NEARFIELD DETECTION OF DIPOLE SOURCES BY THE
GOLDFISH (CARASSIUS AURATUS) AND THE MOTTLED
SCULPIN (COTTUS BAIRDII)

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Summary

Surprisingly few behavioral data exist on dipole source detection by fish, despite the fact that dipole sources more closely approximate biologically relevant signals than do more nearly monopole sources such as loudspeakers, the stimulus used in nearly all fish auditory studies. In this study, dipole source detection is investigated for two fish species that differ in both their auditory and lateral line systems, the two systems capable of detecting dipole sources. Conditioned suppression of respiration in the goldfish and an unconditioned orienting response in the mottled sculpin were used to measure detection of a 6 mm diameter, sinusoidally vibrating sphere as a function of vibration frequency and source distance.

Sound pressure thresholds for the goldfish were nearly independent of distance (15–60 mm) at 800 Hz, but increased with distance at 50 Hz, as they did for the mottled sculpin. The slopes of 50 Hz source level–distance functions, however, differed between the two species. Slopes for the goldfish were independent of distance, remaining at around 8 dB per distance doubling, which is near the 6 dB per distance doubling measured for sound pressure attenuation away from the source, but less than the 18 dB per distance doubling for incompressible flow, measured with an anemometer. Those for the mottled sculpin increased with increasing distance, approaching 18 dB per distance doubling. The nonlinear increase in source level necessary to reach threshold detection was quite similar to the nonlinear decrease in incompressible flow levels measured with the anemometer. Nonlinear increases with distance for 50 Hz sources near the trunk of the mottled sculpin were also similar to those near the head of the fish, where changes in source frequency had little effect on source level–distance functions.

These results indicate that sound pressure detection by the ear is important for dipole detection by the goldfish, but that incompressible flow detection by the lateral line is more important for the mottled sculpin. They also indicate that fish such as the goldfish, with a pressure-sensitive swimbladder, are capable of detecting dipole sources at greater distances than are fish without such structures.

Key words: lateral line, ear, hearing, hydrodynamics, acoustics, goldfish, Carassius auratus, mottled sculpin, Cottus bairdi.
Introduction

The distance from stimulus to receiver has been described as an important factor in distinguishing the function of the lateral line system from that of other mechanoreceptive sensory systems in fishes and aquatic amphibians. Thus, the lateral line has been distinguished from the somatosensory system because it responds to stimuli that are close to, but not actually touching, the animal; hence the term ‘distance touch’ (Dijkgraaf, 1963). At the other end of the continuum, the inner ear has been distinguished from the lateral line because it can respond to vibrating sources at distances beyond that of the lateral line domain (Kalmijn, 1988, 1989). For the low frequencies (<100–200 Hz) to which the lateral line is sensitive, this domain is well within the inner near field—that part of the hydrodynamic field about a vibrating source that is governed primarily by incompressible flow (Morse, 1948; Harris and van Bergeijk, 1962; Kalmijn, 1988, 1989). For most fish, this distance has been estimated to be no more than one or two body lengths away (Denton and Gray, 1983; Kalmijn, 1988, 1989). In contrast, fish auditory systems appear to be capable of responding beyond the inner near field and, in some species (with pressure-sensitive adaptations), even into the far field (Coombs and Janssen, 1990a), where propagated pressure waves predominate.

Despite the farfield hearing abilities of some fish species, Kalmijn (1988, 1989) has argued that both the lateral line and inner ear of fish have evolved to operate in the near field and that dipole (e.g. vibrating spheres), rather than monopole (e.g. loudspeakers), sources more closely approximate the kinds of nearfield phenomena likely to be relevant to the fish. Unfortunately, our understanding of nearfield dipole detection is limited, as there have been very few experimental data collected with dipole sources. Although a number of physiological studies on lateral line function have employed dipole signals (e.g. Kroese et al. 1978; Münz, 1985; Sand, 1981; Montgomery, 1989; Coombs and Janssen, 1990b), most behavioral studies on lateral line capabilities have been performed with surface wave stimuli and nearly all on auditory capabilities have used loudspeakers (for comprehensive listing, see Fay, 1988). Although many of the auditory studies involve nearfield stimulation by a loudspeaker, loudspeakers behave more like monopole than dipole sources (Kalmijn, 1989) and, thus, their near fields are likely to differ from that of a pure dipole source in several ways. For example, the local flow field of a monopole is centered on the source and radially symmetrical about it, whereas that of a dipole is not radially symmetrical and is centered on the source only along the axis of vibration (see Fig. 1) (Kalmijn, 1988). In addition, flow velocity in the inner near field falls off with 1/distance² for monopoles and 1/distance³ for dipoles. These differences have implications for the way in which fish might use mechanosensory systems in localizing and determining the distance of a vibrating source (Kalmijn, 1988, 1989). Thus, if we are to understand how fish detect and localize biologically relevant signals, we must have basic information about their abilities to detect and localize dipole, rather than monopole, sources.

This study provides a systematic and quantitative description of dipole source detection by the mottled sculpin, Cottus bairdi, and the goldfish, Carassius auratus L. The mottled sculpin has recently been used in studies of lateral line function (e.g. Hoekstra and
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Janssen, 1985; Janssen, 1990; Janssen et al. 1987; Coombs and Janssen, 1990b), whereas the goldfish has been extensively in studies of auditory function (see review by Popper and Fay, 1993). In addition, these two species differ significantly in their auditory and lateral line systems, with the most significant differences being (1) that the otophysan goldfish has a mechanical link between the pressure-sensitive swimbladder and the inner ear (von Frisch, 1938), whereas the mottled sculpin lacks a swimbladder, and (2) that the body of the goldfish is covered by thousands of superficial neuromasts (Puzdrowski, 1989), whereas that of the mottled sculpin is covered by only a few, very circumscribed, populations of superficial neuromasts (Janssen et al. 1987).

Threshold detection as a function of distance was measured in both species to determine the rate at which source level had to be increased to maintain threshold detection (a measure of the distance range of the system) and whether this rate was closer to that measured for incompressible flow levels or for sound pressure levels. In addition, threshold detection level as a function of frequency was measured for the goldfish so that comparisons could be made with loudspeaker detection in the same species and with previous measures of frequency effects on dipole detection by the mottled sculpin (Coombs and Janssen, 1990b). Finally, the effects of CoCl₂, which is assumed to block the lateral line but not the inner ear (Karlsen and Sand, 1987), were assessed to determine the extent to which the lateral line system contributes to dipole detection by the goldfish.

Materials and methods

Experimental animals

Mottled sculpin were collected from Lake Michigan near Chicago in 7–10 m of water. Ten animals, ranging in standard length (SL) from 7 to 10 cm were used. Mottled sculpin were anesthetized (MS222, Sigma) before being blinded by either complete removal of the eye or removal of the retina. Fish were housed in individual 22.8 l tanks and fed squid during experimental sessions three times a week.

Goldfish, ranging in size from 10 to 13 cm SL were obtained from local fish dealers and were housed in 91–137 l gallon tanks with 4–6 animals per tank. Goldfish were fed a variety of commercially available foods. Both species were maintained at the same water temperature (14–15 °C). All experimental procedures were approved by the Loyola University Animal Care and Use Committee.

Behavioral procedures

Classically conditioned suppression of respiration, routinely used in psychophysical studies of goldfish hearing (e.g. Fay and Coombs, 1983), was used as a behavioral indicator of dipole source detection in this species. Fish were loosely restrained in a 21.5 cm diameter tank in a cloth bag that covered most of the body (including the eyes) but left the tip of the snout and a 2 cm×3 cm area of the trunk exposed. A thermistor placed directly in front of the fish’s mouth measured water movements created by the respiring fish. Fish were conditioned to reduce their respiration rate during a signal trial by following it with a mild electric shock, delivered through wire screen electrodes at the
tail and head of the fish. This shock in the absence of any signal causes an unconditioned reduction in respiration. The respiration rate and amplitude occurring during the second half of a 7 s interval preceding a signal trial (also 7 s) (A) were compared with the rate and amplitude during the second half of the signal trial (B) to yield a suppression ratio of B/(A+B). Respiratory amplitude and rate were quantified as the length of the voltage waveform in arbitrary units minus the length expected for no respiratory activity. A suppression ratio of 0.5 means that there was no difference between respiration activity measured before and during the stimulus trial. A ratio of 0.4 or less was defined as a detection or ‘yes’ response and is based on previous work (Fay and Coombs, 1983) showing that this value occurs about 12 % of the time by chance and is about one standard deviation below the mean suppression ratio for blank trials. Relatively long inter-trial intervals (varied randomly from 60 to 120 s) were used to ensure reliable suppression behavior.

The unconditioned feeding response of the mottled sculpin was used to measure the ability of the animal to detect the presence of vibrations of a spherical source positioned near either the trunk or the head of the fish (see Coombs and Janssen, 1990b, for further detail). Fish were trained to sit motionless (a normal type of behavior for this benthic fish) on a glass plate located at the bottom of a 52 cm × 52 cm × 20 cm high test tank, filled with water to a height of 8 cm. The glass plate was then moved to position the fish at various distances from the source. Once the fish had been positioned, the experimenter initiated a random inter-trial interval (5–15 s) followed by a 5 s trial during which the sphere was either sinusoidally vibrated or silent. The sculpin’s response was scored as either a detection (a movement towards or a bite at the source) or non-detection (no movement or movement away from the source). For each correct detection of a signal trial, fish were reinforced with small pieces of squid. To ensure that sufficient motivation for the feeding response was maintained, fish were fed limited amounts during experimental sessions only and experiments were run once every other day (see Coombs and Janssen, 1990b, for an experimental evaluation of food deprivation on response reliability).

An adaptive tracking method was used for measuring threshold detection for both goldfish and mottled sculpin. Detection responses resulted in a computer-controlled, 5 dB decrease in the signal level for the next trial, whereas non-detection responses resulted in a 5 dB increase in signal level for the next trial. The signal level midway between consecutively detected and non-detected signal trials was computed as a threshold value and approximately 6 (sculpin) to 10 (goldfish) of these were obtained during a daily experimental session. Thirty to forty of these were averaged from each animal to obtain a final average threshold value for each experimental condition. To ensure that responses were under stimulus control, threshold values from experimental sessions in which blank trial response rates were greater than 20 % were rejected.

Procedures for pharmacologically blocking the lateral line system with CoCl2 follow those of Karlsen and Sand (1987). Fish were initially immersed in 0.1 mmol l−1 CoCl2 solutions made with Ca2+-free deionized water. After 24 h of immersion, fish were removed from the treatment tank and placed in normal aquarium water for immediate threshold testing. Fish were returned to normal aquarium water and were tested again at 72 h post-immersion and on several days subsequent to that. Normal aquarium water was
supplemented with calcium sulfate dihydrate to bring calcium levels up to 1.9 mmol l\(^{-1}\). Calcium levels in deionized and normal aquarium water were measured by flame photometry. After initial testing at CoCl\(_2\) concentrations recommended by Karlsen and Sand (1987) had revealed no effects, the concentration was increased by an order of magnitude (to 1.0 mmol l\(^{-1}\)).

**Stimulus position, generation and measurement**

Both the loudspeaker and the vibrating sphere were driven with sinusoidal signals created with a function generator. Signals were attenuated and amplified before driving the sources. The underwater loudspeaker (University Sound, UW-30) was 18 cm in diameter and was the same as that used in previous studies of goldfish auditory responses (e.g. Coombs and Fay, 1985; Fay and Coombs, 1983). The loudspeaker was buried in coarse sand at the bottom of a cylindrical test tank (21 cm in diameter, 25 cm high). Sand and speaker filled the bottom half of the tank, whereas the fish was positioned in the center of the top half.

A small plastic sphere (6 mm in diameter) attached to a blunt-tipped syringe needle mounted to the center of a small vibrator was used as a dipole source. In both mottled sculpin and goldfish experiments, the axis of sphere vibration was vertical (i.e. perpendicular to the bottom of the test tank) (Fig. 1) and thus parallel to the midsagittal plane of the fish. Source-to-fish distances were measured in a single horizontal plane at the level of the fish as the shortest distance between the projected center of the sphere (onto that plane) and the lateral surface of the fish’s body. In goldfish experiments, the

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Fig. 1. Schematic diagram (not to scale) showing the axis of sphere vibration relative to the bottom and the air/water interface of the test tank. The height of both the sculpin and goldfish trunk lateral line relative to the source is also depicted. The incompressible flow field about the dipole source shows how the axis of flow can differ between distance A and distance B for a sensor below the sphere (−6 mm), but how it stays the same at the height of the sphere center (0 mm).
sphere was positioned at the same height as the trunk canal (Fig. 1), 1–2 cm caudal to the operculum (level with the rostral insertion of the dorsal fin). The benthic position of the mottled sculpin and its average body depth (approximately 1.5 cm at the head and less than 1 cm at the trunk) made it extremely difficult to position the sphere at the same height as both head and trunk canals without the sphere touching the bottom of the tank. Thus, it was necessary to place the sphere center 15 mm above the glass plate on which the fish rested. This was approximately at the eye level of the fish, or about 12 mm above the mandibular canal on the head and 6 mm above the trunk lateral line canal (Fig. 1).

In order to determine the possible effects of source elevation on threshold detection in the mottled sculpin, both source distance and source elevation were varied. Source distance was measured as the distance between the sphere center and the bottom of the tank. Sources positioned near the head of the mottled sculpin were near the eye socket, whereas those positioned near the trunk were located at the junction between the first and second dorsal fins (the same relative position as for the goldfish).

Water flow levels produced by the vibrating sphere were measured directly with a displacement-sensitive hot-film anemometer probe (1 mm long, 51 μm in diameter) placed at varying distances and elevations from the sphere in the absence of the fish (see Coombs et al. 1989, for measurement details). The sensor probe was oriented perpendicular to the axis of sphere vibration (see Figs 1 and 2 in Coombs et al. 1989) for all measurements. In some cases, peak-to-peak displacement (d) levels were converted to peak-to-peak acceleration (a) levels using the relationship \( a = 4 \pi^2 f^2 d \), where \( f \) is frequency. Pressure levels created by both the sphere and the loudspeaker were measured with a hydrophone in the position of, but in the absence of, the fish. The hydrophone was a short cylinder, 17 mm long and 37 mm in diameter (Clevite/Gould, CH-17), positioned vertically in the tank, with its largest face parallel to the vertical axis of sphere vibration. The hydrophone was placed at different distances, measured from sphere center to hydrophone center. Measurements of sound pressure levels at different source elevations were not attempted because of the diameter of the hydrophone (37 mm) relative to the range of source elevations (10 mm) (see also discussion below for limitations of hydrophone pressure measurements).

Results

Effects of source distance and elevation on signal levels

In general, sound pressure levels measured with a hydrophone at different distances from the vibrating sphere declined at rates close to 6 dB per distance doubling. This rate of attenuation (equivalent to 1/distance) is clearly less than the 12 dB per distance doubling (1/distance^2) predicted for dipole sources in the near field (Morse, 1948; Kalmijn, 1988). It is unlikely that these results can be attributed to a distortion of the pressure field by tank boundaries and air/water interfaces, since the source was small relative to the tank and measurements with an extremely small and relatively non-invasive anemometer probe showed that the flow field was undistorted (see Coombs et al. 1989, and following paragraph). Rather, the discrepancy is probably due to the large size of the hydrophone relative to that of the source. For one thing, the presence of
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the hydrophone itself may have altered the pressure field. Second, since the inner near field of a dipolar source is characterized by spatial non-uniformities in the flow field (Kalmijn, 1988, 1989), there will be pressure non-uniformities as well. Unfortunately, these non-uniformities cannot be measured with a transducing element that is larger than the source. In order to get a feel for spatial non-uniformities in the pressure field to which the hydrophone might be exposed, dipole field equations were used to calculate pressure at single points along a 16 mm x 16 mm area corresponding to approximately one-quarter of the surface area of the hydrophone face for a source distance of 15 mm (Table 1). [A computer program, based on the dipole field equations (e.g. Morse, 1948; Kalmijn, 1988), was used to calculate pressure levels at points corresponding to a 16 mm x 16 mm area along the face of the hydrophone. Pressure amplitude \( P \) was calculated as \( P = [(\rho v a^3)/(2r^2)] u \cos \theta \), where \( \omega = 2\pi f \), \( r \) is the distance from the source center, \( \theta = 0^\circ \) along the axis of vibration, \( \rho \) is the density of water, \( f \) is frequency and \( a \) is the source radius. Source amplitude was defined as 1 m s\(^{-1}\).] Pressures (in dB re 0.1 Pa) ranged from minus infinity at the point directly opposite the source center to nearly 37 dB. Minus infinity calculations correspond to a pressure null area in the radiated acoustic field of a dipole (Kalmijn, 1988). It is difficult to predict from these calculations what the output of the hydrophone would be if there were no distortion due to the hydrophone presence. However, calculated drops in pressure corresponding to a doubling of distance from the source range from 0 to 18 dB at single points along the hydrophone and the measured drop (6 dB) falls within this range.

Water flow levels measured with an anemometer at the same elevation (0 mm) as the sphere declined at the predicted rate of 18 dB per distance doubling \((1/\text{distance}^3)\) (Fig. 2, Coombs et al. 1989). For an anemometer 6 mm below the sphere center, flow levels fell off with distance in a nonlinear fashion, with the slopes of level–distance functions increasing with distance and reaching an asymptote of around 18 dB per distance doubling at a distance of about 20 mm. Thus, flow levels were relatively independent of source elevation at distances greater than about 20 mm, but dependent on elevation at distances shorter than 20 mm.

Effects of source elevation on dipole detection by the mottled sculpin

Results on flow levels measured at different distances and source elevations suggested that source elevation might affect threshold detection in a distance-dependent way. To
test this hypothesis, we measured threshold source levels as a function of source elevation for a 50 Hz source near the trunk at distances of 15 and 60 mm. The results of this test for a 50 Hz signal show that a source elevation change of 10 mm results in a 6 dB source level shift at a distance of 15 mm and less than a 3 dB shift (within one standard deviation of the mean) at 60 mm (Table 2).

**Table 2. Effects of source height and distance on detection thresholds of four mottled sculpin**

<table>
<thead>
<tr>
<th>Fish number</th>
<th>Source distance (mm)</th>
<th>Source height (mm)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>15 mm</td>
<td>60 mm</td>
</tr>
<tr>
<td></td>
<td>10  20    10–20    10  20    10–20</td>
<td></td>
</tr>
<tr>
<td>353 Mean*</td>
<td>70.7  64.7  6   50.7  48   2.7</td>
<td></td>
</tr>
<tr>
<td>S.D.</td>
<td>2.4  3.8  2.7  2.7  2.4</td>
<td></td>
</tr>
<tr>
<td>356 Mean</td>
<td>69.7  62.3  7.4  46.5  43.8  2.7</td>
<td></td>
</tr>
<tr>
<td>S.D.</td>
<td>3.1  4.9  2.7  2.7  2.6</td>
<td></td>
</tr>
<tr>
<td>360 Mean</td>
<td>70.7  65.5  5.2  45   43   2</td>
<td></td>
</tr>
<tr>
<td>S.D.</td>
<td>2.6  3   2.5  2.6  2.4</td>
<td></td>
</tr>
<tr>
<td>361 Mean</td>
<td>65.5  59.2  6.3  44.8  41.7  3.1</td>
<td></td>
</tr>
<tr>
<td>S.D.</td>
<td>2.8  2.4  2.8  1.9  1.9</td>
<td></td>
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</table>

*Mean attenuation (dB) of source level at threshold; s.d., standard deviation of the mean.
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**Effects of source distance on dipole source detection by the goldfish and mottled sculpin**

In general, dipole source levels had to be increased with increasing distance to reach detection threshold for both goldfish and mottled sculpin for different vibration frequencies and for sources near the head (Fig. 3) and trunk of the fish (Fig. 4). Tables 3 and 4 show the extent of intra-individual variability for each mean threshold used in generating the functions in Figs 3 and 4. The rate at which dipole source levels had to be increased varied from approximately 2 to 20 dB per distance doubling (Fig. 5), although rates for source distances less than 15 mm away from the head tended to be near zero, and in some cases even less than zero for the mottled sculpin. Rates for sources less than 15 mm away from the trunk were not measured in either the mottled sculpin or the goldfish because of possible tactile detection of the source by the pectoral fin.

For a few individuals, thresholds at these close distances obtained with sources near the head also tended to be more variable (Table 3). This variability is probably due to...
elevation effects, which are more critical at short distances (see previous section) and to the fact that sculpin can alter their head height by propping themselves up on their pelvic fins (Hoekstra and Janssen, 1985). In general, source level–distance functions were nonlinear for the mottled sculpin and the slopes of these functions increased with distance (Fig. 5). In contrast, those for the goldfish at 50 Hz appeared more linear (Figs 4 and 5). Notice that functions in Figs 3 and 4 have been plotted in terms of relative signal levels at the source, rather than at the fish. There are two reasons for doing this. One is that it is difficult to determine a priori whether the relevant stimulus dimension is sound pressure or water flow. The term water flow is used in this paper simply to refer to the local, incompressible flow measured with the anemometer. Thus, the relevant stimulus dimension will depend on how the stimulus is detected and transduced – whether it is detected via a pressure transducer, like a swimbladder or hydrophone, or whether it is detected by a flow transducer, like an anemometer or lateral line neuromast.

Assuming that pressure is the relevant dimension, 800 Hz thresholds obtained from goldfish are nearly independent of distance when plotted in terms of sound pressure levels

Fig. 4. Source attenuation derived as in Fig. 3, but for thresholds measured at 50 Hz for a stimulus near the trunk of both mottled sculpin and goldfish.
A second reason for plotting the results with respect to signal levels at the source is that flow levels at the fish are difficult to determine, since flow levels (Fig. 2) and orientations (Fig. 1) are likely to change with distance in a way that is dependent on source elevation. This is particularly important for interpreting the mottled sculpin results because the source was slightly above the fish. Because of this difficulty, we have not attempted to plot thresholds in terms of water flow levels at the fish. However, we have provided a reference function (dashed line) in Figs 3 and 4 that indicates the maximum rate (1/distance³ or 18 dB per distance doubling) at which incompressible flow declines with distance from the source. In that regard, note that source–level distance functions for the

<table>
<thead>
<tr>
<th>Fish number</th>
<th>Source distance (mm)</th>
<th>Source frequency (Hz)</th>
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<tr>
<td></td>
<td>7.5</td>
<td>15</td>
</tr>
<tr>
<td>S3</td>
<td>Mean 48.3</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>S.D. 5.5</td>
<td>3.2</td>
</tr>
<tr>
<td>S9</td>
<td>Mean 57</td>
<td>57.3</td>
</tr>
<tr>
<td></td>
<td>S.D. 4.1</td>
<td>4.3</td>
</tr>
<tr>
<td>S12</td>
<td>Mean 57</td>
<td>49.5</td>
</tr>
<tr>
<td></td>
<td>S.D. 4.4</td>
<td>2.9</td>
</tr>
<tr>
<td>S211</td>
<td>Mean 60.8</td>
<td>58.8</td>
</tr>
<tr>
<td></td>
<td>S.D. 6.5</td>
<td>4.7</td>
</tr>
<tr>
<td>S3</td>
<td>Mean 87.3</td>
<td>78.8</td>
</tr>
<tr>
<td></td>
<td>S.D. 5.6</td>
<td>2.7</td>
</tr>
<tr>
<td>S12</td>
<td>Mean 85</td>
<td>81.5</td>
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<tr>
<td></td>
<td>S.D. 6</td>
<td>5.6</td>
</tr>
<tr>
<td>S101</td>
<td>Mean 61</td>
<td>69.5</td>
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<td></td>
<td>S.D. 16.74</td>
<td>7</td>
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<tr>
<td>S215</td>
<td>Mean 85.8</td>
<td>78.5</td>
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<tr>
<td></td>
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<tr>
<td>S9</td>
<td>Mean 92.8</td>
<td>95.3</td>
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<td></td>
<td>S.D. 4</td>
<td>4</td>
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<tr>
<td>S12</td>
<td>Mean 90.5</td>
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<tr>
<td></td>
<td>S.D. 4.58</td>
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</tr>
<tr>
<td>S204</td>
<td>Mean 76.5</td>
<td>71.5</td>
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<td></td>
<td>S.D. 11.4</td>
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<td>S102</td>
<td>Mean 79.8</td>
<td>78.5</td>
</tr>
<tr>
<td></td>
<td>S.D. 11.5</td>
<td>8.5</td>
</tr>
</tbody>
</table>
mottled sculpin tend to converge on the 18 dB per distance doubling function (Fig. 3) in much the same way as do signal levels measured at different distances with an anemometer below the source (Fig. 2).

Frequency effects on dipole and loudspeaker detection by the goldfish
With a dipole source positioned 15 mm away from the trunk lateral line, naive goldfish
showed robust suppression of respiration in response to signals at both 50 and 800 Hz within the first 1 or 2 days of training. This rate of response acquisition is similar to that when goldfish are trained using loudspeakers. When plotted in terms of water acceleration levels at the fish (measured with an anemometer at the same elevation as the sphere), the detection curve for the goldfish shows nearly constant acceleration sensitivity below 100 Hz (Fig. 7A). This part of the threshold curve is similar to that obtained from the mottled sculpin (Fig. 7A). At frequencies above 100 Hz, however, acceleration-sensitivity of the mottled sculpin declines, but that of the goldfish increases to its maximum at around 200 Hz. Acceleration-sensitivity of the goldfish does not begin to drop off significantly until frequencies above about 800 Hz. When expressed in terms of sound pressure levels at the fish, goldfish thresholds show best sensitivity in the 100–800 Hz range, which is quite similar to values obtained with the underwater loudspeaker (Fig. 7B).

Effects of CoCl₂ on dipole threshold detection by goldfish

To determine whether conditioned suppression of respiration in response to the vibrating sphere was mediated solely by the lateral line system, goldfish were immersed
in Ca$^{2+}$-free CoCl$_2$ solutions for 24 h prior to testing. Initial testing at 50 Hz of two fish (LL1 and LL7) immersed in 0.1 mmol l$^{-1}$ solutions (the concentration experimentally demonstrated to be effective in the roach, *Rutilus rutilus*, Karlsen and Sand, 1987) indicated no decrease in sensitivity immediately after 24 h of immersion (session 5) and for up to 4 days post-immersion (sessions 6–9, Fig. 8). LL7 showed what could be interpreted as an increase in sensitivity of about 10 dB (the opposite of what was predicted). However, sound pressure thresholds for this animal fluctuated between −10 and 0 dB re 0.1 Pa both before and after CoCl$_2$ treatment and, since the lower thresholds (−10 dB) were frequently associated with high false alarm rates (Fig. 8B), we concluded that the response rate was high in these cases and not under ideal stimulus control. To help rule out the possibility that a 0.1 mmol l$^{-1}$ solution may have been too low for the goldfish, we increased the CoCl$_2$ concentration by an order of magnitude and repeated the test in two additional fish (LL3 and LL4), obtaining similar results (Fig. 8). These concentrations were also ineffective in reducing threshold responses to the underwater loudspeaker at 800 Hz.

**Discussion**

These results indicate that dipole detection by the goldfish and mottled sculpin differ
in a number of fundamental ways, including the frequency and distance range of detection and the stimulus dimensions that govern dipole detection. Since the threshold detection curves for loudspeaker and dipole sources are very similar for the goldfish (Fig. 7B), differences in the frequency range of dipole detection between the goldfish, a fish with a swimbladder, and the mottled sculpin, a fish lacking a swimbladder, are not surprising and merely extend and confirm many earlier studies with loudspeakers showing that fish with pressure-transducing cavities have better sensitivity to higher frequencies (see Popper and Fay, 1993, for a review). A new and interesting aspect of these results, however, is that the goldfish also appears to be able to detect low-frequency sources of a given amplitude at greater distances than the mottled sculpin. Thus, it is conceivable that a major selective advantage of having pressure-sensitive
adaptations has more to do with detecting sources at greater distances than with detecting higher-frequency sources.

In general, dipole threshold detection appears to be governed primarily by sound pressure for the goldfish, especially at higher frequencies. At lower frequencies, however, water flow appears to play a predominant role for the mottled sculpin and perhaps some role for the goldfish. Evidence for sound pressure sensitivity in the goldfish comes from the observation that 800 Hz thresholds, when plotted in terms of sound pressure measured at the distance of the fish, are nearly independent of source distance, changing by less than 2 dB over a 15–60 mm range (Fig. 6). If fish were responding to water flow, sound pressure thresholds would appear to increase with distance, owing to the more rapid attenuation of incompressible flow in the nearfield. This is exactly what happens at 50 Hz, where sound pressure thresholds increase by about 10 dB for the mottled sculpin and 7 dB for the goldfish for a source positioned near the trunk. The latter results are similar to much earlier results obtained from the goldfish at 40 Hz in response to a much larger dipole (approximately 3 cm in diameter) positioned in front of the head at source distances ranging from 13 to 28 cm (Fay, 1969).

The 50 Hz results from the goldfish differ from the 50 Hz results from the mottled

Fig. 8. Sound pressure thresholds from four fish (LL1, LL3, LL4, LL7) to a 50 Hz vibrating sphere before (sessions 1–4), 1–2 h after (session 5) and 2–10 days after (sessions 6–9) 24 h of immersion in CoCl₂ (A). Each data point represents a daily mean of 10 threshold determinations. (B) The false alarm rate associated with each experimental session, typically separated by 1 or 2 days.
sculpin, however, in at least one respect. The slopes of source level–distance functions remain relatively independent of distance at around 8 dB per distance doubling. This rate is quite close to that measured for pressure drops with the hydrophone (6 dB per distance doubling). Most significantly, behaviorally measured slopes are considerably below the 18 dB per distance doubling calculated and measured for incompressible flow dependence (Fig. 5B). In contrast, the slopes of source level–distance functions for the mottled sculpin approach 18 dB per distance doubling (Fig. 5A, B).

These slope differences indicate that the distance range over which sources can be detected is greater for the goldfish than for the mottled sculpin. The most parsimonious explanation for the goldfish results is that threshold detection is influenced primarily by pressure. This explanation is consistent with the idea that the inner ear can account for dipole source detection by the goldfish, since it can be stimulated indirectly by pressure-induced changes in the swimbladder (Fay and Popper, 1975). The rostral–caudal extent of the bipartite swimbladder in the goldfish is approximately 30 mm in a 90 mm fish, with the rostral end at the caudal edge of the operculum (S. Coombs, unpublished observations). In these experiments, this means that the vibrating sphere was directly opposite the swimbladder and that the size of the source was small relative to that of the swimbladder. Given that the slopes of behaviorally measured source level–distance functions are close to the pressure attenuation rates measured with the hydrophone, it is tempting to speculate that the hydrophone and the goldfish swimbladder are integrating and transducing the pressure field in a similar manner.

Although swimbladder stimulation of the lateral line system cannot be ruled out at lower frequencies, Sand (1981) calculated that the displacements associated with the pressure necessary for causing indirect stimulation of the trunk lateral line system via the swimbladder of the roach (*Rutilus rutilus*: Cyprinidae), another otophysan, were between one and two orders of magnitude above displacement thresholds measured with a small dipole source. Thus, according to these measurements, swimbladder effects on the trunk lateral line are unlikely except at very high sound pressure levels.

There are two other lines of evidence to suggest that the inner ear, rather than the lateral line, was the responsible detector in the goldfish. One is that CoCl$_2$ failed to alter dipole detection thresholds for a 50 Hz signal. This frequency is well within the frequency range of detection of all lateral line systems studied to date (Kuiper, 1967; Bleckmann, 1980; Coombs and Janssen, 1990b; Montgomery, 1989; Coombs and Montgomery, 1992) and has also been shown to be an effective stimulus for posterior lateral line nerve (PLLN) fibers innervating the trunk lateral line system of the goldfish (S. Coombs, unpublished results). Thus, if dipole detection at 50 Hz were mediated solely by the lateral line system, we would expect to see significant elevation of thresholds after CoCl$_2$ treatment. This clearly does not happen, even after CoCl$_2$ concentrations had been increased by an order of magnitude. These results and similar results with the loudspeaker at 800 Hz provide further behavioral evidence of the inability of CoCl$_2$ to affect the inner ear.

This line of evidence hinges on the assumption that CoCl$_2$ is an effective lateral line blocker in the goldfish. Since the effectiveness of CoCl$_2$ was not physiologically verified in the goldfish, it is possible that we were unsuccessful in knocking out the lateral line system in this species. If this were the case, however, it would be the first example of its
kind, as previous studies have indicated that the lowest CoCl₂ concentrations used in this study were effective in reducing lateral line responsiveness in a variety of species, including closely (e.g. the otophyisan blind cavefish, Astyanax hubbsi; Hassan et al. 1992) and distantly (Karlsen and Sand, 1987; Janssen, 1990) related fish and amphibian species (Claas et al. 1994).

A second line of evidence is that the frequency range of dipole detection by the goldfish extends to about 1000 Hz, which is well above the frequency range reported for the lateral line system of any other species and well above the frequency range of responsiveness found in PLLN fibers of the goldfish (S. Coombs, unpublished data). In contrast, saccular nerve fibers of the goldfish auditory system respond quite well at these higher frequencies when stimulated with an underwater loudspeaker (Fay and Ream, 1986). In fact, threshold tuning curves from saccular fibers can easily account for the shape of the behaviorally obtained threshold curves, which are quite similar for both an underwater loudspeaker and the vibrating sphere (Fig. 7B). These results are also similar to previously obtained sound pressure audiograms for the goldfish under a variety of stimulus conditions (see Fay, 1988, for review).

Although we conclude from several different lines of evidence that the ear alone can account for dipole detection by the goldfish, we cannot conclude that the lateral line is not also responding. Indeed, our preliminary physiological data suggest that the lateral line system of the goldfish is perfectly capable of responding to dipole sources at vibration frequencies up to around 100 Hz and at sound pressure levels very close to those measured at the behavioral threshold. Similarly, although we argue below that the lateral line system of the mottled sculpin seems to govern dipole detection by the mottled sculpin, we cannot prove that the inner ear is not also detecting the source. The few physiological data we have to date suggest that both lateral line and auditory systems have very similar sensitivities where their frequency ranges overlap (Platt et al. 1989), making it extremely difficult to distinguish the function of the two systems for frequencies up to 100 Hz.

Although sound-pressure-mediated responses of the auditory system seem to play a major role in governing dipole detection by the goldfish, water-flow-mediated responses of the lateral line seem to play a larger role for the mottled sculpin. The shapes of source level–distance functions provide the first line of evidence. The rate at which source levels must be increased to maintain threshold performance increases with distance in a nonlinear fashion (Figs 3–5), much like the attenuation rate of water flow measured with an anemometer several millimeters below the source (Fig. 2). These results would be expected if the sensor were located below the source, as was the case for the lateral line system of the mottled sculpin under the conditions of this experiment (Fig. 1).

Another line of evidence is that a 10 mm change in source elevation causes a much greater shift in the source level required for threshold detection at a source distance of 15 mm than it does at 60 mm (Table 1). These results are consistent with the fact that water flow levels measured with an anemometer attenuate more rapidly with source elevation at distances close to the source than at distances farther away (Fig. 2). As Fig. 1 shows, this effect may be due to the directional sensitivity of the anemometer and to the changes in flow orientation that accompany changes in source elevation and distance. For these experiments, the anemometer was positioned to be most sensitive to flows along the
axis of sphere vibration. Flows perpendicular to that axis (and to the midsagittal plane of the fish) are least effective (Coombs et al. 1989). Given that both Harris and van Bergeijk (1962) and Sand (1981) have shown that lateral line afferent fibers are least sensitive to flows perpendicular to the fish, an interpretation of these results based on lateral line detection of water flow seems quite reasonable. Although it is possible that the inner ear of the mottled sculpin is also responding to local water flows (i.e. by direct acceleration of the fish), previous results with CoCl2 (Janssen, 1990) and other selective pharmacological and mechanical blockers of the lateral line system (Hoekstra and Janssen, 1985) indicate that the orienting response used in measuring these thresholds is dependent on an intact lateral line system.

An alternative or additional explanation for the nonlinearity of source level–distance functions in the mottled sculpin is that a different number of neuromasts may be stimulated at different source distances. The profile of flow levels at the distance of the fish and, thus, the expected excitation patterns across spatially distributed neuromasts depend on the distance from the fish to the source (Gray and Best, 1989). At distances very close to the fish, the spatial profile of stimulus levels is very sharply tuned; that is, stimulus levels fall off very sharply around the projected center of the source. At distances farther away from the fish, the spatial profile is more uniform, with stimulus levels falling off very gradually around the projected center. Thus, it is conceivable that at very close distances, only one or two neuromasts are stimulated but that, as distance increases, the number of neuromasts responding increases until the maximum number of neuromasts possible is recruited. After the maximum has been reached, the system behaves linearly, following the predicted 18 dB per distance doubling. Although the pattern of excitation may be very important for determining the distance and location of the source (Gray, 1984; Gray and Best, 1989), it does not appear to be very important in determining the ability of mottled sculpin to discriminate between different source levels (Coombs and Fay, 1993). Furthermore, behavioral detection thresholds for a source distance of 15 mm can be predicted by threshold response levels in single lateral line nerve fibers (Coombs and Janssen, 1990b). Thus, it remains to be seen whether excitation patterns across different neuromasts and fibers are important in determining threshold detection levels.

In the above discussion, we have assumed that the responsiveness of the mottled sculpin lateral line should be proportional to water flow levels at different distances from the source. It is important to point out, however, that this may be true only for fish such as the mottled sculpin, which are denser than the surrounding water and coupled to the substratum rather than to the surrounding water. The effective stimulus for the lateral line system is net motion between the fish and the surrounding water (Denton and Gray, 1982, 1983; Kalmijn, 1988, 1989). For fish coupled to the substratum, body motion in response to mid-water vibrating sources may be quite minimal. Thus, net motion between the fish and surrounding water would simply be equal to the surrounding incompressible flow alone, which falls off as 1/distance³. For fish such as goldfish, however, which are presumably coupled to the surrounding water, the net motion falls off approximately as 1/distance⁴ (24 dB per distance doubling) (Denton and Gray, 1988). This predicts that the slopes of source–level distance functions for the goldfish, if governed by the lateral line,
would be even steeper than the 1/distance³ function depicted in Fig. 4. This further mismatch between predicted and measured slopes strengthens the argument that the pressure-sensitive auditory system predominates in dipole detection by this species.

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References
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