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Hydrodynamic image formation by the peripheral lateral line system of the Lake Michigan mottled sculpin, *Cottus bairdi*

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Lake Michigan mottled sculpin (*Cottus bairdi*) have a lateral-line-mediated prey-capture behaviour that consists of an initial orientation towards the prey, a sequence of approach movements, and a final strike at the prey. This unconditioned behaviour can be elicited from blinded sculpin in the laboratory by both real and artificial (vibrating sphere) prey. In order to visualize what Lake Michigan mottled sculpin might perceive through their lateral line when approaching prey, we have combined anatomical, neurophysiological, behavioural and computational modelling techniques to produce three-dimensional maps of how excitation patterns along the lateral line sensory surface change as sculpin approach a vibrating sphere. Changes in the excitation patterns and the information they contain about source location are consistent with behavioural performance, including the approach pathways taken by sculpin to the sphere, the maximum distances at which approaches can be elicited, distances from which strikes are launched, and strike success. Information content is generally higher for laterally located sources than for frontally located sources and this may explain exceptional performance (e.g. successful strikes from unusually long distances) in response to lateral sources and poor performance (e.g. unsuccessful strikes) to frontal sources.

Keywords: lateral line; localization; feeding behaviour; prey detection

1. INTRODUCTION

The lateral line system is one of the most primitive, but perhaps least understood of all vertebrate sensory systems, especially given that its general function as a water-current detector has been known for close to a century (Hofer 1908). One of the biggest impediments to understanding how this spatially distributed system works is the inherent difficulty in adequately specifying and measuring hydrodynamic stimuli, which can vary in frequency, amplitude and phase along the sensory surface of the animal. Even the simplest of sources—a sinusoidally vibrating sphere, for example—can produce a rather complex stimulus field. Furthermore, the peripheral excitation pattern that results after the stimulus field has been transduced can be even more complex and depends on a number of factors, including the number, type and spatial distribution of lateral line end organs on the fish, the axis of source vibration, and the distance and orientation of the fish with respect to the source (Denton & Gray 1983; Coombs *et al*. 1996).

For the last few years, we have been interested in the question of what fish actually perceive through their lateral line system. Although it may prove impossible to determine the ultimate percept, we can model 'hydrodynamic images' at the level of the peripheral nervous system and use these models to determine how information about stimulus sources (e.g. location, size, shape, etc.) might be conveyed to the central nervous system. Towards that end, we have used a combination of anatomical, physiological, behavioural and computational approaches to determine (i) the three-dimensional stimulus field about a dipole source (vibrating sphere); (ii) how this field is represented in the activity of peripheral nerve fibres innervating different end organs at different locations within the field; and (iii) how excitation patterns across fibres change as fish approach dipole sources in the biologically relevant context of feeding behaviour (Coombs *et al*. 1996; Coombs & Conley 1997*a*,*b*; Conley & Coombs 1998). The purpose of this paper is to review briefly this multi-dimensional approach and its underlying assumptions, to summarize some of the key findings and testable predictions arising from this approach, and to report some new modelling results, using the latest iteration of our computational model to provide an anatomically correct, three-dimensional model of excitation patterns over the entire lateral line sensory surface of the fish.

One of the keys to the success of this overall strategy is the prey-capture behaviour of Lake Michigan mottled sculpin (*Cottus bairdi*). After responding with an initial orientating response at the time of prey detection, these benthic sculpin approach their prey along the substrate in a saltatory fashion, stopping for several seconds after each

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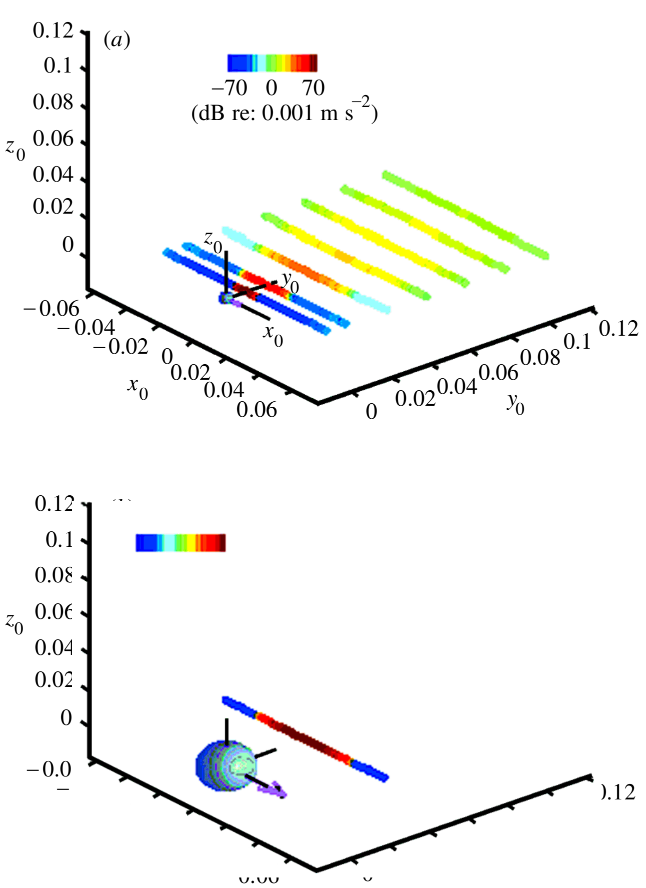

Figure 1. Lateral line excitation patterns as a function of source distance (*a*) and source size (*b*). In (*a*), excitation patterns are modelled along a theoretical linear array of lateral line canal neuromasts spanning the length (100 mm) of a mottled sculpin from head to tail. The array is placed at 10, 20, 40, 60, 80, 100, and 120 mm away from a 50 Hz dipole source, 6 mm in diameter and with a 1 m s^{-1} source velocity. The arrow indicates the axis of source vibration. In (*b*), the excitation pattern is modelled for a source of the same frequency and velocity, but four times the diameter at a distance of 40 mm. In both (*a*) and (*b*), local accelerations (pressure-difference amplitudes) of the surrounding water were computed over 2 mm intervals, the average interpore spacing on the trunk canal of the mottled sculpin. Pressure-difference directions along the long axis of the canal are represented by opposite ends of the spectrum, with positive pressure differences (flow in one direction) at the red end of the spectrum and negative differences (flow in the opposite direction) at the blue end. Thus, saturated colours at either end of the spectrum represent equal amplitudes, but opposite directions. Green is in the middle at zero and represents pressure-difference amplitudes at or below measured estimates of threshold sensitivity (0.002 Pa/2 mm or 0.001 m s^{-2}) for individual posterior lateral line nerve fibres. Axes x, y and z are scaled in units of metres.

movement until they are close enough to launch their final strike (Hoekstra & Janssen 1985). In visually deprived animals, the initial orientating and approach behaviour requires the lateral line (Hoekstra & Janssen 1985; Coombs & Conley 1997*a*; Braun & Coombs, this issue) and relies heavily, if not exclusively, on canal, rather than superficial neuromasts (S. Coombs, C. B. Braun and B. Donovan, unpublished data). Fortunately for us, the prey-capture behaviour can be elicited in the

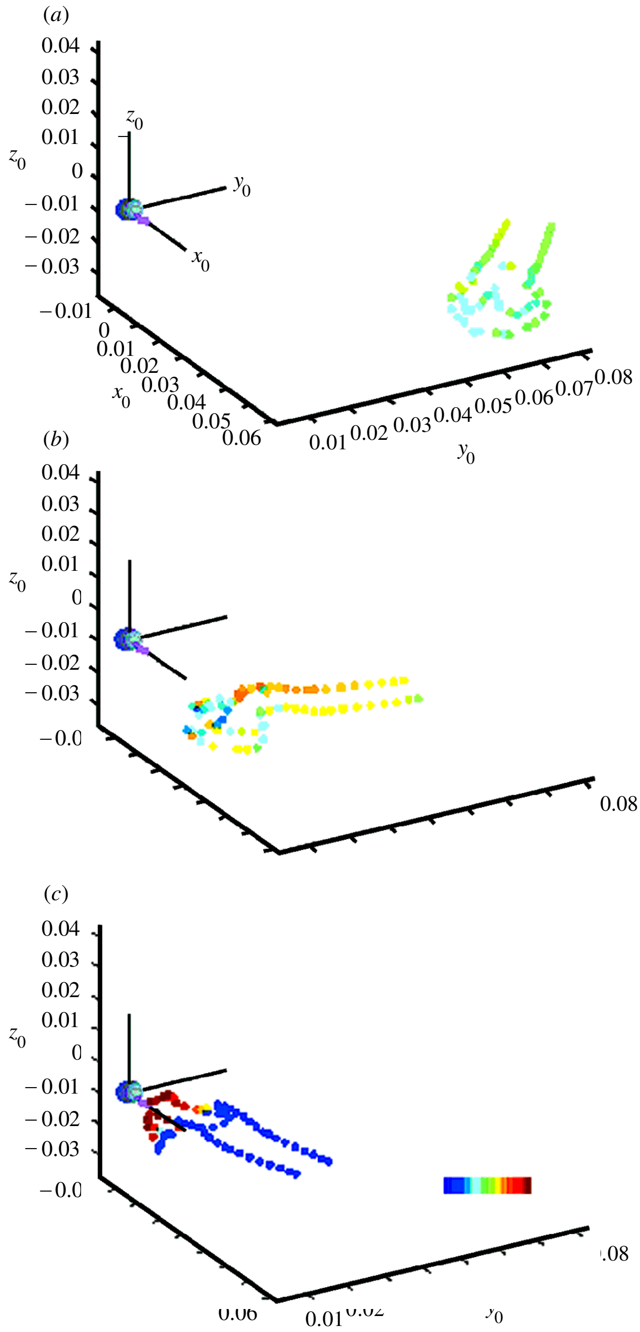

Figure 2. Illustration of how lateral line excitation patterns along the head and body of a mottled sculpin change during an actual prey-capture event, from the time of signal onset (*a*) to the time of strike (*c*). Each coloured dot represents the excitatory input (see figure for explanation of colour code) to different neuromasts housed in one of five canals on the head (supra- and infraorbital canals above and below the eye, the preopercular canal along the cheek, the mandibular canal along the lower jaw, the temporal canal across the top of the head) or in the trunk canal along the body. Neuromasts in all canals are most easily seen in (*a*), which affords a frontal view of the fish. The position of the fish relative to the source was mapped in Cartesian coordinates from a digitized video image of the fish at each step in the pathway and, likewise, the Cartesian coordinates of each canal pore relative to the tip of the fish's snout were determined by using an ocular micrometer on a stereomicroscope.

laboratory from blinded animals with a chemically inert, artificial prey source—a bite-size (6 mm in diameter), vibrating sphere. This has made it possible for us to drive the behaviour with mechanosensory cues alone, to use the same stimulus source in physiological and behavioural experiments, and to use a set of dipole field equations for characterizing the stimulus field and for modelling excitation patterns along lateral line canal neuromasts.

2. ASSUMPTIONS AND VALIDITY OF THE MODELLING APPROACH

Static models of lateral line excitation patterns are computed at the time of maximum sphere excursion and are based on several simplifying assumptions, including (i) that the stimulus field is ideal and unbounded (i.e. tank walls and fish's body have no effect on the stimulus field); (ii) the quantities ka and kr are both much less than 1, where k is the acoustic wave number ($k = w/c$, where c is sound speed and w is circular frequency), a is the source radius, and r is the distance from the source; (iii) there is a single sensory organ (neuromast) between every two pores on any given lateral line canal; and (iv) the response of each neuromast to fluid motions inside the canal is proportional to the outside pressure difference between the two pores, which is also proportional to the acceleration of the surrounding water (Denton & Gray 1983).

The newest version of the model computes the final stimulus to each canal neuromast as the difference between the acceleration of the fish's body and the local accelerations of the surrounding water at the location of the neuromast. Euler's equation and the average pressure along the top/bottom, rostral/caudal and left/right sides of the fish's body are used to determine the whole-body accelerations of the fish, which is treated as a rigid cylinder of approximately the same dimensions (20 mm × 15 100 mm) and density (1072 kg m^{-3}) as the mottled sculpin. Local accelerations of the surrounding water are likewise determined from Euler's equation and the pressure difference between canal pores.

To test the validity of some these assumptions, we used physiological techniques to compare response patterns of single peripheral lateral line nerve fibres to our modelled predictions. In essence, we used the fish and individual posterior lateral line nerve fibres innervating the trunk canal as our stimulus measurement device, so that both the fish's presence and the presence of experimental tank walls were automatically taken into account. Rather than taking the technically difficult approach of simultaneously recording responses from an array of fibres innervating canal neuromasts at different locations along the canal to a fixed source location, we reversed the frame of reference. That is, we recorded the response of a single fibre innervating a single neuromast at a fixed location to a dipole source that slowly changed its location along the length of the canal. The results from this experimental approach revealed that neural responses from many different fibres in both goldfish and sculpin followed both pressure-difference amplitude and direction (phase) predictions of the model rather faithfully, despite the presence of the fish and surrounding tank walls (Coombs *et al.* 1996; Coombs & Conley 1997*b*). These physiological demonstrations give us confidence that our model, while still crude and assumption limited, is a reasonable first approximation of peripheral lateral line excitation patterns under controlled experimental conditions.

3. INFORMATION ENCODING BY LATERAL LINE EXCITATION PATTERNS

Newly modelled excitation patterns for a linear array of canal neuromasts at different distances from the source are quite similar to older models (e.g. Coombs *et al.* 1996) in showing that information about source azimuth is contained in the location of the maximum pressure-difference amplitude, whereas information about source distance is contained in the spread of excitation (figure 1*a*). Thus, unlike visual images, which get smaller as the source gets further away, hydrodynamic images get larger, as do electrosensory images (von der Emde *et al.* 1998). This relatively unusual distance cue is theoretically robust and unambiguous; that is, if source amplitude or size is increased at a given distance, the level but not the spread of excitation increases (e.g. compare the excitation pattern for a small source 4 cm away in figure 1*a* with that of a large source at the same distance in figure 1*b*). Thus, even though peak excitation levels may be the same for a distant, high-amplitude (or large) source and a nearby, low-amplitude (or small) source, there is sufficient information in the spread of excitation to distinguish between the two (e.g. compare the excitation pattern for a large source 4 cm away in figure 1*b* with that for a smaller source 1 cm away in figure 1*a*).

4. UNDERSTANDING AND PREDICTING BEHAVIOUR

By setting model parameters (e.g. fish length, interpore distances, threshold levels of excitation for peripheral lateral line nerve fibres, etc.—see figure 1 legend) to empirically determined values for the mottled sculpin, it also becomes possible to understand behavioural performance in terms of excitation patterns. For example, the maximum distance at which the unconditioned orientating response of the mottled sculpin can be reliably evoked from a given dipole source (that modelled in figure 1*a*) has been measured to be *ca.* 11–12 cm (Coombs 1999; Braun & Coombs, this issue). At these distances, excitation levels range from physiologically measured threshold levels (0.002 Pa/2 mm) at the head and tail to approximately twice the physiological threshold at mid-body locations. Relative to excitation patterns modelled for closer source locations, where peak excitation levels are several orders of magnitude above the threshold, the excitation pattern at this threshold distance is relatively flat (figure 1*a*). Changes in excitation patterns as a function of source distance also predict that information about source location, and therefore the ability of sculpin to pinpoint the exact location of the source, will get increasingly better at shorter distances. Not only do regions of maximum excitation become narrower and more steeply sloped, but also the delineation of these regions at distances less than *ca.* 6 cm is even further enhanced by surrounding regions of excitation in the opposite direction. The fact that over 90% of all successful strikes are made from distances less than 4 cm, with the mean strike distance just under 2 cm (Coombs & Conley 1997*a*), certainly supports the idea that information about source location is best at these close distances.

To determine if other aspects of prey-capture behaviour could be explained on the basis of peripheral excitation patterns, we videotaped the approach behaviour of mottled sculpin for different starting distances and orientations in over 400 trials (Coombs & Conley 1997*a*). Approach pathways depended largely on the initial starting position. Fish pointing towards the source at the time of signal onset tended to approach the source indirectly—either in an arching pattern in which the fish kept the source to one side of its body or in a zigzag fashion in which the fish alternated between keeping the source to the left and right sides of its body. When the source was at the fish's side at signal onset, however, approach pathways tended to be more direct and involved fewer steps (figure 2). In a few of these cases, the initial orientating response was also the final strike response, and of these successful long-distance strikes (greater than one standard deviation above the mean strike distance), 75% were elicited by laterally located sources (e.g. figure 2*b*). In contrast, 83% of unsuccessful strikes (within the mean strike distance) were associated with frontally located sources.

5. UNILATERAL PROCESSING

The general orientating and approach strategies of the mottled sculpin—one step and one side at a time—are consistent with the idea that sculpin are able to extract information about both source distance and azimuth from excitation patterns along a single unilateral sensory surface. This idea is further supported by experiments in which unilateral denervations of specific regions (e.g. head versus trunk) of the lateral line caused site-specific deficits corresponding to the region of denervation, but did not otherwise interfere with the sculpin's ability to localize sources on the intact side or near the intact regions of the denervated side (Conley & Coombs 1998). Examples of poor performance (misses) for frontal sources also suggest that sensory representations on the left and right side of the animal may not be integrated centrally to form frontal images of sensory space, although it is also possible that peripheral morphology (e.g. frontal blind spot) may contribute to this poor performance. So, unlike the vertebrate visual system, which uses both eyes to provide depth of field, or the auditory system of terrestrial vertebrates, which computes source azimuth from time and/or intensity differences at the two ears, the lateral line system theoretically determines both azimuth and distance from a single unilateral sensory surface.

Indirect approach pathways, poor performance (misses) for frontal sources, and exceptional performance ('far' strikes and direct paths) for lateral sources, all indicate that it is advantageous for fish to expose their lateral sensory surfaces to the source. On theoretical grounds, a lateral exposure would confer at least two advantages, maximizing (i) the amount and breadth of stimulus field information that could be represented on a given side of the fish by virtue of the fact that the majority of lateral line organs, as the name suggests, are located on the sides of the animal's body, and (ii) the potential use of a three-dimensional sampling system that includes the rostrocaudally orientated trunk and supraorbital canals, the dorsoventrally orientated preopercular canal and the lateromedially orientated temporal canal—all of which converge at approximately the same location on the side of the fish's head. In this regard, it is interesting to note that weakly electric black ghost knifefish tend to approach their prey with the dorsal surface of the fish forming the leading edge as the fish moves through the water (Nelson & Maciver 1999). Leading with the dorsal edge is thought to have several advantages, including optimizing the exposure of dorsally situated electrosensory receptors, which are two to three times more dense on the dorsal surface than on ventral or lateral surfaces. Thus, active positioning of receptor surfaces, whether they are dorsal in the case of the electrosensory system of the black ghost knifefish, or lateral in the case of the lateral line system of the mottled sculpin, may help animals optimize the information content of incoming signals.

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