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Rheotaxis and prey detection in uniform currents by Lake Michigan mottled sculpin *(Cottus bairdi)*

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Summary

Lake Michigan mottled sculpin, *Cottus bairdi,* exhibit a lateral-line mediated, unconditioned orienting response, which is part of the overall prey capture behavior of this species and can be triggered in visually deprived animals by both live (e.g. *Daphnia magna*) and artificial (e.g. chemically inert vibrating sphere) prey. However, the extent to which background water motions (e.g. currents) might mask the detection of biologically significant stimuli like these is almost entirely unknown, despite the fundamental nature and importance of this question. To examine this question, the orienting response of mottled sculpin was used to measure threshold sensitivity to a nearby artificial prey (a 50 Hz vibrating sphere) as a function of background noise level (unidirectional currents of different flow velocities). Because many fish show unconditioned rheotaxis to uniform currents, we also measured the fish's angular heading relative to the oncoming flow in the absence of the signal. Frequency distributions of fish headings revealed positive rheotaxis to flows as low as 4 cm s^{-1} and an increasing degree of alignment with the oncoming flow as a function of increasing flow velocity. Sculpin positioned in the upstream direction were able to detect relatively weak signals (estimated to be approx. 0.001–0.0001 peak–peak cm s^{-1} at the location of the fish) in the presence of strong background flows (2–8 cm s^{-1}), and signal levels at threshold increased by less than twofold for a fourfold increase in flow velocity. These results are consistent with the idea that lateral line canals behave as high-pass filters to effectively reject low frequency noises such as those caused by slow d.c. currents.

Key words: rheotaxis, prey orientation, lateral line, mottled sculpin, *Cottus bairdi.*

Introduction

The lateral line is a mechanosensory system distributed superficially on the skin surface and in fluid-filled dermal canals on the head and body of all fishes (and superficially in some amphibians). This spatially distributed system allows these aquatic vertebrates to detect water movements produced by both biotic (e.g. nearby swimming fish) and abiotic (e.g. tidal currents) forces as long as there is relative movement between the fish and the surrounding water. Because water movements can arise from many different sources under many different circumstances in the aquatic environment, it is not too surprising that the lateral line is important in many behaviors, including rheotaxis, prey detection, station holding, spawning behavior and schooling behavior (for recent reviews, see Montgomery et al., 1995; Coombs and Montgomery, 1999).

Despite the presence of ambient currents in many aquatic environments and their obvious role in stimulating the lateral line, most behavioral investigations on the sensory capabilities of this system have been conducted under still-water conditions. For example, lateral-line mediated sensitivity and reactive distances of Lake Michigan mottled sculpin (*Cottus bairdi*) to water movements created by live (*Daphnia magna*) and artificial (a small vibrating sphere) prey has been determined in the absence of any background water motions (Hoekstra and Janssen, 1985, 1986; Coombs and Janssen, 1990), although preliminary observations indicate that sculpin can detect artificial prey in the presence of slow (approximately 2 cm s^{-1}) unidirectional currents (Hoekstra and Janssen, 1985). In the natural environment, however, the general background noise created by other biotic and abiotic sources may mask or interfere with the ability of mottled sculpin to detect the small water movements created by their prey. The extent to which background noise masks the detection of biologically significant signals and the extent to which the lateral line system is able to filter out these unwanted noises is almost entirely unknown, despite the fundamental nature of this question.

Although the literature is replete with examples of prey detection by fishes in fluvial environments, only a handful of studies have systematically examined the effects of ambient water motion on lateral line-mediated prey detection.

Montgomery and Milton (1993) showed that mean reactive distance of torrentfish *Cheimarrichthys fosteri* to live, natural prey deteriorated from 6 cm at 0 cm s^{-1} to less than 2 cm at 100 cm s^{-1}. Although this study provides a nice example of how ambient flow can degrade the fish's ability to detect prey signals, the information that it yields about the signal-to-noise processing capabilities of the lateral line system is limited. For example, the amplitude, frequency and duration of prey movement and the position of the fish relative to the prey and flow direction were not controlled in these studies. Thus, signal-to-noise ratios were not characterized and, although care was taken to produce unidirectional, uniform flows, it is quite likely that there were considerable a.c. components (e.g. turbulence) to the background flow at the high flow speeds (10 and 100 cm s^{-1}) used in this study.

In addition to this one prey detection study, a recent series of studies by Montgomery and colleagues on the rheotactic responses of several different fish species to low velocity (<10 cm s^{-1}) currents has demonstrated for the first time an important of role of lateral line superficial neuromasts in rheotaxis (Montgomery et al., 1997; Baker and Montgomery, 1999a,b). Upstream orientation may be an important behavioral strategy for prey detection by fluvial species. It may help fish intercept small, downstream drifting prey or odors from larger upstream prey. Many animals appear to use a combination of odor-conditioned rheotaxis and chemotaxis to localize food odor sources (Weissburg, 2000; Weissburg and Zimmer-Faust, 1993, 1994; Montgomery et al., 1999). Thus, these studies remind us that ambient water currents may function as both signals and noise. The degree to which ambient water currents function to enhance or degrade biologically relevant signals will in large measure depend upon the saliency of different sensory cues and the sensory hierarchies evolved for signal detection in different fish species. In any event, studies on the potential masking effects of uniform flows on prey detection abilities must take the rheotactic behavior of the fish into account.

Despite the near absence of behavioral data on the signal-to-noise processing capabilities of the lateral line, a good deal of information exists on the filtering properties of the lateral line periphery. Both theoretical considerations (Denton and Gray, 1983, 1988, 1989; Kalmijn, 1988, 1989) and neurophysiological measures of afferent fiber responses (Kroese and Schellart, 1992; Coombs and Janssen, 1990; Montgomery et al., 1994) support the idea that the lateral line periphery can be broken down into low-pass (superficial neuromasts) and high-pass (canal neuromast) subsystems with respect to fluid velocity. These biomechanical and hydrodyamic-based differences suggest that canal neuromasts are better suited for filtering out low-frequency, ambient water motions (e.g. uniform flows) and for passing higher-frequency, prey-like signals, whereas superficial neuromasts are better suited for responding to slow, uniform flows while rejecting higher frequency, rapidly changing events (Montgomery et al., 1994).

Indeed, recent physiological studies on goldfish lateral line fibers have shown that although both putative superficial and canal neuromast fibers respond to a 50 Hz dipole source in the absence of background flow, only canal neuromast fibers continue to respond to the source in the presence of a 10–15 cm s^{-1} background flow (Engelmann et al., 2000, 2002). Conversely, superficial neuromast fibers respond robustly to uniform, background flows and increase their firing rate in response to increasing flow velocities (Voigt et al., 2000; Engelmann et al., 2000, 2002), whereas canal neuromast fibers do not (Engelmann et al., 2000, 2002). These findings are in nice agreement with behavioral studies showing that superficial neuromasts rather than canal neuromasts are important to the rheotactic response of fish to low-velocity uniform flows (Montgomery et al., 1997; Baker and Montgomery, 1999a,b), whereas canal neuromasts, rather than superficial neuromasts, appear to underlie prey-orienting responses to discrete, a.c. sources (Coombs et al., 2000b).

In this study, we take advantage of the unconditioned, lateral-line mediated, prey-orienting response of Lake Michigan mottled sculpin to investigate the effects of increasing background flow rates on the ability of sculpin to detect prey-like signals. We also determine the rheotactic response of these benthic sculpin to the same background flows in the absence of prey signals. Given that current-orienting behaviors are subserved by a low-pass (superficial neuromasts) subsystem and that the firing rate of superficial neuromast fibers increases with increasing flow rate, we predict that rheotactic responses in the upstream direction will increase as a function of increasing flow velocity. Likewise, given that the prey-orienting behavior of the Lake Michigan mottled sculpin depends on the high-pass (canal neuromast) subsystem and that uniform (DC) flows are ineffective stimuli for canal neuromast fibers, we predict that increases in flow velocity will have minimal effects on the ability of sculpin to detect the prey-like (a.c.) signals.

Materials and methods

Animal care and collection

Mottled sculpin *Cottus bairdi* Girard (6.3–8 cm in standard length) were collected from Lake Michigan using baited minnow traps placed at depths of 1–4 m in near-shore waters. Upon return to the laboratory, fish were housed in 38 or 76 litre aquaria at densities of 1–5 fish per tank. Water in both the flow tank and home tanks was dechlorinated tapwater, maintained at 15±2°C; this temperature is at the upper end of the temperature range for Lake Michigan sculpin. To control for the possibility that fish might use visual cues, all experimental fish were first surgically blinded. This was done under anesthesia (0.01% MS-222) using (1) complete enucleation, or (2) lens removal followed by aspiration of the retina. After surgery, fish were allowed a minimum of 1 week to recover before experiments began. Fish were hand-fed small pieces of squid delivered by long-nose forceps three times per week. Protocols used in the handling of animals during the course of this experiment were approved by, and on file with, Loyola's Institutional Animal Care and Use Committee.

Flow tank and flow measurements

All experiments were conducted in a ‘flow tank’ of similar design to that reported by Vogel and LaBarbera (1978). The flow tank was placed on a vibration-isolated table (Technical Manufacturing Corp., Peabody, MA, USA) to reduce substrate vibrations. The main body of the tank was a long Plexiglass rectangular channel (44 cm × 18 cm × 17 cm), with a circular opening at each end. The opening at one end was connected to the opening at the other end by a 10.2 cm diameter circular polyvinylchloride (PVC) return tube. Water depth was always kept at 15.5 cm, well above the dorsal surface of these benthic fish, which rarely swim off the bottom. Unidirectional flows were created by a motor-driven impeller placed at the downstream end of the tank, and mounted to a separate bench, so that motor vibrations were not transmitted to the flow tank. Impeller speed was adjusted by a motor controller which also provided a digital readout of the number of revolutions per minute (revs $\min^{-1}$).

A series of two collimators placed upstream of the experimental arena served to reduce turbulence in the flow. Each collimator consisted of approximately 500 soda straws (each 3 cm long) attached together to cover the entire cross section of the tank, and with the long axis of the straws parallel to the flow and long axis of the tank. Fish were placed in an area (22 cm × 17 cm) bounded by the second collimator on the upstream side, and a mesh screen supported by a plastic grid (egg crate) on the downstream side to prevent the fish from being drawn into the impeller. A video camera below the flow tank provided a ventral view of the test arena.

Flow velocities produced by impeller revolutions at different revs $\min^{-1}$ were measured in the experimental arena by two different techniques. Methylene Blue dye streaks were released from pipette tips 12 mm above the bottom of the flow tank at the approximate eye level of the sculpin and at five different locations, separated by 2 cm, along the width of the tank at its upstream end. The movement of the dye downstream was videotaped and the distance traveled by the dye streak from one time-stamped video frame to the next (17 ms frame^{-1}) was used to compute flow velocity. Average mid-stream and focal point velocities (i.e. at the level of the fish) were also measured with a commercially available flow meter (Marsh-McBirney, Model 2000, Frederick, MD, USA) as was done by Facey and Grossman (1992). Visual inspection of time-lapsed video frames revealed that bulk flow was unidirectional and spatially homogenous in the plane of view at all flow velocities tested. Moreover, dye-streak measures of flow velocities at different motor speeds were in excellent agreement with those made with the commercial flow meter.

Signal generation and measurement

Prey-like stimuli for masking experiments were simulated with a small (6 mm diameter) plastic sphere rigidly attached to a mini-shaker (Brüel and Kjaer, Norcross, GA, USA) by a stainless steel, blunt-tipped needle (16 gauge, 15 cm length); sphere vibrations were in the vertical plane. The center of the sphere was placed 12 mm from the bottom of the tank at the approximate eye level of the fish, and at the same level as the dye streak. The shaker assembly was mounted to a support system that was independent of the flow tank and the underlying vibration-isolation table. The amplitude and frequency of oscillation were computer controlled through a Tucker-Davis modular hardware system consisting of a digital-to-analog converter, electronic attenuator, and digital input and output. Sphere vibration (50 Hz) was gated on and off (500 ms on and 500 ms off) with 10 ms rise/fall times with a starting phase of 0°. A light-emitting diode, which could be seen through the camera, was time-locked to each 500 ms signal pulse so that there was a video record of when the signal went on and off.

To ensure that the signal source created sinusoidal water motions at 50 Hz and that the amplitude of water motion was a linear function of signal attenuation, the water motion created by the sphere in the absence and presence of flow was measured with a hot-film anemometry system (TSI, Inc., St Paul, MN, USA) as described in Coombs et al. (1989). Stimulus measurements were taken in the same tank that behavioral experiments were done, but in the absence of the fish. The sensing element was positioned 1 cm from the sphere center and at the same elevation as sphere center. The sensor was oriented to measure the amplitude of water motion along the axis of sphere vibration. The root mean square (RMS) voltage or amplitude of the anemometer response at 50 Hz was measured with a Hewlett Packard Wave Analyzer (3 Hz bandwidth) for different signal levels. The output of the anemometer was also digitized (analog-to-digital converter, Tucker Davis Technologies, Alachva, FL, USA) for suprathreshold signal levels (50 dB SL) and the Fourier transform of the digitized time waveforms was computed in Matlab.

Hot-film anemometer measurements confirmed that the vibrating source created sinusoidal water motions and that the amplitude of these motions declined linearly with signal attenuation. The Fourier transform of the digitized time waveforms for normal experimental conditions revealed a predominant spectral peak at 50 Hz, with increasing levels of low frequency (<30 Hz) energy as flow velocity increased (Fig. 1A). Low frequency energy near 0 Hz was similar for both the 0 and 2 cm s^{-1} conditions and represents the noise floor for ambient substrate vibrations. The amplitude of the second harmonic (100 Hz) was 19 dB less than that of the fundamental for the no-flow condition, but approximately 27 dB down from the fundamental for all flow conditions. Amplitude spectra for control conditions used in signal detection experiments (motor on/flow off) (Fig. 1B) were nearly identical to that for the normal, motor off/flow off condition (dotted line, Fig. 1A), except possibly for the 8 cm s^{-1} motor speed, where the energy below 25 Hz was somewhat higher (see Signal detection experiments, below, for further explanation).

Experimental overview

Two types of experiments were performed: one to measure the rheotactic behavior of fish and the other to measure the ability of fish to detect artificial prey vibrations as a function of background flow rates (signal detection experiments). In

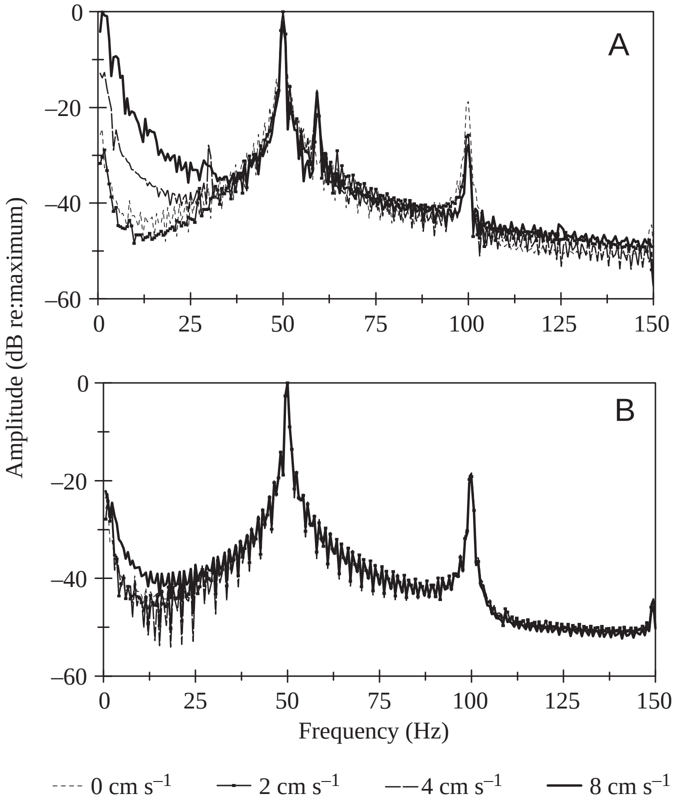

Fig. 1. Average amplitude spectra of digitized anemometer responses to a suprathreshold (15 m s^{-2} (RMS) at the source) 50 Hz vibrating sphere for four different flow velocities (0, 2, 4 and 8 cm s^{-1}). Each amplitude spectrum represents the average of four spectra, each obtained from repeat measures of the time-waveform at a given flow velocity. (A) Amplitude spectra from normal, experimental conditions. (B) Amplitude spectra from control conditions in which the flow-producing impeller blade was removed from the drive shaft, but the drive shaft motions remained coupled to the water for different motor speeds. Note that 60-cycle electrical noise is inexplicably more prominent for the 8 cm s^{-1} flow condition in A.

both cases, flow velocity was varied from 2 to 8 cm s^{-1} (approximately 0.1–1 *BL* s^{-1}; *BL* = body length) – well below the approximate slip speed (12 cm s^{-1}) at which sculpin tend to be displaced downstream by the flow (Webb et al., 1996). These flow speeds are also in the range of focal point velocities (measured with a commercial flow sensor near the head of the fish) reported for stream dwelling populations of mottled sculpin in their natural habitat (Facey and Grossman, 1992).

Experimental sessions for both rheotaxis and signal detection experiments were run 3 days per week (Monday, Wednesday, Friday) and lasted approximately 20–40 min for each fish. Fish were transported to the experimental tank in water-filled, plastic lined nets in order to minimize damage to superficial neuromasts. In both experiments, rheotactic and orientating behaviors were videotaped with a camera placed below the flow tank to yield a ventral view of the fish on the substrate. Rheotactic experiments were run before signal detection experiments and three of the four animals used in these experiments were subsequently used in signal detection experiments. Procedures for conducting rheotactic and signal detection experiments and for analyzing the results are described below.

Rheotaxis experiment

Before each experimental run, a random order of flow speed presentation was determined by drawing numbers corresponding to the three flow speeds (0, 4 or 8 cm s^{-1}) out of a ‘hat’ and recording the sequence. The revolution rate of the impeller was adjusted to the first of three flow speeds and the fish was allowed to acclimate to the flow for several minutes. The fish’s behavior was then videotaped for 5 min. At the end of the first 5 min period, the motor speed was adjusted again to produce the next flow speed in the randomly chosen order. Fish were allowed several minutes to acclimate to the new flow speed before being videotaped for another 5 min period. This procedure was carried out for 1–3 experimental sessions per day until all three flow speeds were tested. A different order of test velocities was then randomly generated for the next set of experimental sessions, and so on until each flow condition had been tested four times for each of four fish.

For data analysis, videotapes of rheotactic experiments were subsequently reviewed frame by frame to determine the position of the fish at different times during the 5 min test period. Because sculpin tend to move frequently, stopping for several seconds at each new position, each stationary position was defined as a potential data point and assigned a number corresponding to the order of occurrence during the test period (e.g. 1, 2, 3...). 25 of these positions, selected with a spreadsheet random-number function, were then captured, digitized and analyzed with a commercially available imaging program (SigmaScanPro, SPSS). For each position, the fish’s heading with respect to the oncoming flow was defined as the angle between the fish’s head vector (a line down the midline of the fish from the snout to the position of pectoral fin insertion) and the flow vector (a line parallel to the flow direction and intersecting the fish head vector at the point of pectoral fin insertion). By convention, an angle of 0° (fish pointing directly into the flow) represents perfect, positive rheotaxis. The frequency distribution of fish headings was then plotted for each fish and test velocity. The vector strength of the distribution (Batschelet, 1981), which can vary from 0 (fish headings randomly distributed across 360°) to 1 (all fish headings the same), was used as a quantitative measure of the degree to which sculpin showed orientation preferences. A modified Rayleigh (*V*) test (Greenwood and Durand, 1955) was used to statistically discriminate between uniform (random) and non-uniform distributions centered on the predicted, upstream direction for positive rheotaxis (0°).

Signal detection experiment

As with rheotactic experiments, the order in which different flow velocities (0, 2, 4 and 8 cm s^{-1}) were used was determined randomly at the beginning of each experimental run. The desired flow speed was then set and the fish was allowed to acclimate to the flow for several minutes. The fish was then lured into a fixed starting position with a small piece of squid dangled at the end of a long-nose forceps. Sculpin were positioned so that (1) the long axis of the fish was parallel (±20°) to the flow vector and facing upstream, (2) the midline of the fish was 5±1 cm away from the center of the signal source and (3) the source was approximately at the rostral/caudal level of pectoral fin insertion on the sculpin. Because lateral line sensitivity to both live (*Daphnia magna*) and artificial (a vibrating sphere) prey is best when the vibrational source is near the head, intermediate when it is near the trunk and poorest when near the tail (Hoekstra and Janssen, 1986; Coombs and Janssen, 1990), we chose the base of the pectoral fin as a convenient and easily identified location near the junction between head and trunk. A target area, outlined on the bottom of the flow tank, enabled easy and precise positioning of the fish relative to the signal source, which was centered in the horizontal plane of the test arena.

Once the fish was in position, the experimenter initiated a computer-controlled trial during which sphere vibrations pulsed on and off for a total of 5 s. The sculpin's response was scored as either a detection [movement towards or strike (bite) at the sphere], or non-detection (no movement, or movement away) response. A perfect orientation towards the source, which was to the side of the fish in the center of the tank, resulted in a 90° deviation from the upstream direction. Detection responses were reinforced by feeding the fish with small pieces of squid. If the fish moved before the trial began, it was repositioned, and a new trial sequence was begun.

To measure threshold sensitivity, an adaptive tracking technique was used in which the fish's response to a trial determined the amplitude of the subsequent trial, such that a detection response resulted in decreasing the amplitude of the next trial by 5 dB, and a non-detection response resulted in increasing the amplitude of the next trial by 5 dB. The signal level midway between that for consecutive 'yes' and 'no' responses was then defined as a transition threshold. This procedure was followed until 10 transition thresholds had occurred for a given flow velocity, which required 1–3 consecutive experimental sessions. After 10 transitions had occurred, the session for that day was terminated, and the next session on the following test day was begun with the next test velocity in the randomly chosen sequence. This procedure was repeated until there were 10 transitions for each test velocity. A new random order of test velocities was then generated, and the entire procedure repeated until a total of 20 transitions per test velocity had been measured.

To measure the probability that orienting responses occurred by chance, 30% of all trials were presented without sphere vibration (blank trials) at randomly distributed times. To control for the possibility that motor-generated acoustic noise or other a.c. flow noises rather than impeller driven d.c. flow noise may have masked signal detection, control conditions were also run with the impeller removed and the impeller drive shaft both in and out of the water.

For data analysis, the mean of 20 transition thresholds at each test velocity was computed for each of five fish. A repeated-measures analysis of variance (RM ANOVA) was used to test for significant threshold differences between fish and between test velocities. Because it was difficult to apply any specific criteria for judging detection and non-detection responses during the real-time execution of the experiment (e.g. fish had to move at least 5° and/or 5 mm towards the source for a detection response), a *post-hoc* video analysis of the fish's position before and after the initial response was performed to determine the distribution of response angles and distances for all blank and signal trials. SigmaScan Pro software was used to measure the fish-to-source angle and distance for each position before and after the response. In cases where the fish did not respond at all, the same position served as both the 'before' and 'after' position.

Results

Orientation preference as a function of flow rate

In the absence of flow, sculpin showed no orientation preference within the flow tank and fish were as likely to orient towards the downstream end (±180°) or the sides (±90°) of the flow tank as the upstream end (0°) (Fig. 2A). A Rayleigh test for circular uniformity on the distribution of orientation angles revealed that distributions for all four fish at 0 cm s^{-1} were not significantly different from random. In the presence of flow, sculpin showed clear orientation preferences in the upstream direction (Fig. 2B,C). A modified Rayleigh (V) test revealed that angular distributions were significantly different from random and grouped around 0° (= directly upstream) ($P<0.01$ for all fish). Finally, increasing flow velocities resulted in increasing degrees of positive rheotaxis, as determined from the vector strengths (**r**) of the angular distributions (Fig. 3). Vector strength was positively correlated with flow velocity ($r^2>0.90$ for all individuals).

Post-hoc *analysis of response angles and distances for threshold detection experiments*

Because the adaptive method of threshold tracking in the threshold detection experiments required the experimenter to make instantaneous judgements as to whether fish moved in the direction of the signal source or not, it is conceivable that the experimenter may not have applied the same response criteria to each trial type (i.e. signal *versus* blank trials). Two types of errors were possible for each trial type. The experimenter may have mistakenly judged that the fish moved towards the source (a so-called 'hit' during a signal trial and a 'false alarm' during a blank trial) when in fact the fish moved away from the source or the movement towards the source was insufficiently large to fulfil the criteria for a positive response (Type I error). Conversely, the experimenter may have mistakenly judged that the fish moved away from the source or did not move at all during the trial period (a 'miss' during a signal trial and a 'correct rejection' during a blank trial) when in fact the fish moved towards the source during the trial period (Type II error).

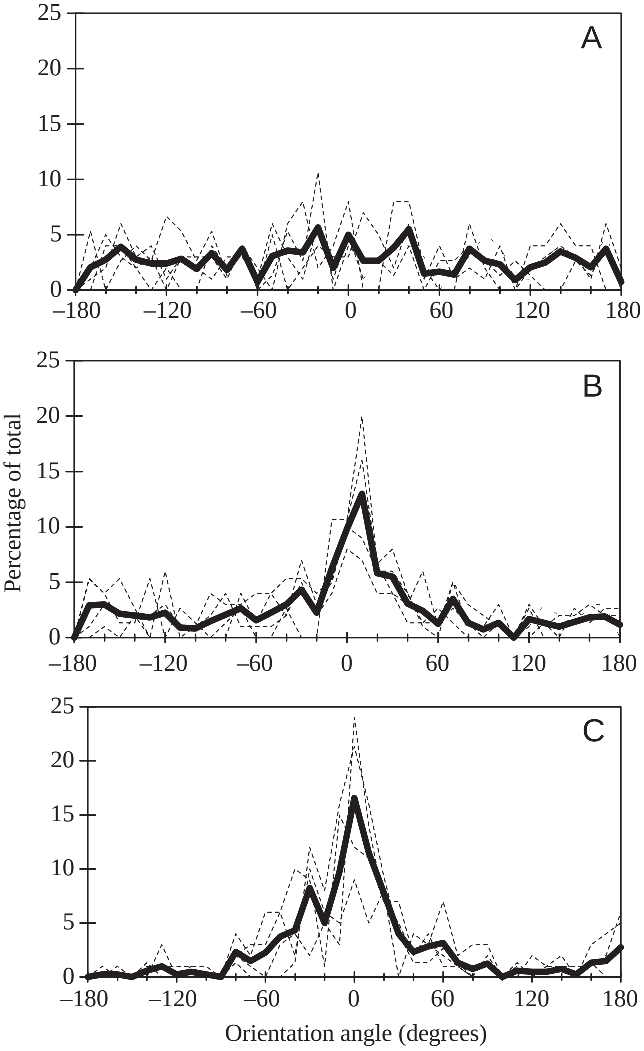

Fig. 2. Frequency distribution of fish orientation relative to the oncoming flow at 0 cm s^{-1} (A), 4 cm s^{-1} (B) and 8 cm s^{-1} (C). An orientation angle of 0° represents perfect positive rheotaxis (fish facing directly upstream). Each dotted line represents the distribution of orientation angles for one of four individuals, while the solid line indicates the mean distribution for all four individuals. Bin width=10°.

A *post-hoc*, videotape analysis of the fish's position before and after each response was used to determine the extent to which experimental errors of these types were made as a function of two different response criteria: the degree by which the fish turned towards the source (the change in fish-to-source angle) and the degree by which the fish moved closer to the source (the change in fish-to-source distance). The distributions of response angles scored as hits (signal trials) (Fig. 4A), misses (signal trials) (Fig. 4B), false alarms (blank trials) (Fig. 4C), and correct rejections (blank trials) (Fig. 4D) were very similar across flow conditions, as were the distributions of response distances for the same judgements (Fig. 5). Pooled distributions across all individuals and conditions also revealed that the experimenter's judgements were consistent for hits and false alarms, as were the judgements for misses and correct rejections (Figs 4E, 5E). That is, the vast majority (>90%) of responses judged to be hits or false alarms were based on fish movements that reduced the fish-to-source angle by greater than 30° or the fish-to-source distance by greater than 10 mm. Likewise, the vast majority of responses judged to be misses or correct rejections were based on movements that reduced the fish-to-source angle by less than 30° or the fish-to-source distance by less than 10 mm. Using the 30° angle and 10 mm distance criteria, type I and II errors occurred at relatively low frequencies (<10% of the time) for both trial types (Table 1). Thus, it is highly unlikely that errors of this type had any systematic or significant effects on the threshold sensitivity results presented here.

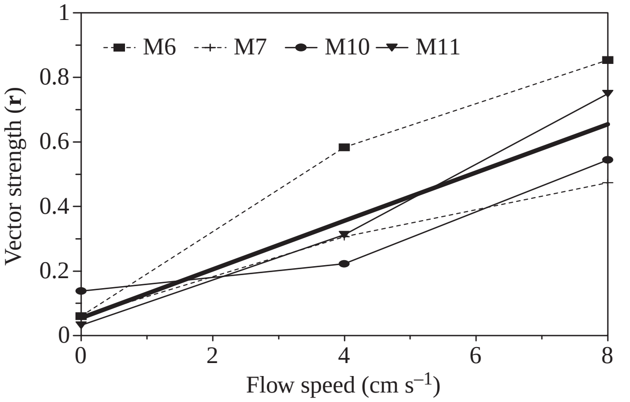

Fig. 3. Vector strength (**r**) as a function of flow speed (cm s^{-1}) for each of four individuals (M6, M7, M10 and M11). The solid heavy line is the linear regression through the data from the four individuals (r^2=0.99).

Signal detection results

Because the rheotaxis experiment clearly showed that sculpin naturally tend to orient upstream (Figs 2, 3), fish were positioned facing upstream for signal detection experiments. Threshold detection results revealed that sculpin were able to detect relatively weak, prey-like signals in the presence of a strong ambient background flow. Peak–peak mean signal levels at threshold ranged from 0.7–1.2 cm s^{-1} at the source for background flow rates of 2–8 cm s^{-1}. Although it is difficult to know the exact signal strength at the fish, the $1/r^3$ law for attenuation of a dipole source (in the absence of flow and fish) predicts that signal levels 4 cm away would be on the order of 0.001–0.0001 cm s^{-1}, several orders of magnitude below the background flow levels. Mean signal levels at threshold were

Table 1. *Percentage of Type I and Type II errors as a function of response (angle* versus *distance) and trial (signal* versus *blank) type*

	Angle criteria		Distance criteria	
	Signal trial	Blank trial	Signal trial	Blank trial
Type I error	7.4	10.0	2.4	1.7
Type II error	5.2	5.4	8.8	8.9

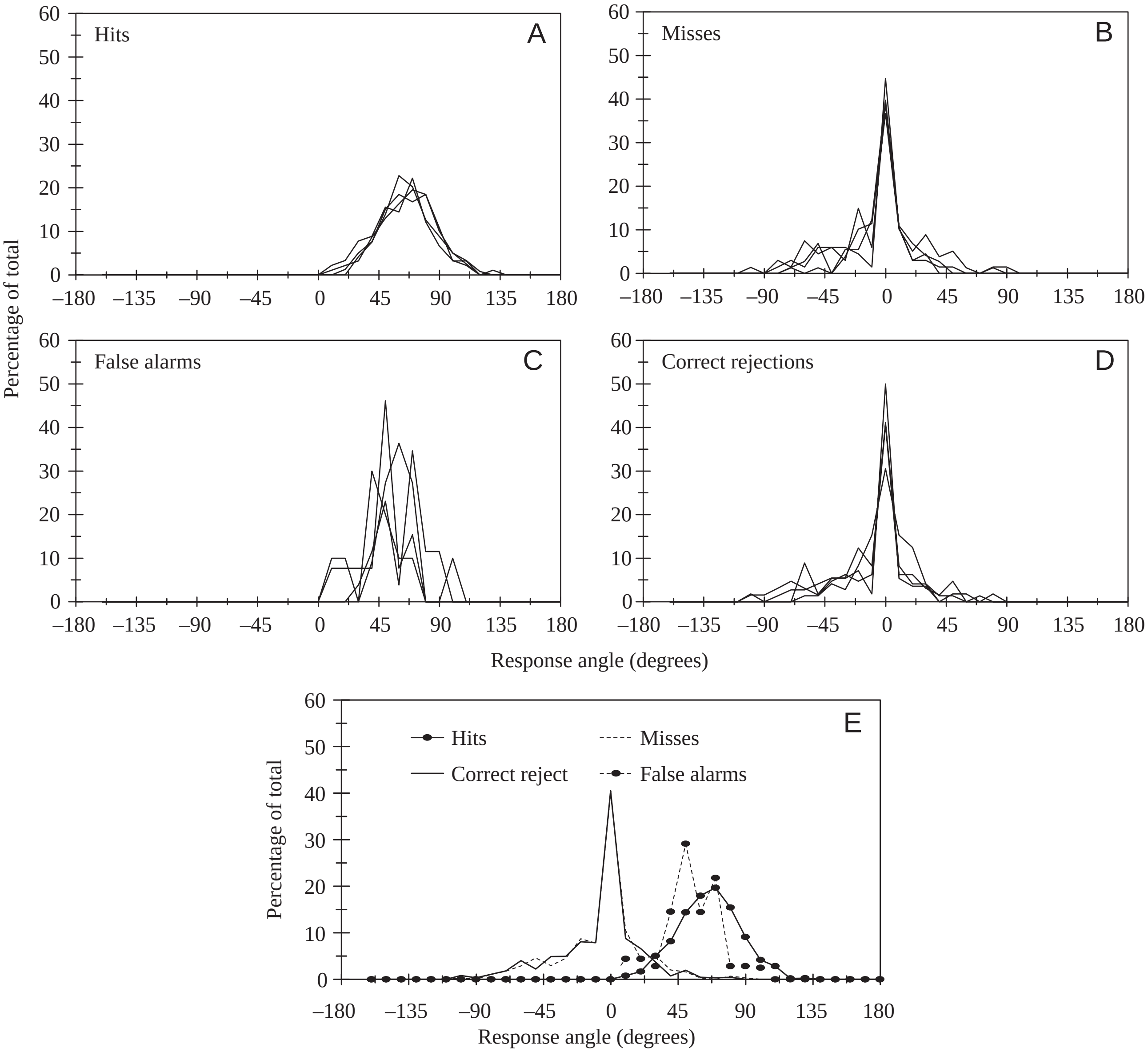

Fig. 4. Frequency distribution of response angles from *post-hoc* analysis of fish-to-source angles before and after orienting responses. Frequency distributions are grouped according to how responses were judged during the real-time execution of the experiment – i.e. as hits (A) or misses (B) for signal trials, and false alarms (C) or correct rejections (D) for blank trials. Each solid line represents the distribution of response angles (pooled from 4 individuals) for one of four flow conditions (0, 2, 4 and 8 $\mathrm{cm\,s^{-1}}$). In E, the mean distributions of all flow conditions are plotted for responses judged as hits, misses, correct rejections and false alarms. Bin width=10°.

approximately fourfold lower in the absence of flow than in the presence of flow and increased by less than twofold for a fourfold increase in current velocity (Fig. 6A). A one-way RM ANOVA of mean thresholds from five individuals showed that different flow conditions (0, 2, 4 and 8 $\mathrm{cm\,s^{-1}}$) had significant effects on threshold sensitivity ($P<0.05$). *Post-hoc* (Tukey's multiple comparison) comparisons of the means revealed that threshold signal levels in the absence of flow were significantly different from those in the presence of flow for all flow velocities (Table 2). In the presence of flow, however, only the lowest (2 $\mathrm{cm\,s^{-1}}$) and highest (8 $\mathrm{cm\,s^{-1}}$) flow velocities produced significantly different thresholds (Table 2). Mean fish-to-source distances at the time of signal onset (measured from *post-hoc* videotape analysis and pooled across all individuals) varied by no more than 2 mm (mean ± S.D. = 56±9, 55±8, 54±8 and 56±7 mm for 0, 2, 4 and 8 $\mathrm{cm\,s^{-1}}$, respectively). Thus, different signal levels at the fish due to different degrees of attenuation with distance are unlikely to account for these threshold differences.

Control condition results

A number of controls were run to determine if threshold

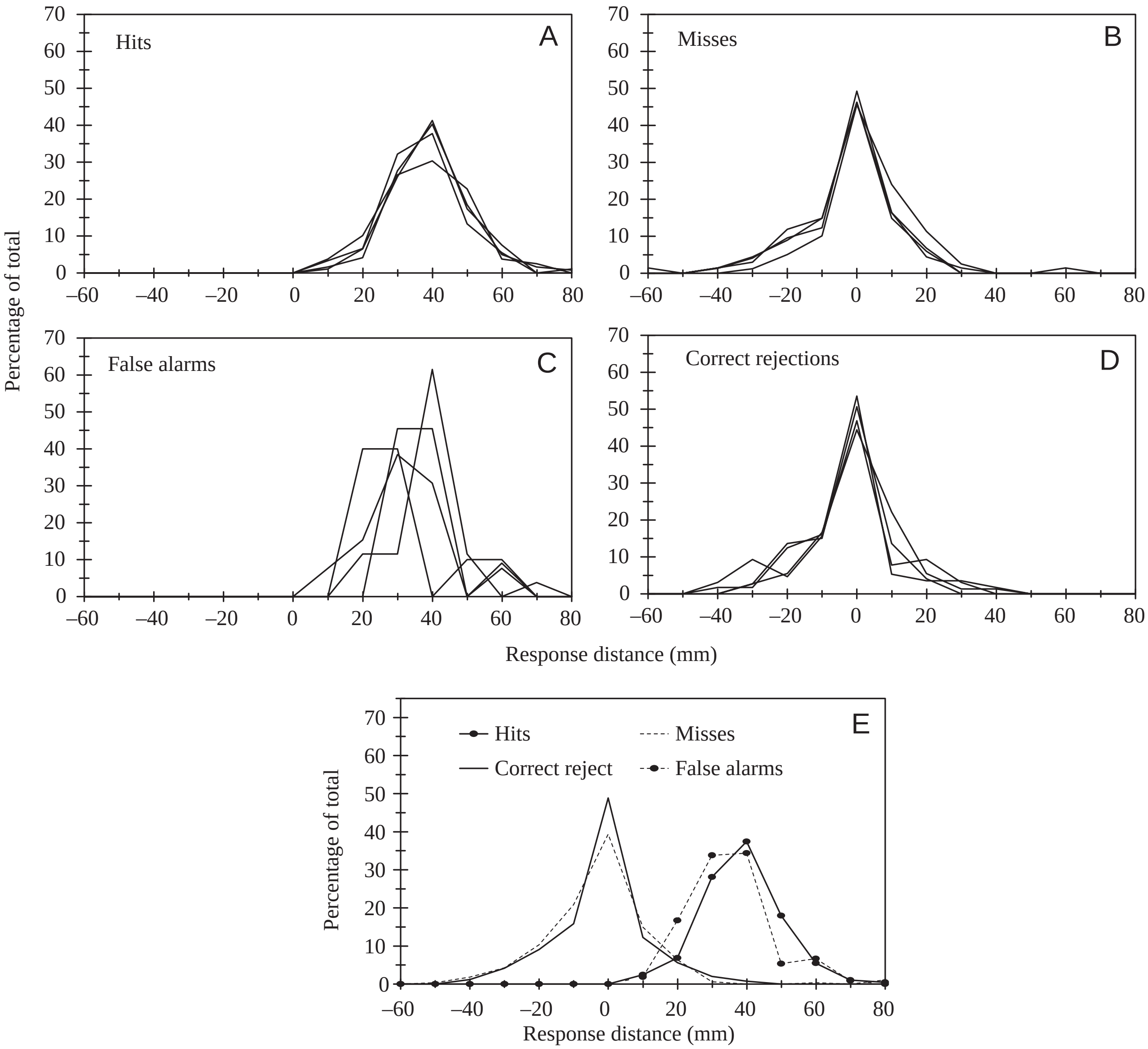

Fig. 5. Frequency distribution of response distances as in Fig. 4. Bin width=10 mm.

Table 2. P *values for Tukey's pair-wise tests of signal detection thresholds under normal conditions at different flow velocities (cm* s^{-1}*) for five individuals*

	Flow speed (cm s^{-1})					
	0 *versus* 2	0 *versus* 4	0 *versus* 8	2 *versus* 4	4 *versus* 8	2 *versus* 8
P	<0.05	<0.01	<0.001	NS	NS	<0.05

NS, not significant.

differences between flow and no-flow conditions were due to masking effects of the flow alone or to some other factor, such as vibrations passed through the impeller drive shaft to the water or the proclivity of sculpin to orient upstream rather than to the side of the tank towards the signal source.

Blank trials were run to determine the propensity of fish to respond in the direction of the source in the absence of any vibration signal. Although response (false alarm) rates to blank trials appear to be somewhat higher in the no-flow condition, they were not significantly different from false alarm rates at different flow rates (Fig. 6B) (RM ANOVA, $P>0.05$).

Motor noise controls were run to assess the possibility that

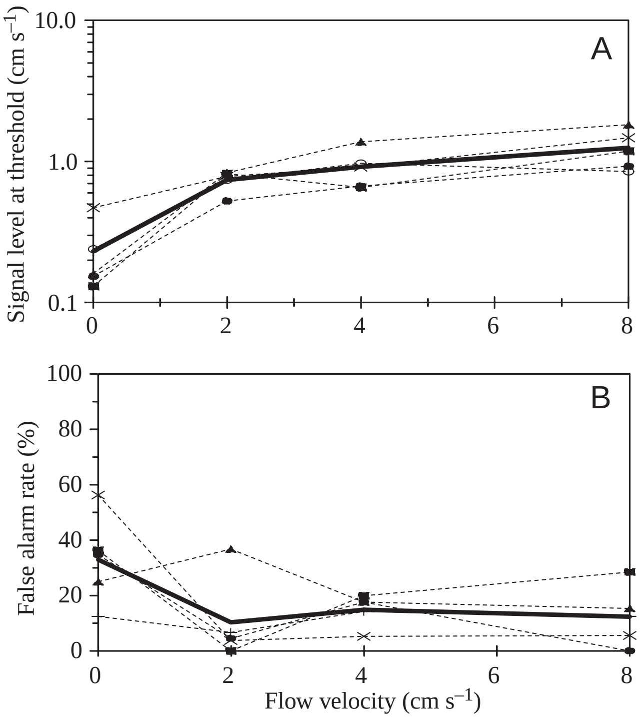

Fig. 6. Signal level (at the source) at threshold (A) and false alarm rates (B) as a function of flow velocity for 5 individuals (dashed lines with different symbols). Mean thresholds in A and false alarm rates in B for normal experimental conditions are plotted as heavy solid lines (N=5).

the motor and the mechanical assemblage (drive shaft plus impeller) may have caused acoustic or a.c. flow noise (in addition to the uniform d.c. flow noise) that interfered with the ability of sculpin to detect the signal vibrations. Two no-flow noise controls were run on three fish. The first control tested the potential masking effects of airborne motor noise alone (transmitted from the air to the water). In this case, the impeller and shaft were removed from the water to prevent flow and any mechanical linkage from the motor to the water through the shaft and impeller. The motor was then run at the speed that would have produced an 8 cm s^{-1} flow if the shaft and impeller had been in the water. Signal levels at threshold for this control condition were not significantly different from those measured in the normal setup with the motor turned off and the flow rate at 0 cm s^{-1} (RM ANOVA, P>0.05). Thus, airborne motor noise alone cannot account for threshold differences between flow and no-flow conditions.

For the second control, the flow-producing impeller blade was removed, but the drive shaft was left in place so that motor-driven vibrations could be directly transmitted to the water. The no-flow threshold was again measured for the highest (8 cm s^{-1} motor) speed and compared to thresholds in the absence of both flow and motor noise. In essence, we wanted to test the hypothesis that elevated levels of low frequency (2–30 Hz) energy produced by motor vibrations alone (Fig. 1B) might have contributed to some of the threshold differences between flow and no-flow conditions. Signal levels at threshold for this motor-on/flow-off control condition were significantly (P<0.01) greater than those obtained in the normal motor-off/flow-off condition, but only by a factor of 2.5 dB (approximately 1.3).

Discussion

In this study, we show that mottled sculpin are capable of a mechanosensory based, positive rheotactic response to low-velocity flows in the absence of visual cues and that, furthermore, the degree of rheotactic alignment with the oncoming flow increases as a function of increasing flow velocity (Figs 1, 2). Although we cannot say for certain whether the mechanosensory basis of this behavior was based on tactile, lateral line or auditory cues, theoretical considerations alone predict that the superficial neuromasts of the lateral line system were responsible, as these low-velocity flows did not cause the fish to be displaced relative to its surroundings. This idea is further supported by recent behavioral studies demonstrating a role of superficial neuromasts in mechanosensory-based rheotaxis to low velocity flows (<10 cm s^{-1}) in several different species (Montgomery et al., 1997; Baker and Montgomery, 1999a,b). Finally, given that rheotaxis at these flow rates is likely to depend on superficial neuromasts, the increase in rheotactic alignment with increasing flow velocity is understandable in light of recent physiological studies showing a firing-rate dependence of superficial neuromast fibers on flow velocity (Voigt et al., 2000).

Recent studies comparing the rheotactic behavior of lake populations with stream populations of mottled sculpin under identical test conditions have confirmed these results, but have also revealed that sculpin tend to spend more time near the sides of the flow tank than in the center (S. Coombs and G. D. Grossman, unpublished results). This behavior, which is most likely a part of the natural shelter-seeking behavior of these animals, occurs even in the absence of flow. Nevertheless, these results raise the possibility that sculpin may be aligning their bodies along the sides of the flow tank and that the orientation of the tank walls is an additional factor contributing to the orientation of the animal's body. Although we cannot completely exclude this possibility, we think it is unlikely to play a significant role, for the following reasons. (1) The random distributions of fish headings in the absence of flow (Fig. 2A) provide compelling evidence that fish orientations are not constrained or biased by the tank size or shape; indeed, the area of the test arena (approximately 2×2.75 fish *BL*) is more than adequate for orientations in any direction. (2) If body orientation were entrained solely by the sides of the tank, we would expect that (i) orientation distributions would be bimodal – half in the upstream and half in the downstream direction – rather than random (no-flow conditions) or unimodal (flow conditions) and (ii) the vector strengths of the distributions would be independent of flow velocity. In summary, the most parsimonious explanation for the results in their entirety is that sculpin exhibit positive rheotaxis to uniform flows.

We further show that sculpin, when oriented upstream, can detect and orient towards relatively weak (approximately 0.001–0.0001 cm s^{-1} at the fish) prey-like signals in the presence of strong (up to 8 cm s^{-1}), background uniform flows. When flow is present, the ability of sculpin to detect the prey-like signal is largely independent of flow velocity, with signal levels at threshold increasing by less than twofold for a fourfold increase in flow velocity (Fig. 5A, Tables 1, 2). In the absence of flow, however, signal levels at threshold are two- to fourfold less than those in the presence of flow (Fig. 5A, Tables 1, 2). Displacement thresholds for the no-flow condition (approximately 10^{-9} m at the fish) are in the same low range as those reported earlier for the lateral line and other hair cell systems (reviewed by Kroese and van Netten, 1989), including those obtained from the mottled sculpin over a decade ago using similar behavioral techniques (Coombs and Janssen, 1990). Threshold results for ambient flow conditions can probably best be understood in terms of the high-pass filtering properties of lateral line canals and a number of different factors that contribute to sensitivity differences between flow and no-flow conditions.

High-pass filtering by lateral line canals

The exquisite sensitivity of sculpin to weak a.c. signals in the presence of strong d.c. flows and the absence of appreciable threshold shifts to increasing flow velocity are consistent with the idea that fish are using the high-pass filtering characteristics of lateral line canals to optimize signal-to-noise ratios for detection tasks involving high-frequency a.c. signals. This idea is further supported by recent physiological results showing that the amplitude-dependent spike rate and phase-locking responses of putative canal neuromast fibers, in goldfish to a 50 Hz dipole source are not significantly degraded in the presence of a 10 cm s^{-1} flow (Engelmann et al., 2001, 2002). When tuning curves from acceleration-sensitive lateral line fibers in the mottled sculpin are plotted as a function of velocity, the low frequency leg of the tuning curve has a slope of –6 dB octave^{-1} (Coombs and Janssen, 1990), as would be expected for canal neuromast fibers, and as has been modeled for simple, straight-sided tubes (Denton and Gray, 1988, 1989). Thus, the lateral line canal is not a very steep filter, and while it may be quite effective in filtering out 0 Hz energy (DC flows), it becomes much less effective as frequency increases. As such, the upward spread of low-frequency (<50 Hz) energy associated with increasing flow velocities (Fig. 1A) may contribute to the elevated thresholds. This explanation is certainly consistent with the decrease in prey-detection distances observed for torrentfish when flow velocities are increased from 10 to 100 cm s^{-1} (Milton and Montgomery, 1993). This upward spread of energy is most likely associated with small scale turbulence produced at the higher flow velocities (Coombs et al., 2001a).

Although the ability of mottled sculpin to detect low-level a.c. signals in the presence of strong d.c. flows is undoubtedly enhanced by the filtering abilities of lateral line canals, it is conceivable that the temporal and/or spatial perturbations caused by the signal in the ongoing flow also contributes to this ability.

Threshold shifts between flow and no-flow conditions

Although the shallow, low-frequency slopes of lateral line canal filters and the upward spread of low frequency energy might explain the modest (<twofold) decrease in threshold sensitivity with a fourfold increase in flow velocity, the two- to fourfold shift in threshold sensitivity between flow and no-flow conditions requires further explanation. One possibility is that elevated thresholds in the presence of flow are due to factors other than the masking effects of flow noise alone, such as the propensity of sculpin to orient upstream rather than in the sidewards direction of the signal source, the presence of artifactual noises (e.g. those produced by the motor-shaft assembly used to generate the flow), and/or alterations in the stimulus field due to complex interactions between the fish's body and the surrounding flow field.

Control conditions, in which the drive shaft (minus its flow-inducing impeller) was driven at the highest motor speed, produced a small elevation in mean threshold above that measured in the normal, no-flow (motor-off) condition. This effect, however, can account for only 10–20% of the total threshold shift, leaving 80% of the difference unaccounted for. Upstream response biases are also unlikely to account for much of the difference. Three lines of evidence argue against them. (1) False alarm rates in the no-flow condition were not significantly higher than those for various flow conditions, as would be expected if sculpin turned to the side more frequently when freed from their 'compulsion' to orient in a forward (upstream) direction. (2) Previous studies have shown that in the absence of flow, sculpin are much more likely to make spontaneous movements in a forward rather than lateral direction (Coombs, 1999). (3) Threshold levels do not increase linearly with flow velocity, as would be expected if upstream orienting biases were a major controlling factor. That is, for a twofold increase in flow velocity (from 4 to 8 cm s^{-1}), the mean vector strength of the rheotactic response doubled, but the mean threshold signal level increased by a factor of only 1.3.

Another confounding factor, impossible to control for but important to understand, is the possibility that when flow is present, the fish's body alters the flow field to the lateral line system in such a way that a new type of a.c. noise interference is created, or the effective a.c. signal level at the fish is attenuated above and beyond what it would be in the absence of the fish. Digital particle image velocimetry (DPIV) has recently been used to determine how 2–8 cm s^{-1} flow fields are altered in the vicinity of the sculpin's body (Coombs et al., 2001a). The results from this study show that fish body parts can significantly alter the local hydrodynamic stimulus field to the lateral line relative to ambient water motions only a few cm away. In particular, flow around the large, extended pectoral fin of the mottled sculpin showed separation at the edge of the fin and a trailing wake, similar to that observed for a flat plate perpendicular to the flow. The high frequency energy in the turbulent wake may have thus introduced an additional noise masker to the detection task.

Finally, it is conceivable that reduced sensitivity in the flow condition is due to a drop in the available energy at the second harmonic (100 Hz). Our anemometer measurements show that while the amplitude of the fundamental frequency varied by no more than 2 dB across all conditions, the amplitude of the second harmonic was about 8 dB less for all flow conditions than for the no-flow conditions (Fig. 1A). Because there was no reduction in the second harmonic for different motor speeds in the absence of impeller-driven flow (Fig. 1B), we can be fairly certain that the reduction in the second harmonic is somehow caused by the flow. Behavioral and physiological measures of threshold sensitivity in the absence of flow show that mottled sculpin are equally sensitive to 50 and 100 Hz dipole signals (Coombs and Janssen, 1990), making the detection and use of energy at the second harmonic plausible if not likely.

In summary, motor driven vibrations of the impeller shaft can account for only a small percentage of the threshold difference between flow and no-flow conditions. A number of other, inter-related factors are likely to make up the remaining difference. These include less energy at the second harmonic for the flow conditions, the upward spread of low-frequency energy associated with increasing flow velocities, and additional noise interference (e.g. shed wakes) created by the interaction between the fish's body and the flow field.

Prey-orienting and current-orienting (rheotactic) behaviors

Both rheotactic and prey-orienting behaviors are naturally occurring, unconditioned behaviors exhibited by many different fish species, including the Lake Michigan mottled sculpin. These behaviors may be inexorably linked, in that the ability to orient upstream is thought to play an important role in the feeding behavior of many fluvial species. Trout, for example, presumably orient upstream to be in the best position to intercept downstream drifting prey. Station holding behaviors in which fish position themselves upstream in current–velocity shelters may also enable fish like trout to hold low-velocity positions adjacent to a high-velocity region, providing them with an abundance of invertebrate drift (Everest and Chapman, 1972; Fausch, 1993). Finally, many animals use a combination of odor-conditioned rheotaxis and chemotaxis to localize food odor sources (Weissburg, 2000; Weissburg and Zimmer-Faust, 1993, 1994; Montgomery et al., 1999). Although it is not known whether Lake Michigan mottled sculpin use rheotactic behavior to detect and localize prey, other similar, non-fluvial, benthic species, such as the antarctic fish, *Trematomus bernachii*, appear to approach prey using a combination of rheosensory and chemosensory information (Montgomery et al., 1999). In any event, currents and flows created by seiches, wind effects and temperature-related mixing are certainly present in lake ecosystems (Goldman and Horne, 1983). Moreover, given that sculpin feed at night when vision is limited (Hoekstra and Janssen, 1985), it is likely that sculpin rely heavily on their non-visual sensory systems. It is reasonable to expect that sculpin may use a combination of different strategies, depending on factors such as current conditions, prey type and prey availability. As a consequence, lake currents may function as both a noise interference for mechanosensory-based detection of moving prey and as a signal for rheosensory-based enhancement of odor source detection and localization. The ability of fish to simultaneously take in and filter out ambient water motions is made possible by two lateral line subsystems – one that passes and processes uniform flow as a behaviorally relevant signal (superficial neuromast system), and one that filters out uniform flow as an interference noise (canal neuromast system). In this regard, it is interesting to note that the uniform flow in these experiments elicited an orienting behavior in the upstream direction of the tank, but that the prey-like source elicited an orienting behavior *away* from the upstream direction and towards the source. Thus, the orientating response to the prey source is clearly capable of overriding the rheotactic response to bulk flow, even at the highest flow velocity tested.

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