RESEARCH ARTICLE

Pectoral fins aid in navigation of a complex environment by bluegill sunfish under sensory deprivation conditions

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SUMMARY

Complex structured environments offer fish advantages as places of refuge and areas of greater potential prey densities, but maneuvering through these environments is a navigational challenge. To successfully navigate complex habitats, fish must have sensory input relaying information about the proximity and size of obstacles. We investigated the role of the pectoral fins as mechanosensors in bluegill sunfish swimming through obstacle courses under different sensory deprivation and flow speed conditions. Sensory deprivation was accomplished by filming in the dark to remove visual input and/or temporarily blocking lateral line input *via* immersion in cobalt chloride. Fish used their pectoral fins to touch obstacles as they swam slowly past them under all conditions. Loss of visual and/or lateral line sensory input resulted in an increased number of fin taps and shorter tap durations while traversing the course. Propulsive pectoral fin strokes were made in open areas between obstacle posts and fish did not use the pectoral fins to push off or change heading. Bending of the flexible pectoral fin rays may initiate an afferent sensory input, which could be an important part of the proprioceptive feedback system needed to navigate complex environments. This behavioral evidence suggests that it is possible for unspecialized pectoral fins to act in both a sensory and a propulsive capacity.

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INTRODUCTION

Many fishes inhabit complex underwater environments and navigating through such habitats requires perception of the presence and location of surrounding obstacles. For example, bluegill sunfish, *Lepomis macrochirus* Rafinesque 1819, maintain an association with the littoral zone throughout part, if not all, of their lives for the benefits of higher prey densities and greater protection from predators (Crowder and Cooper, 1982; Ellerby and Gerry, 2011; Mittelbach, 1981). Visual and mechanosensory cues, such as those detected by the lateral line neuromasts, aid in obstacle avoidance and prey detection for fishes inhabiting complex littoral environments (Coombs and Van Netten, 2005; Stewart et al., 2013; Webb, 1989).

Bluegill sunfish have color vision and can discriminate between green (536 nm) and red (620 nm) peak absorption frequencies, as well as rhodopsin for low-light identification (~480 nm) of shapes (Hawryshyn et al., 1988; Hurst, 1953; Tamura and Niwa, 1967). Visual acuity increases through ontogeny because of the continuous growth of the retina and increase in receptor density; therefore, older bluegill can see smaller prey items than younger bluegill (Hairston et al., 1982). However, reduced illumination and turbidity have a significant effect on the vision and reactive distance of bluegill sunfish (Vinyard and O'Brien, 1976).

In low-light or dark conditions, fish may rely more heavily on sensory input from the lateral line to ascertain their surroundings in a novel environment (Sharma et al., 2009). Both sighted and blind morphs of the cavefish *Astyanax mexicanus* are known to use a wall-following behavior, relying on their lateral line system for sensory

information regarding nearby obstacles (Patton et al., 2010; Sharma et al., 2009; Windsor et al., 2008; Windsor et al., 2010a; Windsor et al., 2010b).

The lateral line system of bony fishes is composed of a series of superficial neuromasts on the skin and canal neuromasts in canals that lie just below the skin surface and are open to the outside environment *via* pores (Coombs and Van Netten, 2005; Webb, 1989). Hair cells within the neuromasts are anatomically polarized such that hydrodynamic loading from a certain direction will result in afferent stimulation relaying hydrodynamic information (Coombs and Janssen, 1990; Coombs and Van Netten, 2005; Engelmann et al., 2000; Webb, 1989). A complex environment modifies local fluid dynamics and increased flow speeds decrease the resolution of hydrodynamic signal detection by the lateral line in fish (Bassett et al., 2006; Coombs and Janssen, 1990; Engelmann et al., 2002; Engelmann et al., 2000; Montgomery et al., 1997).

Recent neurobiological studies have found that bluegill sunfish have putative mechanosensitive nerve endings in the distal ends of their pectoral fins and that these structures convey feedback in response to bending of the pectoral fin rays (Hale and Williams, 2012; Williams et al., 2013). This is a particularly exciting finding in light of extensive research that has failed to find proprioceptive receptors in fish with non-specialized fins (like those in bluegill sunfish) capable of providing sensory information regarding hydrodynamic loading (Ballintijn, 1972; Bone, 1978; Ono, 1979). Being able to interpret the bending of fin rays has obvious propulsive benefits in terms of controlling the shape and resulting hydrodynamics of flexible pectoral fins. Adoption of bending

proprioception as a mechanosensor used to relay information about nearby obstacles would be a great advantage, allowing fish to inhabit and navigate complex environments.

While the issue of obstacle avoidance has been a subject of interest for control algorithms for robotic fish (Bandyopadhyay et al., 1997; Liu and Hu, 2006; Shao et al., 2005; Shin et al., 2008; Yu et al., 2004), we are not aware of any research that has investigated how live fish are able to successfully navigate obstacles in a complex environment if visual or lateral line sensory input is impeded. It has been observed that blind cavefish will make contact with walls using their pectoral fins during wall-following behavior (Sharma et al., 2009; Windsor et al., 2008). We hypothesized that bluegill sunfish would swim through an obstacle course at low speeds, using pectoral fin swimming (Gibb et al., 1994; Lauder and Jayne, 1996). Under circumstances of visual or lateral line sensory deprivation, we expected that bluegill sunfish would use pectoral fins as a secondary source of mechanosensory input. We further hypothesized that bluegill sunfish would not make pectoral fin contact with obstacles under normal conditions because that would compromise the locomotor function of the pectoral fin during swimming. To test these hypotheses, we investigated the swimming of bluegill sunfish through obstacles under normal conditions, sensory deprivation conditions (with loss of either visual input or lateral line sensory input, or both) and with different flow velocities of water moving through the obstacles.

MATERIALS AND METHODS
Fish
Four bluegill sunfish (mean ± s.d. total length=18.5±1.29 cm) were collected from White's Pond (Concord, MA, USA) and kept in individual 40 l aquaria under a 12 h:12 h light:dark cycle. Fish were handled ethically according to Harvard University Institutional Animal Care and Use Committee guidelines, protocol 20-03.

Behavioral experiments
The obstacle course was constructed from eight 2.22 cm (7/8 inch) clear acrylic tubes (McMaster-Carr, Princeton, NJ, USA, part 8532K17) that were spaced 10 cm apart on center and extended the vertical height of the water column in the flow tank. The course arena was 25×25 cm length × width. A variety of course designs were tried during preliminary experiments to be sure that the fish could see the obstacles under light conditions and that the fish were able to swim through the course without contacting the obstacles inadvertently; the obstacle course used in this study was chosen because it satisfied both of these conditions.

Fish were exposed to different sensory deprivation conditions to assess the effect sensory loss had on the usage of pectoral fins for navigation. Four different treatment cases were used: (1) no alteration to visual or lateral line input (+V+LL), (2) loss of visual input by filming in total darkness (–V+LL), (3) loss of lateral line input by cobalt chloride block (+V–LL), and (4) loss of both visual and lateral line inputs (–V–LL). Fish swimming under normal vision conditions (+V) were recorded at 250 frames s^{-1}. Visual input was restricted by filming in total darkness using infrared lighting, which, because of low infrared light levels, were recorded at 125 frames s^{-1}. The lateral line was temporarily blocked using cobalt chloride hexahydrate (Sigma-Aldrich, St Louis, MO, USA), which competitively inhibits the binding of calcium at the sensory hair cells of the superficial and canal neuromasts (Karlsen and Sand, 1987; Schwalbe et al., 2012). Fish were placed in a solution of 0.15 mmol l^{-1} cobalt chloride hexahydrate and calcium-free DI water for 3 h immediately prior to the start of experiments (Karlsen and Sand, 1987; Liao, 2006;

Schwalbe et al., 2012). Concentrations and procedures exactly followed Liao (Liao, 2006). Temporary blockage of the lateral line was confirmed for up to 5 h after cobalt treatment by the absence of an escape response when a jet of water hit the caudal half of the body; fish exhibited an escape response prior to cobalt treatment and 24 h following experiments. As a second method to assess the efficacy of cobalt treatments, the cobalt procedure was replicated on separate fish and followed by 2-h staining in 0.008% 2-(4-(dimethylamino)styryl)-N-ethylpyridinium iodide (DASPEI) (Van Trump et al., 2010). Functional neuromasts would have been visualized as bright cells after having taken up the fluorescent DASPEI stain; however, following cobalt treatment we saw negative staining of the lateral line hair cells (Schwalbe et al., 2012; Van Trump et al., 2010). While this morphological evidence does suggest that cobalt chloride was effective in temporarily blocking the lateral line, it should be noted that the physiological response of modified fish behavior is a better indicator that the fish sensory system has been altered. Combined, the confirmation of both behavioral modifications and negative neuromast staining in fish that underwent cobalt chloride treatments demonstrate the efficacy of cobalt chloride in successfully inactivating the lateral line neuromasts (Karlsen and Sand, 1987; Liao, 2006; Schwalbe et al., 2012). Using cobalt chloride as an agent to temporarily eliminate the lateral line in behavioral studies has been extensively discussed recently by Schwalbe et al. (Schwalbe et al., 2012).

Fish did not experience the same order of experimental treatments. Each fish was filmed on two separate days, one under normal lateral line (+LL) conditions, and one following cobalt treatment (–LL), to reduce the exposure to cobalt over the course of the experiments. On each filming day, the order of light (+V) and dark (–V) was alternated so that no fish experienced the same sequence of all four trials.

Experiments were conducted in a 600 l flow tank with a 26×26×80 cm working area, as in previous work on bluegill locomotion (Flammang and Lauder, 2008; Flammang and Lauder, 2009; Flammang et al., 2011). Fish were recorded swimming through the obstacle course using two synchronized high-speed video cameras (Photron USA, San Diego, CA, USA) that simultaneously captured the lateral and ventral views in 1024×1024 pixel resolution. Each of the four fish was recorded swimming through the obstacle course under each sensory deprivation treatment condition (+V+LL, –V+LL, +V–LL, –V–LL) and flow speed (0.0, 0.5, 1.0 body lengths s^{-1}) five times, resulting in a total of 240 sequences analyzed. Fish were motivated to swim through the course using a wooden rod to swirl the water behind the fish (after having entered the obstacle area) without making physical contact. The experimenter wore night vision goggles to ensure the fish were not touched by the wooden rod during the dark trials.

Data analysis
The two video views were calibrated in three-dimensional space using direct linear transformation and digitized using custom MATLAB (R2011a, MathWorks, Natick, MA, USA) scripts written by Dr Ty Hedrick (Hedrick, 2008). A total of nine points were digitized in every 10th (when recorded at 125 frames s^{-1}) or 20th (when recorded at 250 frames s^{-1}) frame in each video sequence: (1) anterior tip of the lower jaw, (2) insertion point of the right pelvic fin, (3) insertion point of the left pelvic fin, (4) the anterior origin of the anal fin, (5) the ventral insertion point of the caudal fin, (6) the ventral insertion point of the left pectoral fin, (7) the distal tip of the third (and longest) left pectoral fin ray, (8) the ventral insertion point of the right pectoral fin, and (9) the distal tip of the third (and longest) right pectoral fin ray. A direct linear

transformation residual of less than 0.1 mm was used as a standard for accuracy and precision was monitored by redundant analysis of random data sets by undergraduate research assistants (see Acknowledgements) and B.E.F.

Using these digitized anatomical points, 10 variables of interest were calculated for each sequence: maximum swim velocity ($\mathrm{cm\,s^{-1}}$), number of times the fin contacted the obstacle structure (herein referred to as fin taps), duration of fin taps (ms), maximum pectoral fin angle from body (deg), change in heading following fin tap (deg), length of path traveled by fish through the course (cm), straight line distance from the point the fish entered and exited the course (cm), circuitousness (the ratio of path length to straight line distance), maximum body curvature ($\mathrm{mm^{-1}}$) and body pitch (deg). Data were tested for normality (Shapiro–Wilk test) and equal variance. A two-way repeated-measures ANOVA was calculated for each variable to determine the source of variation and interaction effects of sensory deprivation treatment, flow speed and individual fish. Pairwise multiple comparisons were performed using the Holm–Sidak method. All statistical tests were carried out using SigmaPlot 12.0 (Systat Software, San Jose, CA, USA).

RESULTS

Fish swam through the obstacle course without difficulty under all treatment conditions (Fig. 1). Locomotion was controlled primarily by pectoral fins and little use of median fins or body undulation was observed. Forward motion was produced by simultaneous beats of left and right pectoral fins between locations of obstacle posts. There was no significant effect of treatment, flow speed or individual on the maximum velocity at which the fish swam through the obstacle course (Table 1).

Fish made pectoral fin contact with the obstacle posts under all sensory deprivation treatment (Fig. 2) and flow conditions. There was a statistically significant difference in the number of fin taps among treatments ($P<0.001$; Table 1, Fig. 3) and speeds ($P=0.020$; Table 1, Fig. 3). Fish used their pectoral fins to contact the posts more frequently in the dark than in the light ($P<0.001$, Holm–Sidak), and when the lateral line was blocked than when it was not ($P=0.002$, Holm–Sidak; Fig. 3). Pectoral fin tapping was also more frequent during trials with flow ($P=0.014$, Holm–Sidak).

The duration of a single fin contact with an obstacle post was significantly different among treatments ($P=0.018$; Table 1, Fig. 3) and flow speeds ($P<0.001$; Table 1, Fig. 3). Fin contact was longest under normal swimming (+V+LL) conditions and shortest when the lateral line was blocked (–V–LL, $P=0.013$, Holm–Sidak; Fig. 3). Fin contact was nearly twice as long under no flow conditions ($P<0.001$, Holm–Sidak; Fig. 3).

Mean maximum pectoral fin angle, the angle of the pectoral fins outstretched relative to the body, was not significantly different among treatments, flow speed or individual ($P>0.05$; Table 1). Pectoral fin excursion appeared in all cases to reach a maximum angle of 90.0±1.0 deg from the mid-sagittal plane of the fish body.

There was no significant difference to changes in heading following fin taps among treatments, flow speeds or individuals ($P>0.05$ for all cases; Table 1). Changes in heading following a fin tap ranged between 20.4 and 64.0 deg (mean=48.9±8.2 deg, $N=6$) to the opposite side of the body as the fin that made contact with an obstacle post (supplementary material Movie 1).

The path length traveled by the fish through the course differed statistically by treatment ($P=0.002$; Table 1, Fig. 3). There was also an effect of treatment on the straight line distance between the points at which the fish entered and exited the obstacle course ($P=0.019$; Table 1). Fish covered a greater distance inside the obstacle course
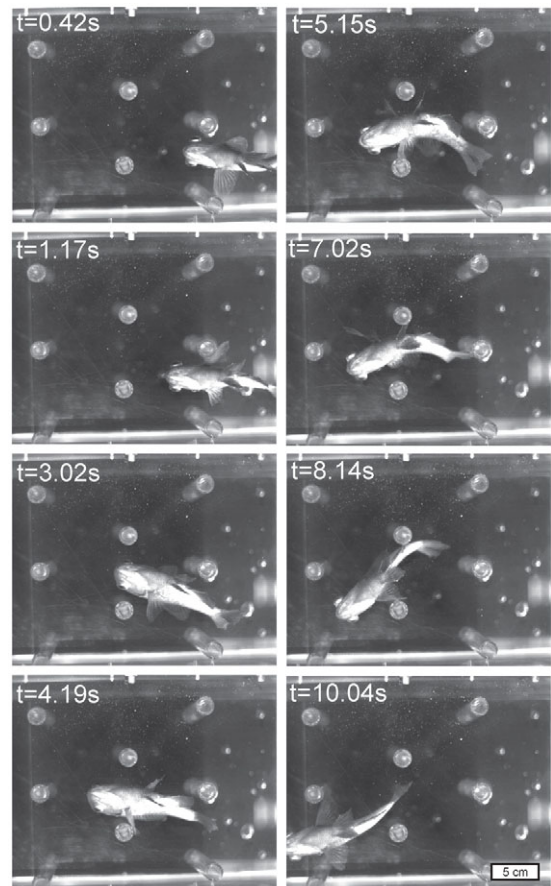

Fig. 1. Ventral view of bluegill sunfish swimming through an obstacle course. In this sequence, there is no flow and the fish can see (+V) but the lateral line has been temporarily blocked (–LL). This video is available as supplementary material Movie 1.

under no vision (–V) conditions. However, there was no effect of treatment, flow speed or individual on the circuitousness measure, the ratio of the path length to the straight-line distance ($P>0.05$; Table 1).

There was an effect of individual on body curvature while swimming through the obstacle course ($P=0.008$; Table 1). Body curvature means for fish A, B, C and D were 0.0066, 0.0078, 0.0066 and 0.0051 $\mathrm{mm^{-1}}$, respectively. There was no significant effect of treatment, speed or individual on body pitch ($P>0.05$; Table 1), which suggests that all fish were exhibiting similar body angles when swimming through the obstacle course under all conditions.

DISCUSSION
Effect of sensory deprivation treatments

Our initial hypothesis was that fish would not contact the obstacles when other sensory inputs were intact because it would interfere with the propulsive stroke of the pectoral fins. However, under normal conditions (in the light with the lateral line intact), bluegill sunfish contacted obstacle posts, often multiple times, as they passed them. While it is certainly possible that initial contact with an obstacle may have been due to the fact that bluegill sunfish use pectoral swimming at low speeds, subsequent contacts in which fins often wrapped around the obstacle post (Fig. 2) did not result in locomotion. Additionally, propulsive fin beats occurred in the open area between obstacle posts. Under conditions of reduced visual

Table 1. Two-way repeated-measures ANOVA results for each of 10 measured kinematic variables describing bluegill sunfish ($N=4$) swimming through an obstacle course under different sensory deprivation and flow conditions

Variable	Treatment		Speed		Treatment × Speed	
	P	$F_{3,18}$	P	$F_{2,18}$	P	$F_{6,18}$
Mean maximum velocity (cm s^{-1})	0.289	1.462	0.529	0.709	0.173	1.723
Number of fin taps	**<0.001**	17.547	**0.020**	3.806	0.095	2.168
Tap duration (ms)	**0.012**	6.587	**<0.001**	25.87	**0.021**	3.150
Mean maximum pectoral fin angle (deg)	0.233	1.714	0.519	0.733	0.649	0.706
Change in heading (deg)	0.269	1.545	0.278	1.599	0.206	1.595
Path length (cm)	**0.010**	7.087	0.939	0.063	0.455	1.000
Straight distance length (cm)	**0.040**	4.236	0.862	0.152	0.081	2.286
Ratio of path to straight distance length	0.451	0.963	0.788	0.247	0.216	1.559
Mean maximum body curvature (mm^{-1})	0.703	0.482	0.935	0.0679	0.198	1.621
Body pitch (deg)	0.124	2.515	0.596	0.565	0.679	0.664

Statistically significant values ($P<0.05$) are in bold.

and lateral line sensory input, fish tapped posts more frequently and for shorter periods of time.

Fin contact with the post resulted in bending of the distal tips of the fin rays (Fig. 2); fish did not appear to push off of the posts to change heading or move forward. Forward motion did not initiate until the beat following the tapping contact with the obstacle posts. These data provide behavioral evidence that fish use their pectoral fins to contact surrounding obstacles while navigating a complex environment, regardless of whether other sensory modalities are limited.

Pectoral fins as mechanosensors

Numerous studies have shown that the pectoral fins of fishes are typically used in a propulsive role, especially during swimming at slow speeds (Drucker and Jensen, 1997; Drucker and Lauder, 2003; Gibb et al., 1994; Lauder et al., 2006). There are a couple of reports of specialized sensory nerve endings in fish fins but these have only

been identified in a few fishes with highly modified pectoral fins, such as squirrel hake (*Urophycis chuss*), searobins (*Prionotus* sp.) and gurnard (*Aspitrigla cuculus*) (Bardach and Case, 1965; Ono, 1979). It is unknown whether these specialized fins relay proprioceptive information that is obtained by pressure, stretch or tension. Our data suggest a new hypothesis: that unspecialized pectoral fins are capable of acting simultaneously as propulsors and sensors and that fish are actively using input from pectoral fin bending to assist in navigation through complex environments.

Underlying the possibility of this mechanoreceptive ability is the fundamental prerequisite that pectoral fins must be flexible in order to produce bending-initiated afferent feedback. The flexible fin rays of fin-rayed fishes are notable for a myriad of hydrodynamic locomotor advantages (Alben, 2008; Alben et al., 2007; Flammang et al., 2013). However, flexible fins also have the ability to change shape passively and conform to obstacles in the environment. Deformation of the entire fish pectoral fin around a complex-shaped

With lateral line (+LL)   No lateral line (−LL)
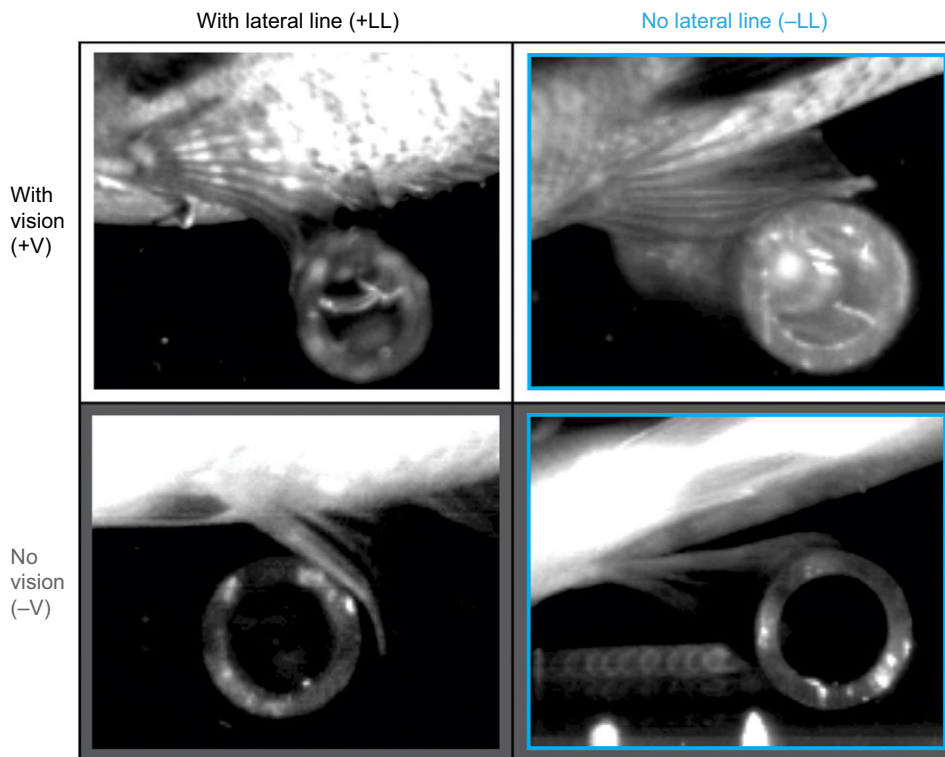
With vision (+V)

No vision (−V)

Fig. 2. Examples of pectoral fin contact with obstacle posts under all four sensory deprivation treatment conditions. Image brightness and contrast were increased to make the pectoral fins more visible.
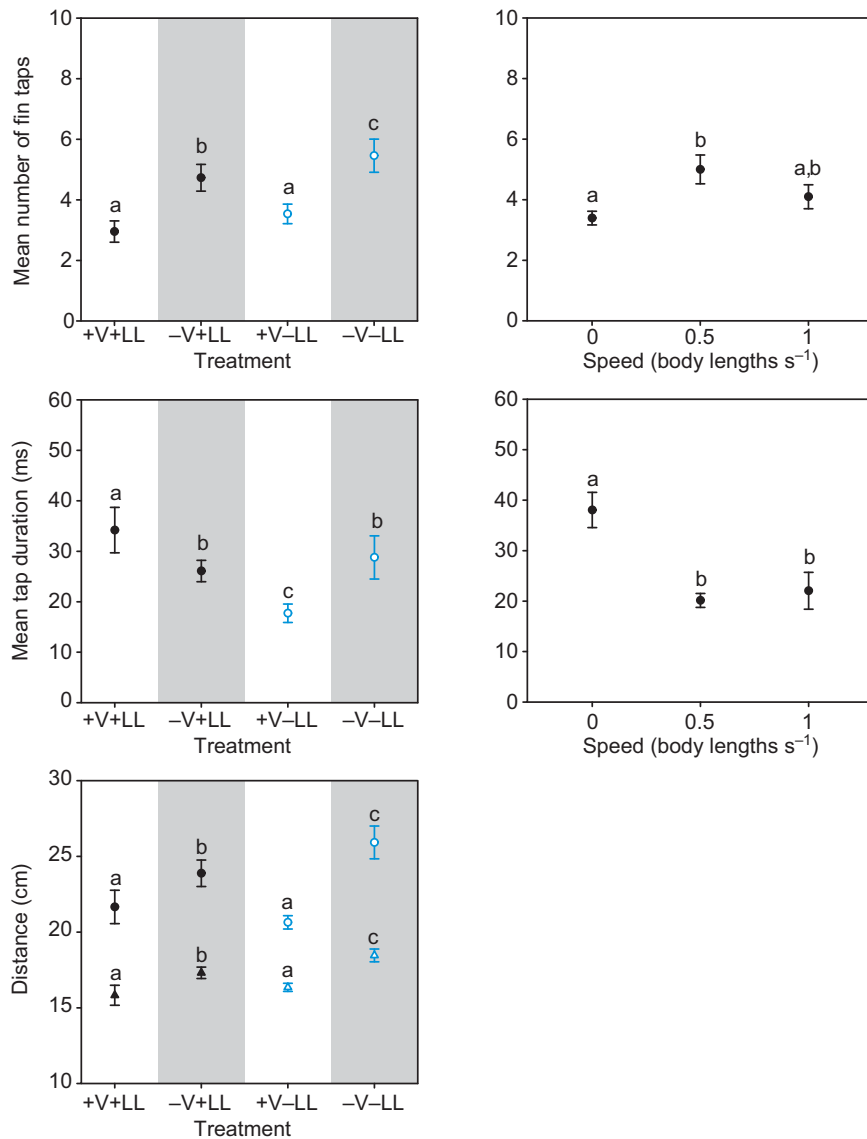
Fig. 3. Plots of variables showing significant variation from statistical tests (Table 1) due to sensory deprivation treatment and flow speed. Variables found to differ significantly included the mean number of pectoral fin taps, the mean duration of pectoral fin taps, and the path distance (circles) and straight line distance (triangles) the fish traveled through the obstacle course. Error bars represent ±1 s.e.m. Treatments are abbreviated as +V+LL (no sensory deprivation; black points, light background), –V+LL (no vision; black points, dark background), +V–LL (no lateral line; blue points, light background), and –V–LL (no vision or lateral line; blue points, dark background). Alphabetic designations represent significant differences among treatments from Holm–Sidek *post hoc* tests.

obstacle (e.g. Fig. 2) would create differential bending maxima along the lengths of parallel fin rays, thereby transmitting information about the shape and size of the obstacle around which the fish is trying to navigate.

Researchers interested in the bioinspired design of autonomous underwater vehicles have already focused on programming the obstacle avoidance behavior of robotic fish (Bandyopadhyay et al., 1997; Liu and Hu, 2006; Shao et al., 2005; Shin et al., 2008; Yu et al., 2004), but have not yet looked to the biological mechanisms by which live fish accomplish this task. Robotic fish are programmed to avoid obstacles. But the results of this study show that fish repeatedly use their pectoral fins to contact obstacles before passing them in a cluttered environment. We expect that further research into understanding the neurobiological mechanoreceptive feedback system of fish pectoral fins will be a crucial component in developing a fully autonomous bioinspired robot.

AUTHOR CONTRIBUTIONS

B.E.F. and G.V.L. conceived and designed the study; B.E.F. executed the study, interpreted the results and drafted the article; and B.E.F. and G.V.L. revised the article.

COMPETING INTERESTS

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