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The overlapping roles of the inner ear and lateral line: the active space of dipole source detection

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The problems associated with the detection of sounds and other mechanical disturbances in the aquatic environment differ greatly from those associated with airborne sounds. The differences are primarily due to the incompressibility of water and the corresponding increase in importance of the acoustic near field. The near field, or hydrodynamic field, is characterized by steep spatial gradients in pressure, and detection of the accelerations associated with these gradients is performed by both the inner ear and the lateral line systems of fishes. Acceleration-sensitive otolithic organs are present in all fishes and provide these animals with a form of inertial audition. The detection of pressure gradients, by both the lateral line and inner ear, is the taxonomically most widespread mechanism of sound-source detection amongst vertebrates, and is thus the most likely primitive mode of detecting sound sources. Surprisingly, little is known about the capabilities of either the lateral line or the otolithic endorgan in the detection of vibratory dipole sources. Theoretical considerations for the overlapping roles of the inner ear and lateral line systems in midwater predict that the lateral line will operate over a shorter distance range than the inner ear, although with a much greater spatial resolution. Our empirical results of dipole detection by mottled sculpin, a benthic fish, do not agree with theoretical predictions based on midwater fishes, in that the distance ranges of the two systems appear to be approximately equal. This is almost certainly as a result of physical coupling between the fishes and the substrate. Thus, rather than having a greater active range, the inner ear appears to have a reduced distance range in benthic fishes, and the lateral line distance range may be concomitantly extended.

Keywords: hearing; mechanosensory; auditory; multisensory

1. SOUND DETECTION UNDERWATER: THE PRIMACY OF THE NEAR FIELD

The mechanisms of sound perception by aquatic organisms are often difficult to appreciate fully since the nature of sound and sound sources can be so different in air and in water. We commonly define sound as a propagating wave of compressions and rarefactions of the conducting medium, but this pressure wave is only one portion of the stimulus field surrounding a vibratory source. If the medium is relatively incompressible, as water is, then other aspects of the stimulus field ascend in importance. Any mechanical disturbance, such as the vibrations of an appendage, the burrowing or swimming motions of animals and communicatory stridulations or vocalizations, will generate a steep gradient in pressure close to the source, whether or not they actually give rise to the propagating pressure wave we commonly label 'sound'. Given the incompressibility of water, this steep gradient in pressure will give rise to a net flow of water. Close to the source, this bulk water flow will eclipse the magnitude of the oscillatory compressions and rarefactions (particle motions) that make up the propagating pressure wave. Thus for many, particularly low frequency, sources, this

acoustic near field is of utmost biological importance. Detection of the particle accelerations associated with these pressure gradients is almost certainly the primitive mode of vertebrate hearing (Kalmijn 1989) and remains the most taxonomically widespread. These steep gradients in pressure surrounding a hydrodynamic source are also detected by the lateral line system. Both the lateral line and the inner ear, then, are responsive to many of the same stimulus fields. In order to understand the function of either system, or the primitive mode of sound detection generally, it is imperative to move beyond speculative evolutionary considerations of the relationship between auditory and lateral line systems and actually begin to investigate the overlap in the functions of these two systems that detect different aspects of the same sources.

We have been investigating the relative contributions of both sensory systems to the detection and analysis of vibratory dipole sources by the Lake Michigan mottled sculpin (*Cottus bairdi*), a benthic fish that uses sound and vibration to detect prey, particularly in the absence of visual cues (Hoekstra & Janssen 1985). Cottids in general lack a swimbladder and are apparently insensitive to pressure *per se* but have a typical complement of otolithic endorgans, and could use inertial audition to detect sound sources. Mottled sculpin have a lateral line that is typical of Scorpaeniformes, with simple canals on the surface of

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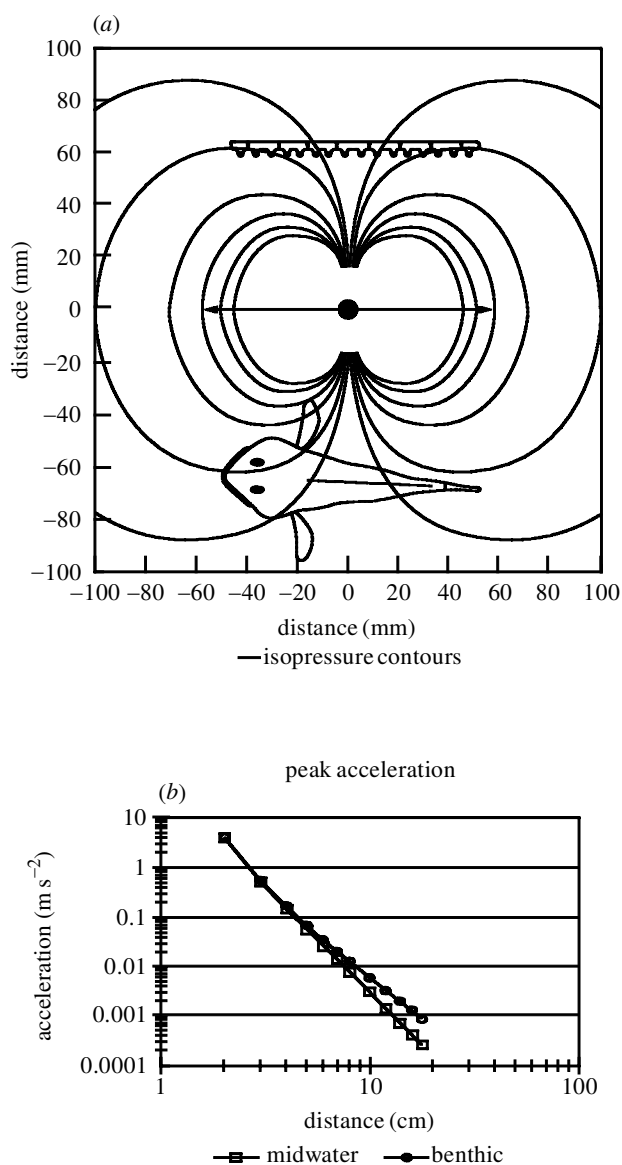


Figure 1. (a) Illustration of the difference in sampling scale between the lateral line system and the inner ear. The lateral line (at the top of the field), with multiple closely spaced sampling points, requires a steep spatial gradient to achieve stimulation, but is capable of resolving that gradient in fine spatial detail. The auditory system of a sculpin may respond to a similar pressure gradient, but by integrating the differences in pressure along opposing sides of the entire body (note the difference in scale of a fish body, bottom, and any single canal segment, above). The inertial sensors of the inner ear are thus incapable of resolving the fine spatial detail of the stimulus field. Isopressure contours were modelled after dipole flow field equations (Kalmijn 1988). (b) Modelled accelerations of the canal fluid in response to a vibrating dipole. The peak acceleration along a linear canal positioned at a range of distances from an orthogonally vibrating source (as in the behavioural experiments discussed in the text) is plotted as a function of source distance. The open squares represent the net accelerations of canal fluids in a midwater, neutrally buoyant fish. The open circles represent the accelerations of canal fluids in a benthic fish that does not move at all as a result of the imposed sound field. Note the difference in the slopes of the two functions.

the head and a single trunk canal. A small number of superficial neuromasts are also present paralleling the main canals and in independent lines on the head and tail (Janssen *et al.* 1987). Several lines of evidence indicate that the superficial neuromasts play a negligible role in dipole source detection (Coombs & Braun 2000), so we will restrict the present discussion to canal neuromasts. Our experiments have focused on the distance range of the lateral line and the inner ear in an attempt to define an active space within which each system operates. Only then can we begin to address questions of spatial or temporal resolution of hydrodynamic source localization and perception.

Before turning to our behavioural data, it is necessary to explore the roles each sensory system might theoretically play in the detection of the pressure gradients. Although both the lateral line and otolithic organs are responsive to the same stimulus fields, the mechanisms of transduction and thus the type of information extracted differ greatly. Accelerations of the water surrounding a vibratory source are efficiently transmitted to a nearby fish due to the similarity in density of the fish and the surrounding water. The otoliths, having a greater density, will lag behind the motions of the fish, providing the animal with three-dimensional cues to the motions of its own body (Fay 1984). This inertial form of audition will be particularly important within the acoustic near field, where bulk flow predominates, but it may also be of importance within the intermediate or far field, allowing the animal to detect the particle displacements that make up the propagating pressure wave (Kalmijn 1988). Close to the source, the steep gradients of pressure will give rise to highly non-uniform patterns of water flow. The spatially distributed accelerometers of the lateral line system are well suited to resolving the fine spatial organization of these pressure gradients. In principle, the accelerations imparted to the lateral line canal fluid are similar to those imparted to the fish itself. In the case of the fish, pressure differences between opposing sides of the body give rise to accelerations of the whole body. In the case of the lateral line system, pressure differences between adjacent canal pores give rise to accelerations of the fluid within that canal segment. This difference in the size of the sampling interval (whole fish versus single canal segment) and sample numbers (single body versus multiple canal segments) predicts that within threshold distances of the lateral line system, the lateral line will always provide a greater spatial resolution of the stimulus field than the inner ear. This enhanced spatial resolution may allow both a more detailed analysis of both the spatial configuration of the field and the precise location of the source by the lateral line system (figure 1*a*). To date there have been no studies that directly examine the spatial resolution of either the lateral line or inertial auditory systems.

In addition to this difference in sampling resolution, we must consider the difference in the mode of transduction of the stimulus field by the lateral line system and the inner ear. The inertial sensors of the inner ear detect a near field stimulus by measuring the motion imposed on the fish itself. The lateral line, on the other hand, measures the motion imposed on the canal fluids. If these canals are themselves moving, the resulting motion

within the canal is the result of the difference between the pressure difference at the two pores and the motion of the canal itself, i.e. motion within the canals is proportional to the difference in the motion of water outside that canal and the motion of the canal itself (Denton & Gray 1983). The motion of the fish therefore effectively reduces the magnitude of fluid motion within the canal. The degree of reduction will depend on the relationship between the orientation of the fish's motion and the orientation of the canals. Additionally, the decrease in lateral line stimulation will increase with increasing source distance (figure 1*b*). While the water motions outside the fish will attenuate as the reciprocal of the distance cubed, the net water motions in the canals of a fish displaced by a sound field will, in the most extreme case modelled by Denton & Gray (1983), actually attenuate as the reciprocal of the distance to the fourth power. Furthermore, Denton & Gray (1983) argue that when the distance to the source is great relative to the length of the fish, the motions of the water will be very similar in magnitude along the entire length of the fish, effectively eliminating any lateral line stimulation. They and many other subsequent workers have therefore suggested that the distance range of both the lateral line and the inner ear are related to the body length of the fish, but with differing relationships. Accordingly, the inertial sensors of the inner ear may be responsive to distances in the order of several body lengths but the lateral line would be limited to one or two times the body length at most, even for relatively intense sources.

2. EXPERIMENTAL PROCEDURES

We have used two behavioural approaches to explore the ability of mottled sculpin to detect a vibrating bead. Given the theoretical considerations outlined above in §1, and the many statements in the literature that the inner ear has a greater distance range than the lateral line, we chose to determine empirically the distance range for both systems using a fixed intensity dipole source presented to the fishes at a range of distances. What is the maximum detectable distance of this source by the lateral line and inner ear? In all experiments, our source was a vibrating bead (6 mm diameter), sinusoidally driven by a minishaker with a displacement of 3 mm, accelerating 300 m s^{-2} at 50 Hz. The axis of vibration was always parallel to the long axis of the fishes, and the bead was located along a transect originating at the centre of mass of the fishes (at the level of the pelvic fin) and forming a right angle to the long axis of the fishes. All experiments were performed either on enucleated animals or in darkness. All procedures conformed to the Loyola University Institutional Animal Care and Use Committee guidelines.

Naive mottled sculpin will orientate to, approach, and eventually strike at a vibrating bead with high frequency. We used the first component of this innate behaviour as a measure of source detection in blinded animals. Briefly, animals were placed in a large behavioural arena and videotaped from below. We analysed the distribution of the change in angle of the fishes relative to the source (after the first response) during trials when a signal was present and when a signal was absent over a range of source distances (2–20 cm).

We also used classical conditioning to determine the detectability of the same source in a similar configuration. In this

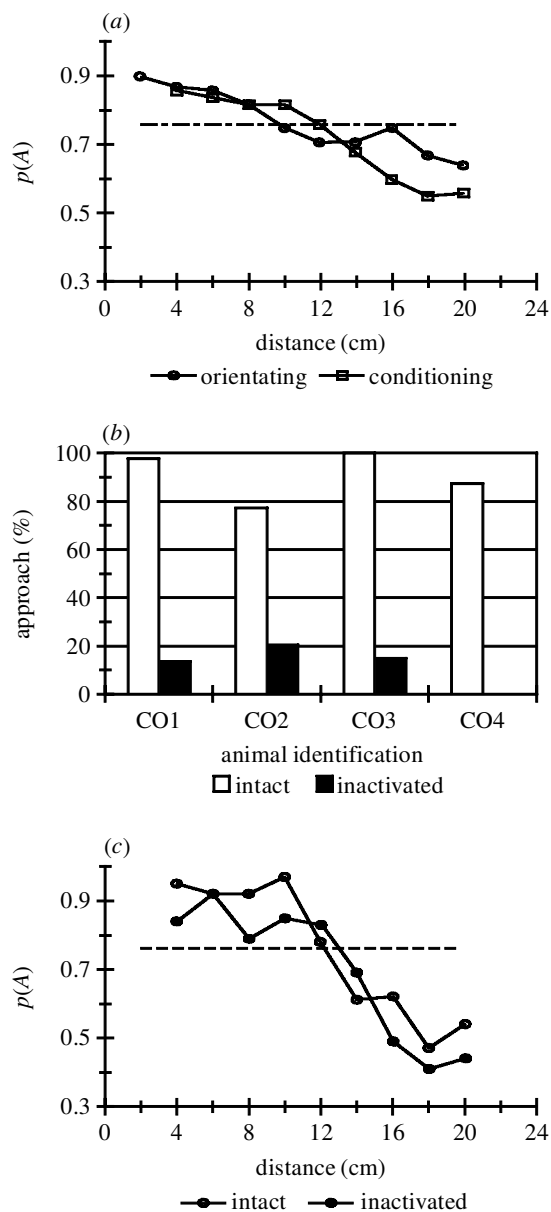


Figure 2. (a) Dipole source detection by the mottled sculpin, plotted as a function of source distance. The detectability of the source ($p(A)$), which decreases with source distance, fell below chance levels ($p(A) < 0.76$) at a distance of *ca.* 11 cm, regardless of which behavioural measure was used (pooled data from four animals). (b) The effect of CoCl_2 on the frequency of untrained approaches to a dipole source in four individual sculpin. Prior to pharmacological inactivation, nearly all presentations of a vibrating bead caused the fishes to approach to source. After CoCl_2 treatment, approaches to the source were nearly abolished. (c) The effect of CoCl_2 on source detectability as measured with conditioned suppression of respiration. CoCl_2 inactivation had no substantial effect on this animal's performance, indicating that its behaviour may be completely explained with reference to the inner ear alone (functions from the responses of a single animal before and after treatment).

paradigm, animals were conditioned to suppress respiration when they detected the source by repeated pairing of the source and a small electric shock. We measured respiration before and during the stimulus presentation to calculate a suppression ratio.

Both behavioural measures, suppression ratios and changes in angular relations to the source were compared during signal and non-signal trials according to the tenets of signal detection theory by calculating receiver operating characteristic (ROC) curves. The area underneath the ROC curve, $p(A)$, is a measure of detectability and is plotted as a function of distance for both behavioural measures in figure 2. $p(A)$ is a measure of the separation between the distribution of responses recorded when a signal is present and when it is absent. A $p(A)$ -value of 0.5 indicates completely overlapping distributions and a $p(A)$ -value of 0.76 indicates a separation between the means of the distributions of one full standard deviation and is typically used as a threshold response. For a complete discussion of ROC curves, see Gescheider (1997).

To determine the sensory substrates of our behavioural measures, we used CoCl_2 to inactivate the lateral line system. Overnight immersion in 0.1 mM CoCl_2 inactivates the lateral line for up to two weeks, but has no effect on the inner ear hair cells (Karlsen & Sand 1987). We compared the frequency of approaches to a nearby (< 5 cm) source before and after CoCl_2 treatment to determine the role of the lateral line system in unconditioned orientating responses. We also examined the effect of CoCl_2 treatment on detection of the source as assessed by conditioned suppression of respiration.

3. THE DISTANCE RANGE OF DIPOLE SOURCE DETECTION IN MOTTLED SCULPIN

The psychometric functions for both behavioural measures (figure 2a) are quite similar. In both behavioural approaches, the threshold distance is approximately 11 cm. The fishes used in these experiments ranged from 7–10 cm standard length (SL), so the range of dipole detection is *ca.* 1–1.5 body lengths. While both behavioural measures gave very similar estimates of the distance range of source detection, each behavioural measure apparently relies on a different sensory modality. CoCl_2 treatment nearly eliminated the unconditioned orientating responses to the source (figure 2b), but appears to have had no effect on the behavioural performance in the conditioning paradigm (preliminary data are shown in figure 2c). Orientating responses therefore depend on lateral line information but conditioned responses may be explained by use of the inner ear alone.

Surprisingly then, both the inner ear and the lateral line system may have very similar operating ranges in the mottled sculpin. How can we explain the similarity in distance range for these two systems? The most obvious explanation lies in the fact that mottled sculpin are benthic fishes. These fishes are generally denser than the surrounding water, decreasing the acceleration imposed on the fishes by any given pressure gradient. In addition, friction coupling between the fishes and the substrate would also act to reduce the acceleration of the fishes. While this has never been explicitly explored, it is also possible that benthic animals might have active postural control systems that act to limit their motions in response to accelerations of the surrounding water (perhaps simply as a means of producing negative lift to keep the fishes on the substrate). All of these factors contribute to a decrease in the relative effectiveness of a stimulus to the inner ear, but would have an opposite effect on the lateral line.

On the contrary, reduction of fish motion may actually act to increase the distance range of the lateral line. As described above, fish motion effectively reduces the intensity and alters the spatial pattern of lateral line stimulation, particularly in the outer reaches of the near field (Kalmijn 1989). If the fish is held rigidly due to friction with the substrate or active postural control mechanisms, the pattern and intensity of stimulation of the lateral line may be closer to the conditions of the stimulus field itself. The same factors that act to decrease inner ear stimulation would thus also act to increase lateral line stimulation.

4. FUTURE DIRECTIONS

The studies described above suggest several fruitful avenues for ongoing research. For example, what is the actual range of fish motion in response to vibratory sources? How does imposed fish motion depend on the habitat and morphology of the fish, and do active postural control mechanisms exist that limit or enhance fish motion? Furthermore, do midwater fishes actually have a reduced lateral line distance range relative to benthic fishes? Conversely, do midwater fishes have an enlarged inner ear active space?

Empirical determination of the spatial resolving power and localizing abilities of both the lateral line and otolithic endorgans is desperately needed. Currently we are investigating the difference in spatial resolution of dipole sources in intact and lateral-line-impaired sculpin. We predict that spatial discrimination will be severely reduced in lateral-line-inactivated sculpin. For midwater fishes, if there is a larger difference in the distance range of the inner ear and lateral line system, there should also be a reduction in spatial resolving power in the intermediate range, where inertial audition is still effective but the lateral line is not.

While controversies over the nature of the stimulus (note the diversity of views expressed in the chapters and discussions contained in Cahn (1967)) no longer plague the field of acousticolateralis research, the biological role and actual sensory capabilities of inertial audition and the lateral line system are still in dire need of empirical research. The elegant behavioural experiments of Dijkgraaf (1963) and theoretical treatments of Kalmijn (1988, 1989) have effectively argued for the importance of spatial gradients of water motion as the stimulus to the auditory and hydrodynamic senses, but few relevant experimental data have been collected. Behavioural responses to relevant stimuli, such as a near field dipole source, are the best means of determining the hydrodynamic sensory capabilities of aquatic organisms.

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