearly half as likely to respond to flow as motionless larvae. However, the latency between stimulus and response was unaffected by swimming or the direction of flow. Therefore, swimming creates changes in the hydrodynamics or neurophysiology of a larval fish that diminish the probability, but not the speed, of their response to a flow stimulus. These findings demonstrate a sensory benefit to the intermittent swimming behavior observed among a broad diversity of fishes.

Key words: lateral line system, predator–prey interaction, foraging, hydrodynamics.

INTRODUCTION

Locomotion can challenge the ability of an animal to sense changes in its environment. As an aquatic vertebrate swims forward, its visual, olfactory, vestibular and lateral line systems may receive signals that are generated entirely by its own motion. In order to respond to changes in the environment, sensory systems must distinguish self-induced signals from external stimuli. This ability is potentially of great importance in the ecology of larval fish, which are preyed upon by suction-feeding fish predators. Larvae detect the flow created by a predator's strike to trigger an evasive escape response (Blaxter and Fuiman, 1989; McHenry et al., 2009). However, this sensory system is potentially compromised by interference created by self-induced flow. Therefore, the main goal of the present study was to test the effect of swimming on the response of larval fish to the flow of a predator's strike.

There are a variety of hydrodynamic and physiological mechanisms that could affect a fish's ability to respond to a flow stimulus while swimming. For example, swimming creates a flow field that could attenuate a stimulus by hydrodynamic interaction before the signal reaches any of the lateral line receptors on the surface of the body. Signals of sufficient magnitude to reach the body surface could be indistinguishable from the flow created by swimming if similar in the frequency and amplitude of velocity (Engelmann et al., 2000). The central nervous system can reduce the sensitivity of hair cells within the lateral line receptors by efferent activation during swimming (Roberts and Russell, 1972). Finally, it may be more difficult for the motor system to initiate an escape response when transmitting the patterns that drive routine swimming (McLean et al., 2007). Therefore, it is reasonable to anticipate that a swimming fish may be less likely to respond to a flow stimulus or may do so more slowly than a motionless fish.

Alternatively, a fish's nervous system may have the capacity to suppress self-induced flow to detect environmental stimuli. Efferent signals are capable of elevating the sensitivity of lateral line hair cells (Flock and Russell, 1973b; Roberts and Meredith, 1989). Furthermore, the flow created by swimming is highly stereotyped and can be slower than the impulsive signal created by a predator (Day et al., 2005). The central nervous system may be capable of distinguishing alarming environmental stimuli by coordinating the sensitivity of the lateral line system with the motor patterns that drive swimming such that the lateral line system behaves as an adaptive filter (Bell, 1989; Bodznick et al., 1999; Tricas and Highstein, 1991).

Evaluating the effect of swimming on the responsiveness to flow is technically challenging. With few exceptions (e.g. Tricas and Highstein, 1991), neurobiological studies on the lateral line system examine paralyzed animals because of the inherent difficulty of attempting physiological recordings in a freely moving body. These studies generally neglect the influence of efferent activity when considering the effects of flow (e.g. Engelmann et al., 2000), or neglect flow when focusing on the dynamics of efferent stimulation (e.g. Flock and Russell, 1973a; Roberts and Russell, 1972). Behavioral studies offer the opportunity to evaluate the combined influence of all neurophysiological and hydrodynamic effects on performance. For example, behavioral measurements of freely swimming blind cavefish (*Astyanax fasciatus*) established that they were more than 6 times more likely to collide with an obstacle during tail beating than when gliding (Windsor et al., 2008). However, it is difficult to expose a moving animal to a repeatable and well-characterized flow stimulus. A vibrating sphere provides an excellent signal in these respects for the canal neuromasts of the lateral line system, which sense pressure gradients (Coombs and Conley, 1997a; Coombs and Conley, 1997b; Curcic-Blake and van Netten, 2006; Sane and McHenry, 2009). However, the lateral line of larval fish includes only velocity-sensitive superficial neuromasts (Blaxter and Fuiman, 1989; Iwai, 1967; Iwai, 1980; Van Trump and

McHenry, 2008). A vibrating sphere is poorly suited to generate a simple velocity signal because of the complexity of viscous hydrodynamics (McHenry et al., 2008; van Netten, 2006; Windsor and McHenry, 2009).

We developed the impulse chamber to expose swimming fish to a flow stimulus (McHenry et al., 2009) that is similar to the suction feeding of a predator (Day et al., 2005; Skorczewski et al., 2010; Wainwright et al., 2001). This flow is created by a computer-controlled linear servo motor that pulls a hydraulic piston (Fig. 1A) to generate a pressure gradient within a working section that contains a group of larval fish. Larvae respond to this flow with an escape response that presumably aids in predator evasion (Kimmel et al., 1974). McHenry et al. found that pharmacologically blocking the hair cells within the lateral line system caused this response to diminish (McHenry et al., 2009), but this manipulation did not affect the ability to maintain balance or respond to sound. Therefore, high responsiveness to the impulse chamber stimulus requires lateral line input, but may also depend on inputs provided by other sensory organs, such as the inner ear (Zeddies and Fay, 2005). The present study used the impulse chamber to compare the responses of swimming and motionless fish and to consider the influence of the direction of flow velocity.

Zebrafish (*Danio rerio*) larvae were selected as the subject for this investigation because these animals have emerged as a focus of study on both the lateral line system and the hydrodynamics of swimming. Aided by advances in visualization techniques, zebrafish larvae have provided major insight into the neuroanatomy, development and physiology of the lateral line (Alexandre and Ghysen, 1999; Bricaud et al., 2001; Fame et al., 2006; Faucherre et al., 2009; Gompel et al., 2001a; Gompel et al., 2001b). Furthermore, its locomotor behavior is well characterized (Budick and O'Malley, 2000; Fuiman and Webb, 1988; Muller and van Leeuwen, 2004), and the motor control (Fetcho et al., 2008; Masino and Fetcho, 2005; McLean et al., 2007) and hydrodynamics (McHenry and Lauder, 2005; McHenry and Lauder, 2006; Muller et al., 2000; Muller et al., 2008) of this swimming are active areas of investigation. Therefore, the zebrafish offers excellent potential for integrating our understanding of the neurobiological and biomechanical principles that govern behavior.

MATERIALS AND METHODS

Animal husbandry

Zebrafish larvae were cultured using standard techniques. A wild-type (AB) zebrafish (*Danio rerio*, Hamilton 1922) breeding colony was maintained in a flow-through tank system (Aquatic Habitats, Apopka, FL, USA) at 28°C on a 13 h:11 h light:dark cycle. Batches of fertilized eggs from randomized breeding were maintained according to standard protocol (Westerfield, 1995) and larvae were raised in a flow-through aquarium system. Experiments were performed on these batches of larvae, which included between 10 and 30 individuals.

All experiments followed a consistent protocol for exposing larvae to light. This became necessary upon finding in a pilot experiment that the spontaneous swimming of larvae was influenced by changes in light exposure. According to this protocol, on the afternoon of the fourth day of post-fertilization (4 d.p.f.), larvae were transferred from our aquaria for culturing to the impulse chamber. After this transfer, larvae were maintained on the same light schedule, which changed to darkness at 20:00 h. However, larvae were held in the dark on the following morning until the beginning of experimentation, at between 09:00 h and 11:00 h. At that time, we turned on an infrared (IR, 940 nm) LED panel beneath the impulse chamber and a diffuser (Fig. 1A), which permitted the observation of larvae by camera. Larvae were then exposed to a 20 min period of white light using a broad-spectrum 250 W halogen lamp directed to the side of the impulse chamber at a distance of 0.3 m. After this period, all light but the IR panel was turned off and one of two experiments was performed. In one experiment, we characterized the patterns of spontaneous swimming by recording the proportion of swimming larvae as a function of time after turning off the white light. Most batches of larvae were used in the second type of experiment, which exposed larvae to a flow stimulus at 5 min after the light change.

Spontaneous swimming activity

We characterized the influence of a change in illumination on the swimming behavior of larvae. In particular, we measured the proportion of larvae that were swimming over a 1 s period at 2 min intervals before and after the change from illuminated to darkened conditions. These measurements were based on video recordings (1280 pixels × 1024 pixels, 30 frames s^{-1}, 12 bit monochromatic, Marlin F131, Allied Vision Technologies Inc., Newburyport, MA, USA) of larvae within the working section of the impulse chamber (Fig. 1A) from 10 min before to 30 min after the transition. The results of these measurements were used as the basis for deciding to expose larvae to a flow stimulus at 5 min after the light transition. As described in Results, a large proportion of larvae were observed to be swimming at this time.

Behavioral responses to a flow stimulus

We measured the responses of larvae to a well-characterized flow stimulus using the impulse chamber (Fig. 1A). The software used to control the hydraulic piston of the chamber (STA1112 Servotube Linear Actuator, Accelnet ACJ-090-09-S Micro Panel Digital Drive, Copley Motion Systems, Canton, MA, USA) also recorded the velocity of the motor over the course of an experiment. Through an application of the principle of continuity, the flow velocity within the chamber was calculated as the product of the motor velocity and the ratio of cross-sectional area within the piston (62.5 mm^2) to that within the chamber (326.3 mm^2) [verified with flow visualization (McHenry et al., 2009)]. As demonstrated by repeated measures, the flow speed generated within the impulse chamber is highly repeatable (Fig. 1B). The electronic trigger used to initiate the motion of the motor [a 5 V transistor–transistor logic (TTL) pulse] was used to synchronize the period of video recording for a high-speed video camera (1280 pixels × 1024 pixels, 500 frames s^{-1}, Fastcam 1280 PCI, Photron USA Inc., San Diego, CA, USA) that was focused on the working section of the impulse chamber. These recordings provided the basis for observations of larvae before and after their exposure to flow.

For the period just prior to the flow stimulus, we recorded the orientation of larvae and whether they were swimming. Orientation was measured by finding the coordinates for the centroids of the dark eyes of a larva (see McHenry and Lauder, 2005) with custom-designed software developed in Matlab (v. 2009a, Mathworks, Natick, MA, USA). The angle of orientation was calculated as that between the vectors of the velocity of flow and the position of the left eye relative to the right eye. The zero orientation angle therefore occurred where the flow velocity was directed toward the head of a larva. Any larvae that were not more than 0.5 body lengths away from other individuals or the walls of the tank were excluded from consideration.

In the period after the stimulus, we recorded whether each larva responded with an escape response. The escape response was

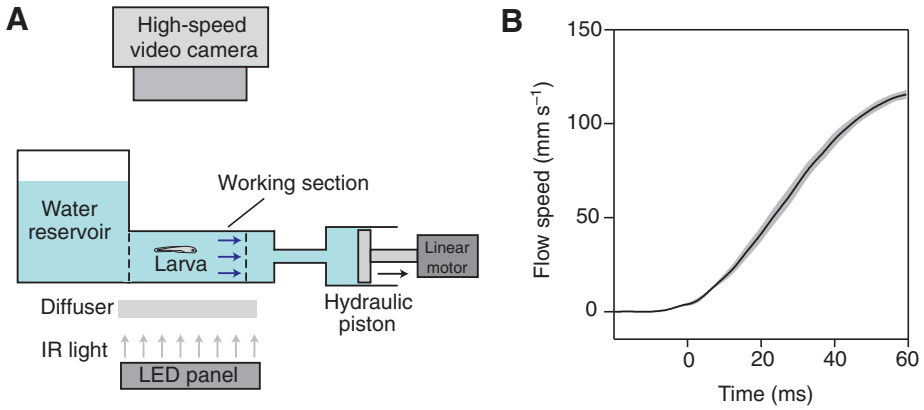

Fig. 1. The impulse chamber used to expose larval fish to a well-characterized and repeatable flow stimulus. (A) A schematic illustration of the impulse chamber (not to scale) shows how a computer-controlled linear servo motor actuates a hydraulic piston. This piston draws water (blue area) from a reservoir and through the working section with a laminar velocity profile (blue arrows). A high-speed camera (500 frames s^{-1}) recorded responses of larvae backlit by a panel of infrared (IR, 940 nm) LEDs with a diffuser. Larvae are kept in the working section by 130 μm mesh panels (dashed lines) at either end. (B) The flow speed within the working section was calculated from position recordings of the linear servo motor. The mean speed (black line) and 95% confidence intervals (gray area) for these calculations are plotted as a function of time (N=16 trials).

identified by a rapid curling of the body of a larva into a 'C' shape, which is characteristic of the first stage of a fast-start response (Kimmel et al., 1974). The response probability was calculated as the proportion of all larvae that initiated an escape response within 60 ms of the stimulus. The latency of this response was considered to be the period between the first movement of the hydraulic piston and the first video frame at which the rostrum of a larva visibly moved laterally to initiate an escape response.

Statistics

Statistical tests evaluated the effects of swimming and the direction of flow on the probability and latency of escape responses. Response probability and latency provided the two dependent measures of behavioral responsiveness in these tests. We calculated 95% confidence intervals for response probability and latency respectively by assuming binomial and normal probability distributions. These measures of variation were used to compare groups in *post-hoc* comparisons of significant differences. We tested for significant differences in response probability using a Chi-square test for goodness of fit (Sokal and Rohlf, 1995). This determined whether the observed number of responding fish significantly deviated from an equal probability distribution in each category. The two categorical variables were swimming and flow direction. Flow direction was divided into 20 deg bins in order to survey responses over the entire range (from 0 deg to 180 deg), while maintaining a reasonably large sample size (~15 individuals per bin). Differences in latency were tested with analysis of variance (ANOVA). All analyses were coded in Matlab (with Statistics Toolbox, v. 7.3).

RESULTS

We found that the spontaneous swimming behavior of larvae varied with changes in illumination. The great majority of larvae (86.8%) were observed to swim in darkness in the 2 min following a 20 min period of exposure to white light (Fig. 2). Although this proportion decreased monotonically from the time of transition, the majority of larvae remained active at 5 min. It was at this time that we exposed larvae to the stimulus in our flow experiments. In the flow experiments, a smaller proportion of larvae were observed to be swimming at the time of the stimulus (e.g. Fig. 3). This discrepancy is due to the short period for identifying a swimmer (4 ms) just prior to the stimulus, rather than the 1 s interval considered in the spontaneous swimming measurements (Fig. 2).

The results for our flow experiments suggest that swimming adversely affects the responsiveness of larvae to a flow stimulus. Many swimming larvae exhibited no response within 60 ms from exposure to flow. Non-responsive larvae would generally continue routine swimming despite their bodies being rapidly displaced by the stimulus (Fig. 3A). Those larvae that did respond would interrupt their routine undulatory swimming by rapidly curling the body into the C-shape that is characteristic of stage 1 of a startle response (Kimmel et al., 1974). This response was exhibited by the majority of motionless larvae (Fig. 3B,C), with a mean response probability of 0.76 (L_1=0.67, L_2=0.83, where L_1 and L_2 are respectively the lower and upper 95% confidence intervals for a binomial distribution, N=121). In contrast, the mean response probability for swimming larvae (0.40, L_1=0.24, L_2=0.58, N=25) was nearly half the value of motionless larvae (Fig. 3C).

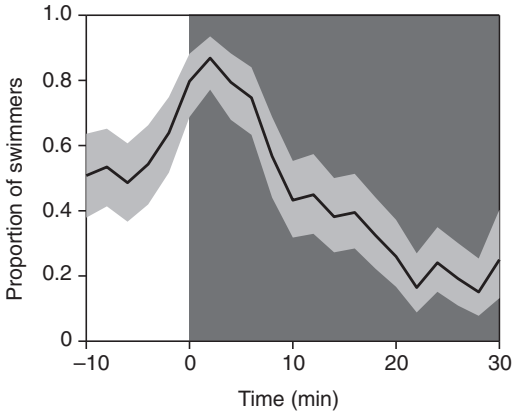

Fig. 2. Spontaneous swimming activity in response to a change in illumination. For a period of 10 min in white light (white area) and 30 min in darkness (dark gray area), batches of larvae varied in the proportion of individuals observed to be swimming within a 1 s period at 2 min intervals. The mean values (black line) are shown with 95% confidence intervals (light gray area) for varying sample sizes (from N=8 to N=22) among five batches of larvae.

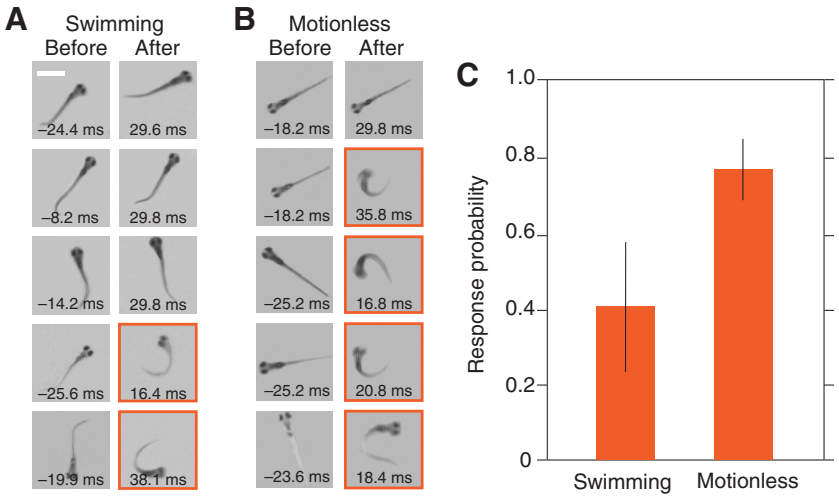

Fig. 3. The effect of routine swimming on the probability of an escape response to the flow stimulus. (A-B) Individual video frames are shown from a dorsal perspective for 10 representative larvae that were either swimming (A) or motionless (B) at the time of the stimulus. Each frame pair shows a larva before (left column) and after (right column) the stimulus. Larvae that responded to the stimulus (orange border) are shown in the middle of stage 1 of the startle response. The value of time listed for each frame is defined relative to stimulus onset (as in Fig. 1B). The white scale bar in the top-left frame has a length of 2 mm. (C) The response probability for larvae swimming (N=25) or motionless (N=121) at the onset of flow stimulus. The bar length and error flags respectively denote the mean and 95% confidence intervals for each group. Swimming larvae were significantly less likely to exhibit an escape response than stationary larvae (Chi-square test, P<0.001).

Response probability was also affected by the direction of flow with respect to a larva's body. Larvae were free to adopt any orientation with respect to the working section of the impulse chamber prior to exposure to a flow stimulus, though we only considered the effect of flow direction on motionless larvae. Among the numerous larvae tested, we found that orientation had a significant effect on response probability (Chi-square, P<0.001, N=155). Although significant, the effect of orientation was highly variable among individuals. When binned by intervals of 20 deg, the 95% confidence intervals overlapped in any comparison between two bins (Fig. 4B). The lowest probabilities were elicited by a head-on (orientations between 0 deg and 20 deg) and a tail-on velocity (from 160 deg to 180 deg). Head-on and tail-on velocities respectively elicited response probabilities of 0.53 (L_1=0.29, L_2=0.76, N=19) and 0.58 (L_1=0.34, L_2=0.80, N=19). In contrast, a velocity toward the side of the body (from 80 deg to 110 deg) showed a probability of 0.88 (L_1=0.47, L_2=0.99, N=8). Therefore, larvae tended to be less likely to respond to flow velocity parallel to the body than velocity directed to the side of the body.

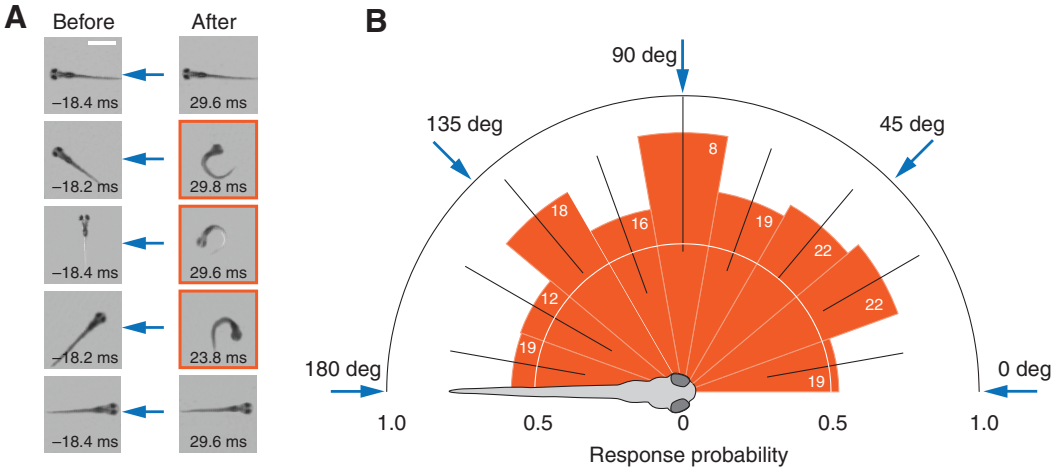

Fig. 4. Response probability as a function of the direction of flow toward the body of motionless larvae. (A) Representative video stills are shown for 5 individuals from a dorsal perspective before (left column) and after (right column) exposure to the flow stimulus. Before the stimulus, each individual has a different orientation with respect to the velocity of the flow stimulus (blue arrows). Some responded with an escape response (orange border), while others did not. The white scale bar in the top-left frame has a length of 2 mm. (B) A polar plot displays measurements of response probability as a function of the orientation of flow in the larva's frame of reference. Blue arrows denote the direction of flow relative to the larval body (drawn schematically in gray from a dorsal perspective), ranging from head-on (0 deg) to tail-on (180 deg) at 20 deg intervals. The wedge length and error flags respectively denote the mean and 95% confidence intervals and sample sizes are given (in white type) for each group. These data demonstrate that orientation significantly affects the probability of a response (Chi-square, P<0.001, N=155).

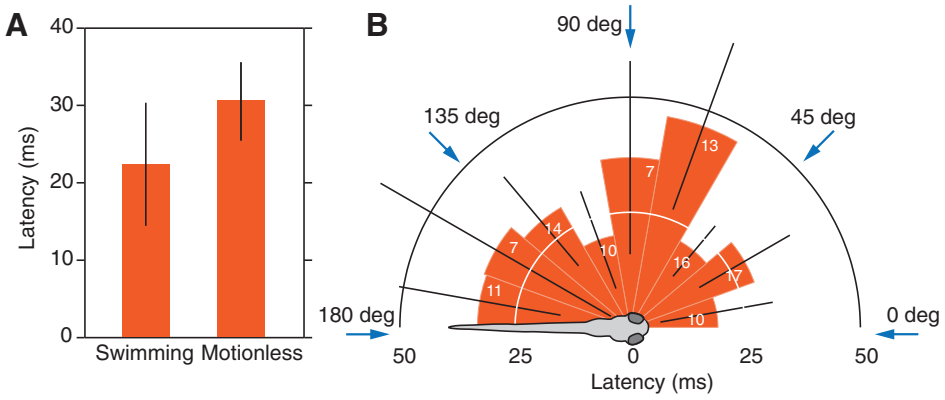

Fig. 5. Effect of routine swimming and flow direction on response latency. The bar length and error flags respectively denote the mean and 95% confidence intervals for each group. (A) The mean response latency for larvae swimming (N=14) and motionless (N=92) at the onset of the flow stimulus. There was no significant difference in response latency between these groups (Student's t-test, P=0.22). (B) A polar plot of response latency as a function of flow direction. Blue arrows indicate the direction of flow velocity in the larva's frame of reference (sample sizes in white). These measurements indicate that orientation to flow did not have a significant effect on response latency (one-way ANOVA, P=0.09, N=105).

We found little evidence for an effect of swimming or flow direction on the latency of the escape response. The mean latency of swimming larvae (22.3 ms, L_1=14.4 ms, L_2=30.3 ms, N=14), was statistically indistinguishable from that of motionless larvae (30.5 ms, L_1=25.5 ms, L_2=35.6 ms, N=92), according to an unpaired Student's t-test (P=0.22) (Fig. 5A). Latency values grouped by flow direction in bins of 20 deg exhibited a high degree of variation within each bin (Fig. 5B). As a consequence, flow direction had no significant effect on response latency, as determined by a one-way ANOVA (P=0.09, N=105).

DISCUSSION

There are at least four mechanisms by which swimming could reduce the responsiveness of a larval fish to a flow stimulus. (1) The flow created by swimming could directly attenuate a stimulus through hydrodynamic interaction, (2) the signals detected by the neuromasts from swimming could mask the stimulus signal, (3) the sensitivity of the lateral line system may be reduced by efferent nervous activity, and (4) the motor control of swimming may be challenged to initiate a startle response while driving routine swimming. A careful consideration of each of these hydrodynamic and neurophysiological mechanisms is necessary to evaluate how they may be distinguished experimentally. Irrespective of its mechanistic basis, the reduction in response probability with swimming demonstrates a cost in the ability to sense the environment that has implications for the locomotor behavior of fish.

Hydrodynamic interference created by swimming

The flow field created around the body of an undulatory swimming fish may directly interfere with the hydrodynamics of a flow stimulus. The waves of bending that propagate down the body create oscillatory pressure gradients that drive water flow (Muller et al., 1997; Tytell and Lauder, 2004). The viscosity of water dampens this flow and creates a gradient in velocity at the body's surface, known as the boundary layer (Anderson et al., 2001). The fluid forces created by a stimulus must penetrate these patterns of flow to be detected by the lateral line receptors at the body's surface. Therefore, the flow created by swimming may contribute to lowering the response probability by directly interfering with the fluid forces created by a stimulus.

Interference may also be generated at the level of individual receptors. In larval fish, these receptors are composed of superficial neuromasts, each of which includes a rosette of around 10 mechanosensory hair cells within the skin (Blaxter and Fuiman, 1989; Iwai, 1967; Iwai, 1980). These cells are coupled to a bullet-shaped extracellular matrix, the cupula, that extends into the water. By detecting deflections of the cupula, the superficial neuromast functions as a sensor of the shear stress created by the velocity of flow relative to the body (McHenry et al., 2008; McHenry and van Netten, 2007; Windsor and McHenry, 2009). Swimming may generate sufficient shear stress to saturate the neuromasts such that they become insensitive to a flow stimulus. Alternatively, the signals created by locomotor flow may mask a stimulus if similar in frequency and amplitude. Such masking was observed in the lateral line nerve of adult goldfish (*Carassius auratus*) and trout (*Oncorhynchus mykiss*), where the action potentials generated by a 50 Hz vibrating sphere were found to be increasingly indistinguishable from unidirectional flow at faster flow speeds (Engelmann et al., 2002; Engelmann et al., 2000). Similarly, the flow stimulus considered in the present study does not greatly contrast with the flow likely to be generated by swimming. Zebrafish larvae routinely swim forward at a rate ranging from 10 mm s^{-1} to 100 mm s^{-1} with a tail-beat period of ~30 ms (Budick and O'Malley, 2000; Buss and Drapeau, 2001; Fuiman and Webb, 1988). In that period, the velocity of the flow stimulus in our experiments reached little more than 60 mm s^{-1} (Fig. 1B) and was much less in the fish's frame of reference as the body moved down the pressure gradient with the surrounding water. Therefore, swimming has the potential to create substantial receptor-level interference.

Both receptor-level and direct hydrodynamic interference have the potential to create a latency in the response to flow. As its velocity increased with time (Fig. 1B), the flow stimulus in the present experiments became increasingly large relative to these sources of interference. If a threshold flow velocity above the interference was required to trigger an escape response, then that threshold should have been achieved later in swimming fish than in motionless fish. We found no such difference in latency (Fig. 5A), but instead found a trend toward lower latency (though not statistically significant) in swimming fish. This suggests a more complex model for the stimulus–response relationship that depends on how the central nervous system processes lateral line signals.

Neurophysiological effects of swimming

The neurophysiology of the lateral line and motor systems can be altered during swimming in ways that could adversely affect the ability to respond to a flow stimulus. Lateral line hair cells receive efferent input during swimming that can cause a reduction in the rate of afferent action potentials, which presumably reduces lateral line sensitivity (Art and Kroese, 1982; Flock and Russell, 1973a; Hashimoto et al., 1970; Russell and Lowe, 1983; Russell and Roberts, 1972; Russell, 1968; Russell and Roberts, 1974). However, there are instances where efferent input may have the reverse effect and elevate afferent sensitivity (Flock and Russell, 1973b; Roberts and Meredith, 1989). Our finding that response probability is lower in swimming fish (Fig. 3C) favors the hypothesis that the efferent system reduces lateral line sensitivity during swimming. However, if the efferent system simply functioned to reduce sensitivity, then swimming fish should exhibit a greater latency to a stimulus that increases in magnitude with time relative to motionless fish. We did not find this effect (Fig. 5A), which suggests that the role of the efferent system may be more sophisticated than the tonic suppression of sensitivity. For example, efferent signals transmitted to the lateral line hair cells could reduce sensitivity to particular frequencies by coordinated activity with the motor pattern for routine swimming (Bodznick et al., 1999; Tricas and Highstein, 1991). The flow created by swimming could thereby be adaptively filtered at the level of the neuromasts through a mechanism of efferent feedback, similar to what has been observed in the electroreception of weakly electric fishes (Bell, 1989).

Alternatively, the reduced sensitivity that accompanies swimming could be related to motor control. Initiating an escape response in a swimmer requires disruption of the motor pattern and mechanics of undulatory swimming to initiate the escape response (McLean et al., 2007). This disruption could require a greater stimulus to trigger an escape response than in a motionless fish that has an inactive motor system. Adult fish are capable of executing an escape response during swimming with only minor differences in kinematics compared with motionless fish (Jayne and Lauder, 1993), but it is unclear whether swimming reduces the probability of response in these animals. Neurophysiological preparations of fictive swimming (e.g. Masino and Fetcho, 2005) offer the potential to resolve the effects of efferent inputs to the lateral line system and the muscles on lateral line sensitivity.

The effects of flow direction

The effects of flow direction are likely a consequence of hydrodynamics. Flow direction was not a dominant effect, but it did show a mediating influence on response probability that was statistically significant (Fig. 4B). For example, a larva is 66% more likely to respond to flow directed to the side of the body than toward its head on average (Fig. 4B). Given that the lateral line system in larval fish is composed entirely of superficial neuromasts, this result predicts that flow normal to the longitudinal axis of the body generates greater shear stress than flow parallel to the body. This prediction is consistent with classical fluid dynamics models of cylindrical bodies at low Reynolds numbers (Happel and Brenner, 1973), which provide a reasonable approximation for the flow around a larval fish.

Implications for locomotor behavior

Our results suggest that intermittent locomotion offers a sensory advantage over continuous swimming for predator evasion. Such a benefit has previously been examined for the visual system, where intermittent swimming has the potential to aid in visualizing prey and predators (Chesney, 2008; Fuiman and Magurran, 1994; Fuiman et al., 2006; Hunter, 1972; Kramer and McLaughlin, 2001; McLaughlin and Grant, 2001). Our results extend this view by including the effects of swimming on the lateral line system. By interrupting swimming with bouts of inactivity, intermittent motion provides periods of time when a larva is nearly twice as likely to respond to the flow of suction feeding with an escape response as during swimming (Fig. 3C). However, it is not clear how effectively this response permits predator evasion. Evasion should depend on a wide variety of factors, including the speed and accuracy of the predator's strike, and the direction and rate of the propulsive phase (i.e. stage 2) of the response (Weihs and Webb, 1984). It remains to be demonstrated how the differences in response probability that we report affect survivorship, but an escape response is likely superior to no response in many predator–prey interactions.

Intermittent swimming is hypothesized to minimize the energetic cost of locomotion in larval and juvenile fishes (Fuiman and Webb, 1988; Webb and Weihs, 1986; Weihs, 1980). Although this view is not exclusive of the sensory advantage hypothesis, its basis has been challenged by observations of foraging in the field and hydrodynamic analysis (Fuiman and Batty, 1997; McHenry et al., 2003; McHenry and Lauder, 2005; McHenry and Lauder, 2006; McLaughlin and Grant, 2001). Therefore, the sensory benefits of intermittent swimming could be of greater consequence to the fitness of a fish species than its energetic effects.

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