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RESEARCH ARTICLE

Lateral line sensitivity in free-swimming toadfish *Opsanus tau*

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ABSTRACT

A longstanding question in aquatic animal sensory physiology is the impact of self-generated movement on lateral line sensitivity. One hypothesis is that efferent modulation of the sensory hair cells cancels self-generated noise and allows fish to sample their surroundings while swimming. In this study, microwire electrodes were chronically implanted into the anterior lateral line nerve of oyster toadfish and neural activity was monitored during forward movement. Fish were allowed to freely swim or were moved by a tethered sled. In all cases, neural activity increased during movement with no evidence of efferent modulation. The anterior lateral line of moving fish responded to a vibrating sphere or the tail oscillations of a robotic fish, indicating that the lateral line also remains sensitive to outside stimulus during self-generated movement. The results suggest that during normal swim speeds, lateral line neuromasts are not saturated and retain the ability to detect external stimuli without efferent modulation.

KEY WORDS: Efferent, Hair cell, Self-generated movement, Modulation

INTRODUCTION

The mechanosensory lateral line in fishes detects water displacement and is used in schooling (Partridge and Pitcher, 1980), rheotaxis (Montgomery et al., 1997), hydrodynamic imaging (Weissert and von Campenhausen, 1981), hearing (Higgs and Radford, 2013; Montgomery et al., 1995) and predator–prey interactions (Montgomery et al., 1995). The lateral line is composed of both superficial and canal neuromast sensory organs which contain sensory hair cells that are innervated by both afferent and efferent nerve fibers. Physiological recordings from afferent nerves during respiration (Montgomery et al., 1996; Montgomery and Bodznick, 1994), and swimming movements of restrained fish (Ayali et al., 2009; Russell and Roberts, 1974) as well as freely swimming fish (Palmer et al., 2005) have documented self-stimulation of the lateral line.

The question remains as to how fish avoid saturation of the lateral line afferents and/or detect external stimuli during swimming while the hair cells are stimulated by water flow. One hypothesis is that the efferent system inhibits hair cell activity when self-motion is expected to saturate afferent firing (Roberts and Meridith, 1989) or that filtering occurs in higher order brain centers to reduce the effect of self-generated movement on the neuromasts (Bell et al., 1997). Recent work has suggested an alternative hypothesis that if the fish head is rotated in phase with side-to-side motion, the effects of movement on the lateral line may be reduced but not eliminated, therefore minimizing reliance on the efferent system to distinguish between external and self-generated stimuli (Akanyeti et al., 2016). Efferent fibers originate from the octavolateralis efferent nucleus in the hindbrain and, with rare exceptions, efferent innervation is a fundamental feature of all vertebrate hair cell systems (Roberts and Meridith, 1989). Mechanical and visual stimulation (Edgar et al., 2014; Roberts and Russell, 1972; Tricas and Highstein, 1990), gilling (Montgomery and Bodznick, 1994) and motor activity (Tricas and Highstein, 1991; Weeg et al., 2005) have been shown to depress lateral line afferent activity through efferent modulation. However, difficulties in recording lateral line input from free-swimming fish have prevented analysis of neural activity during swimming.

The oyster toadfish, *Opsanus tau*, is a benthic ambush predator with a well-mapped anterior lateral line that contains external superficial neuromasts surrounded by finger-like projections and several rows of canal neuromasts (Clapp, 1898). Previous investigations using chronically implanted electrodes have shown that the toadfish lateral line has a role in both predation (Palmer et al., 2005) and detection of intraspecific vocalizations (Radford and Mensinger, 2014); however, these neural recordings were conducted primarily in stationary fish. Additionally, the electrodes were permanently affixed, limiting the number of obtainable axons and the duration of the recording. The recent development of a 3D-printed, implantable micromanipulator has provided access to a greater number of fibers and the ability to record for longer periods of time (Rogers et al., 2017). This advancement allowed us to investigate the sensitivity of the lateral line in fish during swimming.

MATERIALS AND METHODS

Animal husbandry

Adult toadfish *Opsanus tau* (Linnaeus 1766) (mean±s.d. 31.5±3.5 cm standard length, n=12) of both sexes were obtained from the Marine Biological Laboratory, Woods Hole, MA, USA. The fish were maintained in large flow-through seawater tanks at local ambient seawater temperatures (19–21°C). All experimental procedures conformed to institutional animal care protocols.

Microwire electrode and implantation

Microwire (three wire) electrodes were fabricated and implanted into the anterior lateral line nerve using implantable micromanipulators (25×15×30 mm and 5.28 g) that were fabricated with a high-resolution desktop Formlabs Form 2 3D printer (Somerville, MA, USA). Additional details on electrode fabrication and implantation are available in Rogers et al. (2017).

Action potentials were differentially amplified (Dagan, Minneapolis, MN, USA) and monitored on a portable computer using Spike2 for windows software (Cambridge Electronic Design Ltd, Cambridge, UK). Following electrode implantation, the fish was transferred to the experimental tank and allowed to recover for 90 min, after which the three electrode wires were attached with a

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waterproof connector to a 2.5 m long, flexible tether that terminated in the differential amplifier.

Experimental design and statistical analysis

The experimental tank consisted of a Plexiglas aquarium 0.75×0.67 m with water depth maintained at 10 cm which completely immersed the fish and protruding micromanipulator. All tethered fish started on the left side of the arena with the anterior margin of the toadfish approximately 30 cm from the near end wall and 30 cm from the vibrating sphere, which was positioned 15 cm inside the far end wall. A small brush was run over the surface of the fish to pinpoint the location of the innervated lateral line neuromasts. Spontaneous and mechanically evoked neural activity was recorded using ADInstruments Powerlab. Waveform analysis was performed on the data, using Spike2 software (Cambridge Electronic Design Ltd, version 7), to discriminate individual units in the extracellular recording.

A solid plastic sphere (15 mm diameter) was attached to a mini-shaker (Bruël and Kjaer, model 4810) by a 15 cm metal shaft and suspended vertically midway in the water column. An externally triggered function generator (Tektronix FG 501A, Beaverton, OR, USA) was used to drive the mini-shaker at 50 Hz. The sphere's vertical displacement (peak to peak) was as follows: −40 dB, 0.01 mm; −20 dB, 0.05 mm; and 0 dB, 0.75 mm. The vibrating sphere was positioned 15 cm from the near side and end wall of the arena. All experiments started with the fish head positioned facing the sphere approximately 30 cm away from the near wall and approximately 17–20 cm from the closest side wall. Fish were allowed to either spontaneously swim or were induced to swim by contacting the tail with a probe. After each swim, the fish was returned to its original position. Alternatively, the fish was affixed by a single plastic electrical tie around the middle of its body to a movable sled (12.5×7.5×2.5 cm) of clear photopolymer resin that was fabricated with the 3D printer. A long, thin cable was attached to the front sled and the sled was pulled forward by a RC electric motor (Uxcell, Hong Kong) at either 2.2 or 5.8 cm s^{-1} and then returned to its origin. A pulley system maintained the cable along the bottom of the tank to minimize interference. A minimum of 5 trials were performed for each fish at each speed (Fig. 1).

A lateral line stimulus was provided by a vibrating sphere operated at 50 Hz located at a linear distance of 30 cm from the front of the fish head and positioned to be within 2.5 cm of the outside portion of the fish operculum at the point of closest pass. Alternatively, a robotic zombie Aquabot hexbug shark (Greenville, TX, USA) was attached by an L-shaped piece of piano wire to the sled and positioned with its tail lateral and in close proximity to the area where the neuromast was localized. The tail movements were initiated when the shark was placed in the water and the tail oscillated at frequencies of 3, 5 and 10 Hz, with the frequency automatically changing every 15 s.

The experiments were viewed overhead with a Logitech C920 HD Pro Webcam (30 frames s^{-1}; 640×480 resolution) that was run using Spike2 Video and paired with Spike2 for later analysis. The position of the fish and movements were monitored with a water-proofed miniature triaxial accelerometer (ICP® Model 356A12). Waveform analysis was performed on the data, using Spike2 software (Cambridge Electronic Design Ltd, version 7), to discriminate individual units in the extracellular recording. To compare spontaneous and movement-evoked firing rates, the average spontaneous firing rate was calculated for 5 s before movement and compared with the firing rate while the fish was moving for 5 trials for each fish at each sled speed or for at least 10 free swims. Data were analyzed prior to movement (30 cm from sphere), during initial movement (30 to 20 cm), mid-movement (20 to 10 cm), near the sphere (±5 cm of the sphere) and at the end of the sled's track after movement (15 cm past sphere).

SigmaPlot version 13.0 was used to analyze afferent fiber firing rates. All data were tested for normality using Shapiro–Wilk tests, and one-way analysis of variance (ANOVA) with Holm–Sidak *post hoc* tests were used to compare spontaneous firing rates with sled speeds. Student's *t*-tests were used to compare spontaneous firing rates with free swim speeds. Data are presented throughout as means±1 s.d.

Neural responses to the 50 Hz vibrational stimulus were quantified for evoked spike rate and vector strength. To determine whether the anterior lateral line responses were phase locked, phase histograms were generated for each unit. The coefficient of synchronization (R) was calculated from the phase histograms to represent phase-locking strength (Goldberg and Brown, 1969). However, R is likely to be misinterpreted when the sample size is small. To correct this issue, the Rayleigh statistic (Z) was used as a combined measure of the number of discharges and the strength of phase lock (Lu and Fay, 1993, 1995). Z is defined as $N \times R^2$, where N is the total number of spikes (Batschelet, 1981; Radford et al., 2013)

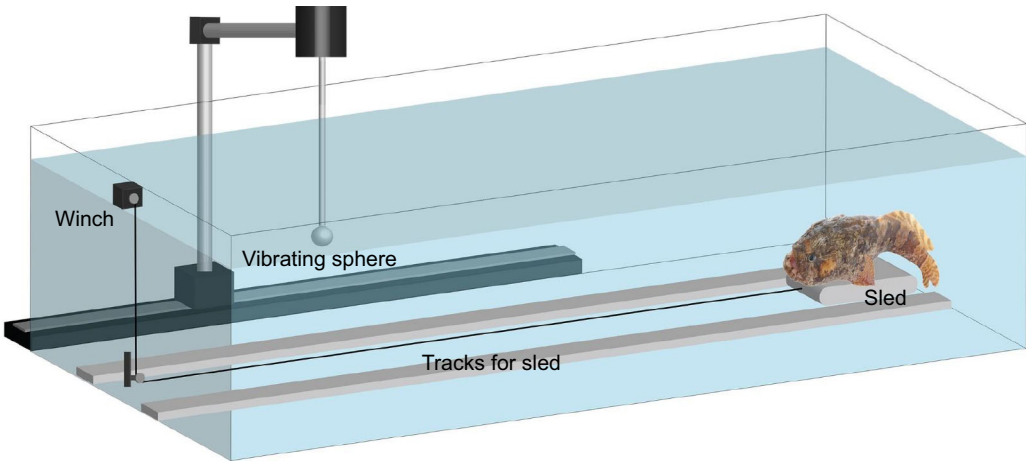

Fig. 1. Schematic representation of the testing arena. For sled experiments, the toadfish was placed on the sled at one end (near wall) of the arena and pulled forward by means of a motorized winch at either slow (2.2 cm s^{-1}) or fast (5.8 cm s^{-1}) sled speeds. Two strips of plastic acted as tracks to maintain the sled in the proper position. The vibrating sphere was placed near the opposite wall (far wall) of the arena and lateral to the toadfish path.

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and represents the response magnitude of the anterior lateral line nerve afferents. An afferent was significantly phase locked if $Z>6.91$ ($P<0.001$). To describe the strength of phase locking of the afferents, a previously published criterion (Lu and Fay, 1993, 1995) was applied to distinguish strongly phase-locked afferents ($R\geq0.5$) from weakly phase-locked afferents ($R<0.5$).

RESULTS

Chronic electrodes were successfully implanted into 12 toadfish, and 30 afferent lateral line units were analyzed for this study. These afferent lateral line units displayed spontaneous activity ranging from 2 to 42 spikes s^{-1} and increased firing rates during respiration or fish movement. Several efferent fibers ($n=3$) were also isolated, which were identified by their low spontaneous frequency (<1 spikes s^{-1}) and lack of modulation to movement, touch or outside stimulus.

Spontaneous or evoked free swimming speeds ranged from approximately 6 to 14 cm s^{-1} Alternatively, fish were pulled forward on a sled at two different speeds: 2.2 cm s^{-1} (slow) or 5.8 cm s^{-1} (fast). Both free swimming and sled movement increased the firing rate of afferent fibers above their spontaneous activity. In toadfish (TF) A, the spontaneous firing rate (2.3±1.1 spikes s^{-1}) at rest significantly increased (ANOVA, d.f.=2, $F=173.853$, $P<0.001$) to 32.3±3.6 spikes s^{-1} with the slow sled (Holm–Sidak, $P<0.001$) and 30.8±1.6 spikes s^{-1} with the fast sled (Holm–Sidak, $P<0.001$); however, there was no difference in firing rate between the slow and fast speeds (Holm–Sidak, $P=0.429$). In TF B, the spontaneous rate (13.8±0.5 spikes s^{-1}) significantly increased (ANOVA, d.f.=2, $F=51.720$, $P<0.001$) during movement to 19.5±0.5 spikes s^{-1} with the slow sled (Holm–Sidak, $P<0.001$) and 18.7±1.1 spikes s^{-1} with the fast sled (Holm–Sidak, $P<0.001$); however, there was no difference in firing rate between the slow and fast speeds (Holm–Sidak, $P=0.200$) (Fig. 2A). Firing rates also significantly increased during free swimming (Fig. 2B). In TF A, the spontaneous rate (2.3±1.1 spikes s^{-1}) significantly increased (Student's t-test, $t=-3.758$, d.f.=12, $P=0.00273$) to 11.2±4.6 spikes s^{-1} during swimming. In TF C, the nerve fired an average of 49.9±12.9 spikes s^{-1} during movement, which was significantly greater (Student's t-test, $t=-4.003$, d.f.=12, $P=0.00175$) than the resting rate (19.0±2.6 spikes s^{-1}).

Most neuromasts were localized near or posterior to the eye, which placed their location approximately 5 cm from the anterior margin of the fish and therefore 35 cm from the sphere. Forward sled movement increased the firing rate of the afferent lateral line fibers, which continued to fire throughout the transit but did not display phase locking to the vibrating sphere when it was off or operated at low amplitude (−40 dB, −20 dB) (Fig. 3). However, when the sphere's relative amplitude was increased to 0 dB, afferent lateral line fibers displayed an increase in the mean frequency of the firing rate (Fig. 3) and showed significant phase locking ($Z>6.91$; $P<0.001$) when the fish was near (±5 cm) the sphere.

Fig. 4 shows the phase-locking activity of the neuromasts as the fish was in motion past the vibrating sphere operated at low (−40 dB) and high (0 dB) amplitude. At low amplitude, although movements caused an increase in the firing rate of the fiber, no phase locking was observed. However, at the higher amplitude, strong ($R>0.50$) and significant ($Z>6.91$) phase locking occurred as the fish passed in the vicinity of the sphere.

Free-swimming fish also started approximately 30 cm from the sphere and passed the target at various speeds (6–14 cm s^{-1}), distances (2–20 cm), angles [lateral line parallel (0 deg) to perpendicular (90 deg) to sphere] and sides (contralateral or ipsilateral to the implanted electrode). Therefore, the sphere was not within the range of the neuromasts for all passes. Fig. 5A,B shows the recording of two spontaneous swims close by the vibrating sphere from an afferent lateral line fiber with a low spontaneous firing rate of 4 spikes s^{-1}. The fiber's mean firing rate increased during swimming (~10 spikes s^{-1}) and was elevated (~40 spikes s^{-1}) in the vicinity of the sphere. In contrast, efferent lateral line fibers did not alter firing rates during free swimming (Fig. 5C).

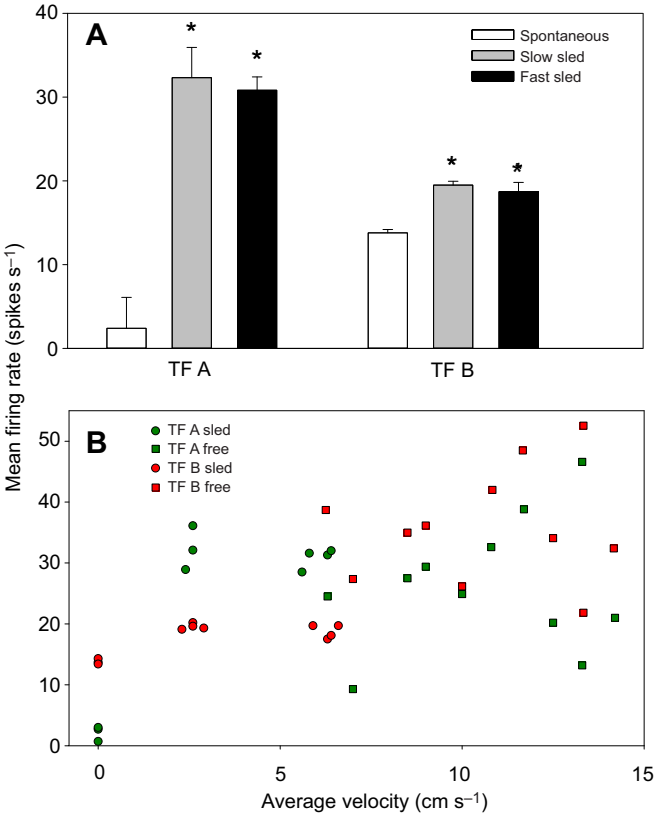

Fig. 2. Anterior lateral line afferent firing rates. (A) The mean firing rate of two lateral line afferent fibers is plotted for each fiber's spontaneous activity, and slow sled (2.2 cm s^{-1}) and fast sled (5.8 cm s^{-1}) speeds for two toadfish (TF A and B). Means±1 s.d. are shown. Asterisks indicate a significant difference from spontaneous (ANOVA, $P<0.001$). (B) The mean firing rate during both sled movement (circles) and free swimming (squares) is plotted versus average velocity. The spontaneous activity of the fiber is indicated at zero velocity. Each data point represents one movement.

Lateral line fibers also responded in phase to the oscillations of a robotic fish tail prior to fish movement. Fig. 6A shows the response of a stationary fish to the robotic fish tail oscillating at 3 Hz and Fig. 6B shows the same fish during sled movement responding to tail oscillation at 3 Hz and then to an increase in oscillation to 5 Hz.

DISCUSSION

These experiments show for the first time that the lateral line of free-swimming fish remains sensitive to external stimuli without the need for efferent modulation. Previous hypotheses proposed that self-generated noise is filtered by efferent modulation or in higher order brain centers (Bell, 2001; Montgomery and Bodznick, 1994). However, under the current experimental conditions, efferent modulation was not observed and appeared unnecessary for the toadfish to detect stimuli while moving.

Efferent input to the lateral line has been noted in several earlier studies; however, none involved free-swimming fish. Decerebrate

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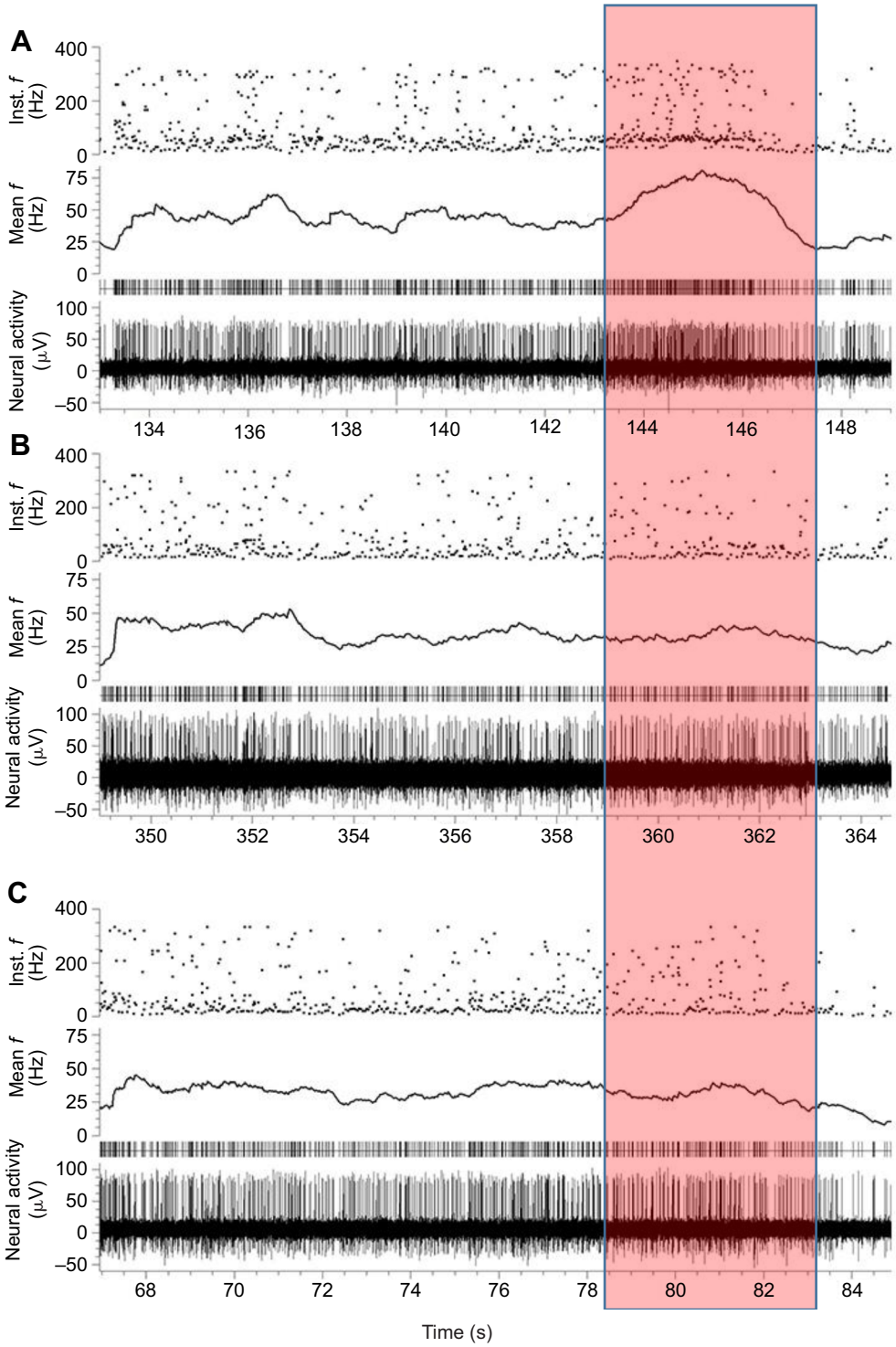

Fig. 3. Anterior lateral line recording during fish movement. Each panel (top to bottom) shows the instantaneous firing rate (frequency, *f*), the mean firing rate (spikes s^{-1}), vertical lines corresponding to action potentials, and neural activity from the anterior lateral line nerve during fish movement on a sled past a vibrating sphere at 50 Hz operated at the following amplitudes: (A) 0 dB (high), (B) −20 dB (medium) and (C) −40 dB (low). The shaded red rectangle indicates when the fish was within 5 cm of the sphere.

sharks showed a decrease in lateral line activity with tail movement, but efforts to correlate the efferent modulation with this reduction were complicated by the large amplitude of the movements (Roberts and Russell, 1972; Russell and Roberts, 1974). Experiments in the scorpionfish *Scorpoena papiliosus* correlated a reduction in lateral line response to ventilation movements with increased activity in ascending efferent neurons, suggesting an adaptive filter of self-generated movement (Montgomery and Bodznick, 1994). Additionally, previous work in the oyster toadfish showed efferent modulation of the lateral line in response to visual cues (Tricas and Highstein, 1991). During fictive sound production in the plainfin midshipman, *Porichthys notatus*, a member of the toadfish family (Batrachoididae), efferent modulation was noted to both the hearing organs and the lateral line (Weeg et al., 2005).

Though the initial goal of this study was to examine the lateral line activity in free-swimming toadfish and their detection of an external stimulus (i.e. vibrating sphere), coercing the toadfish to swim past the sphere at consistent speeds and distances proved challenging. Additionally, the toadfish lateral line had a limited detection range to the vibrating sphere (approximately 10 cm for

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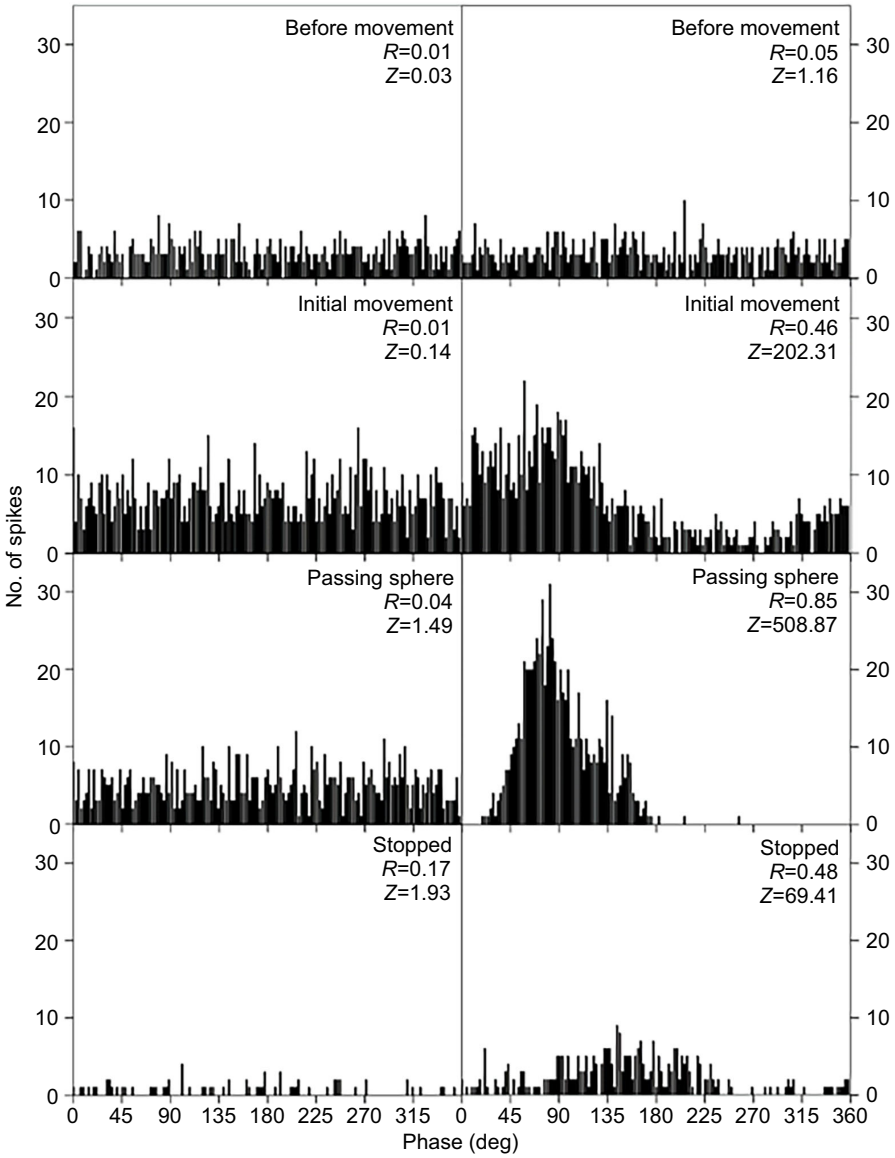

Fig. 4. Phase histograms for anterior lateral line fibers during sled movement past a vibrating sphere. Fibers were binned in 1 deg increments. Fish distance relative to the sphere was as follows: −30 cm (before movement), −25 to −15 cm (initial movement), −5 to +5 cm (passing sphere), +15 cm (stopped). The 50 Hz vibrating sphere was operated at −40 dB (left) and 0 dB (right). *R* is the coefficient of synchronization with strong phase locking indicated by *R*>0.50. *Z* is the Raleigh statistic and indicates significant phase locking when *Z*>6.91.

fish in this study) and even during nearby passes, free-swimming fish were only in range of the sphere for 1 or 2 s; thus, each pass was unique and it was difficult to statistically analyze the swims by the vibrating sphere because of the large variation in speed and direction. However, afferent activity significantly increased during free swimming and rates increased further during passes in the vicinity of the sphere (±5 cm), indicating that the free-swimming fish detected the sphere. In contrast, efferent fibers did not increase firing rate during swimming.

To correlate lateral line neural activity with movement and stimulus detection, a tethered sled was developed to allow controlled and quantified approaches to the vibrating sphere. The toadfish is a relatively sedentary fish with sustained swimming rarely seen in captivity and their murky estuarine habitats make field observations difficult. Most toadfish movements observed in tanks consist of short-distance (<1 m), slow 'hops' interspersed with stationary periods. They are also capable of short (one body length), rapid bursts during predatory strikes (Palmer et al., 2005).

The sled speeds were within the range of natural toadfish movements; the fast sled speeds overlapped with the lower range of toadfish swim speeds recorded in this study and the slow sled speeds were consistent with the hops observed in captivity. Forward sled movement increased neural activity, consistent with that observed during free swimming. Phase locking to the sinusoidal movements of the vibrating sphere indicated that the lateral line was detecting the stimuli. Although firing rates increased during movement, there was no indication that phase locking occurred when the sphere was off or operated at low amplitude. At higher sphere amplitudes, strong and statistically significant phase locking was observed ±5 cm to the sphere

Decreases in afferent activity were not observed with movement, suggesting that efferent fibers did not modulate firing activity. While it remains possible that efferent modulation requires voluntary movement and was not detected because of the artificial movement of the sled, free-swimming fish also displayed increased afferent firing rates without apparent efferent input, and afferent firing rates also increased during prey strikes (Palmer et al., 2005). Additionally, numerous efferent fibers, which are characterized by a relatively low (<1 Hz) firing rate, were recorded during this and previous studies (Maruska and Mensinger, 2015; Radford and Mensinger, 2014), and were not modulated by external stimuli or movement.

Several alternative hypotheses exist for the failure to record efferent modulation. It is possible that efferent modulation occurred

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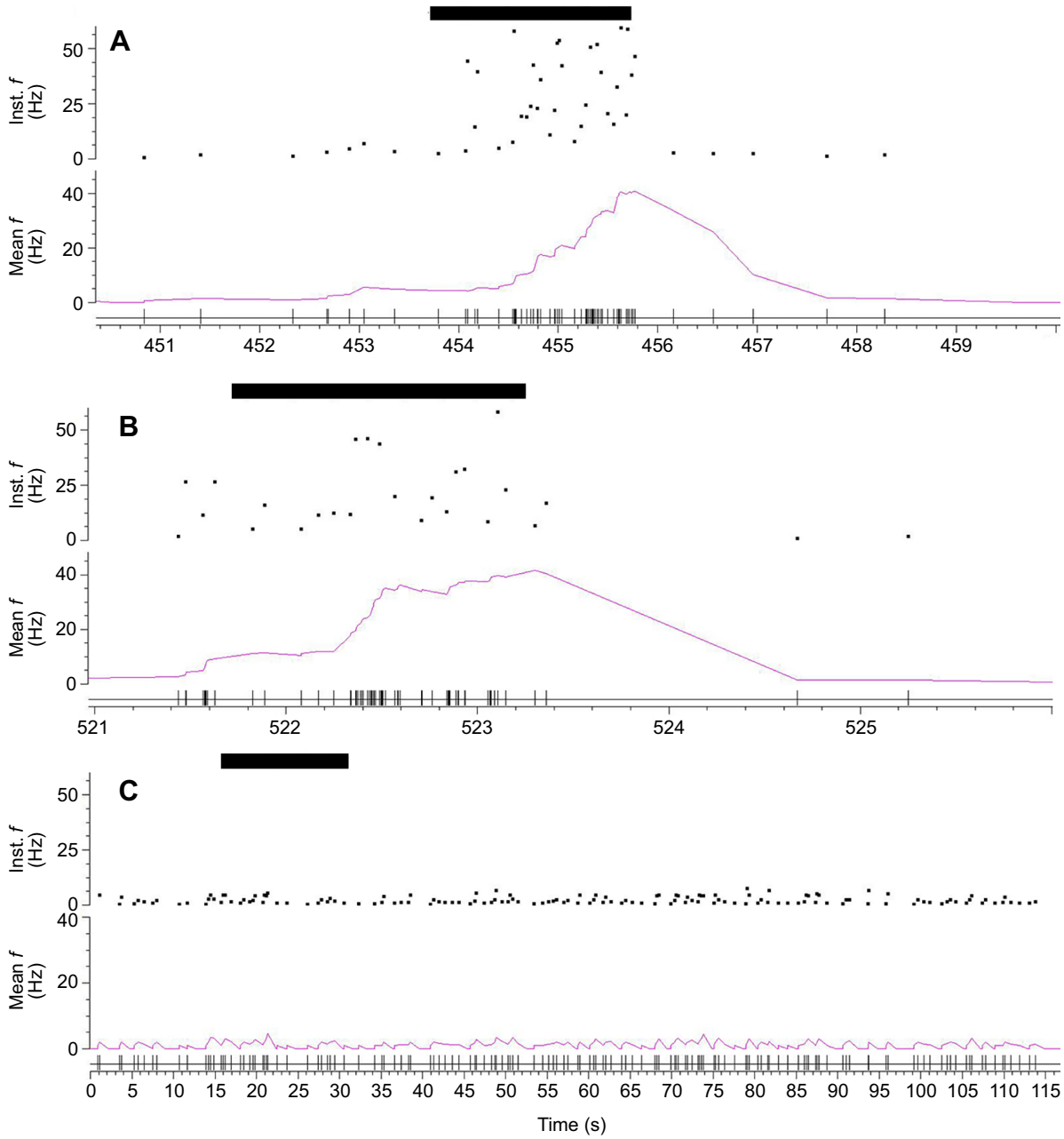

Fig. 5. Free-swimming fish. Each panel (top to bottom) shows the instantaneous firing rate, the mean firing rate (spikes s^{-1}) and vertical lines corresponding to action potentials during spontaneous swimming. The black solid rectangle above each panel indicates the duration of the swim. (A,B) A free-swimming toadfish moving past a vibrating sphere at 50 Hz (A, ~2 s swim duration, 10 s total time; B, ~2 s swim duration, 5 s total time). (C) A recording from an efferent fiber during a free swim (~15 s swim duration, 115 s total time) in the experimental tank.

and depressed the firing rate of the afferent fiber, preventing the lateral line from being saturated. However, for efferent modulation to occur and not be detected, it would have to be instantaneous with movement. If it was delayed, then firing rates during movement should have declined, which was not observed. Additionally, the implanted efferent fibers did not show modulation during swimming. It remains possible that the implanted lateral line afferents were not subjected to efferent modulation; however, these afferents innervated neuromasts found along the lateral and anterior margin of the toadfish head, which would be logical locations for the fish to monitor self-generated movement. Additionally, while numerous efferent fibers were identified, only three were retained for implantation and although none showed increased firing rate during movement, it is possible that there is another population of efferent fibers in the nerve that does react to movement. Although this study cannot completely rule out efferent modulation of the lateral line, it does demonstrate that fish can detect stimuli while moving without detectable efferent modulation at the speeds and stimuli tested.

The need for fish to be able to filter out self-generated movement was thought to be necessary for schooling. The robotic fish was used to recreate a quasi schooling situation as the mechanical fish constantly moved its caudal fin during toadfish movement. While there is no evidence that toadfish school, the experiment served as a proxy for two fish swimming side by side in a school. The toadfish responded to all three different tailbeat frequencies of the robotic fish, indicating that moving fish can detect motions of nearby fish.

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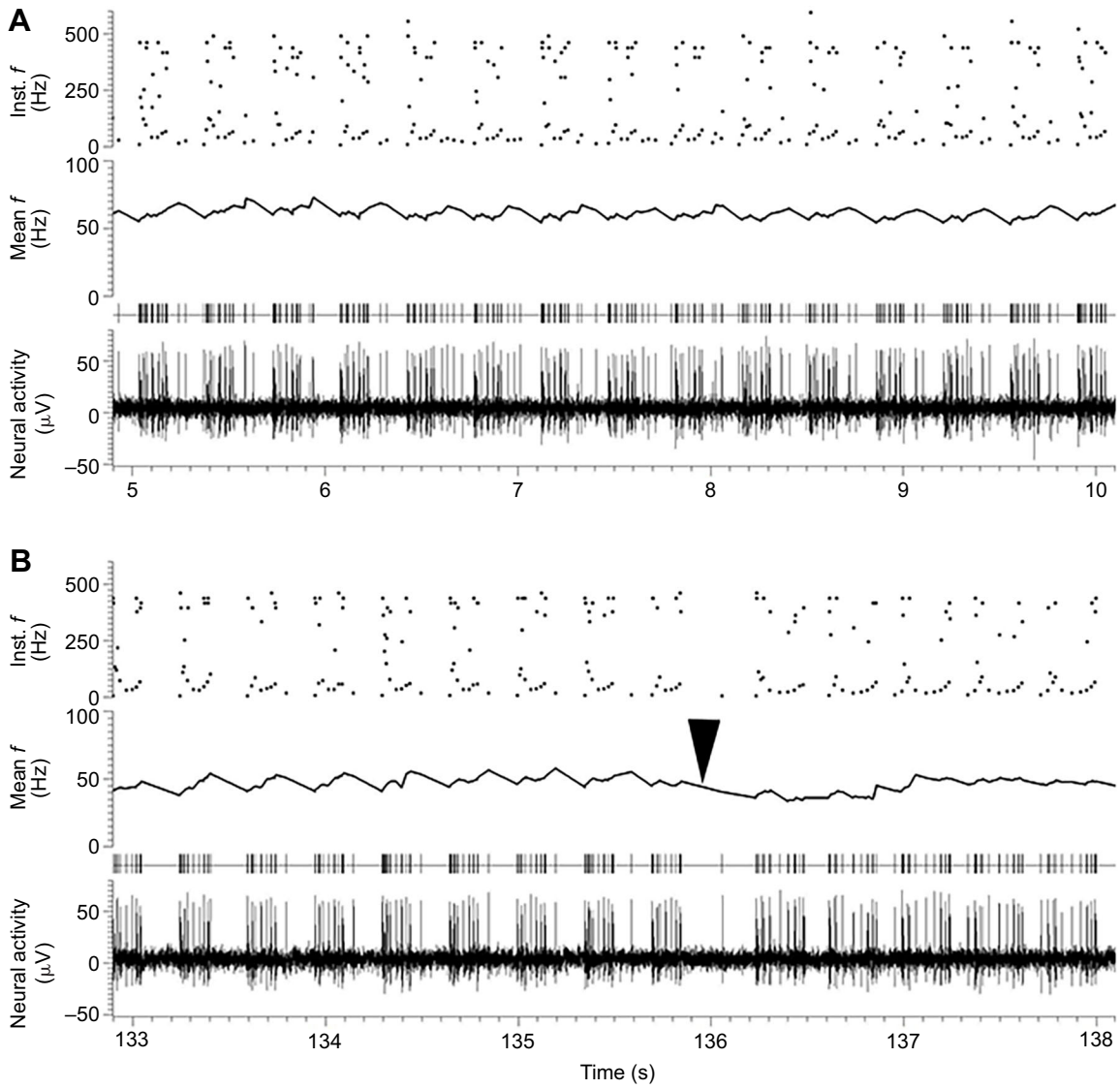

Fig. 6. Anterior lateral line response to robotic fish tail oscillations. Each panel (top to bottom) shows the instantaneous firing rate, the mean firing rate (spikes s^{-1}), vertical lines corresponding to action potentials and the neural activity in response to the robotic fish tail movements. (A) Stationary fish anterior lateral line fiber firing in response to 3 Hz tail oscillations. (B) Toadfish moving on a slow sled parallel to the robotic fish with the tail beating at 3 Hz and then changing to 5 Hz (arrowhead).

The lateral line fibers encoded forward fish movement yet still remained sensitive to other stimuli. Presumably, self-generated movement displaces neuromast stereocilia to send impulses to the brain to indicate that the fish is moving; however, the hair cells remain pliable to react to other stimuli. For example, at low sphere displacement amplitudes, forward movement stimulated the neuromasts, but when the fish passed the sphere, the firing rate did not increase and phase locking was not observed. Only at high amplitudes (0 dB) did afferent firing rates increase and strong phase locking occur, showing the hair cells have the plasticity to respond to the presumably stronger stimulus.

Much of the previous work on lateral line efferents involved decerebrate, immobilized, anesthetized or stationary fish (Bodznick et al., 1999; Roberts and Russell, 1972; Tricas and Highstein, 1991). While important information was certainly obtained from these studies, the implantable electrodes used in the present study provided fish with sufficient time to recover from anesthesia (90 min), metabolize the muscle relaxant (pancuronium bromide) and resume normal behaviors such as active feeding and swimming (Palmer and Mensinger, 2004). This experiment has shown the effect of forward movement on the lateral line in free-moving or swimming fish for the first time. Efferent modulation was not detected and appeared unnecessary for the fish to detect outside stimuli during movement. Whether this phenomenon is consistent across other fish or amphibians will require further study.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: A.F.M.; Methodology: A.F.M.; Formal analysis: A.F.M., J.C.V.W., L.S.R.; Investigation: J.C.V.W., L.F.R.; Resources: A.F.M.; Writing - original draft: A.F.M.; Writing - review & editing: A.F.M., J.C.V.W., L.S.R.; Supervision: A.F.M.; Project administration: A.F.M.; Funding acquisition: A.F.M.

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