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Detection of infrasound and linear acceleration in fishes

O. Sand* and H. E. Karlsen

Department of Biology, The University of Oslo, PO Box 1051 Blindern, N-0316 Oslo, Norway

Fishes have an acute sensitivity to extremely low-frequency linear acceleration, or infrasound, even down to below 1 Hz. The otolith organs are the sensory system responsible for this ability. The hydrodynamic noise generated by swimming fishes is mainly in the infrasound range, and may be important in courtship and prey–predator interactions. Intense infrasound has a deterring effect on some species, and has a potential in acoustic barriers. We hypothesize that the pattern of ambient infrasound in the oceans may be used for orientation in migratory fishes, and that pelagic fishes may detect changes in the surface wave pattern associated with altered water depth and distant land formations. We suggest that the acute sensitivity to linear acceleration could be used for inertial guidance, and to detect the relative velocity of layered ocean currents. Sensitivity to infrasound may be a widespread ability among aquatic organisms, and has also been reported in cephalopods and crustaceans.

Keywords: acoustic fish barrier; fish migration; inertial navigation; infrasound; linear acceleration; orientation

1. PHYSICAL CONSIDERATIONS

Infrasound is usually defined as sound with frequencies below 20 Hz, which is roughly the lower-frequency cut-off for the human audiogram. The possibility that fishes might detect infrasound was not thoroughly investigated until fairly recently, mainly because most of the early studies on fish hearing employed sound sources unable to produce undistorted tones below 20–30 Hz. Furthermore, the sound pressure audiograms obtained in these studies indicated a steadily declining sensitivity towards lower frequencies, making the idea about infrasound detection in fishes less interesting. However, the unaided otolith organs of the inner ear are not sensitive to sound pressure. The hair cells are directional sensitive displacement detectors, and the receptor current is dependent on the hair bundle displacement. The apical hair bundles of vertebrate hair cells are coupled to a variety of accessory structures, an otolith, a cupula or a tectorial membrane. It is the combined physical properties of these structures and the hair cells that determine the adequate stimulus, sensitivity and the frequency range of the organ.

The otolith organs in fishes may be treated as simple harmonic oscillators (figure 1*a*), as outlined by de Vries (1950). Otolith organs are nearly critically damped, and at frequencies below the natural frequency of the system the deflection of the otolith relative to the sensory epithelium follows the acceleration of the fish. Such a system is thus an accelerometer, and figure 1*b* shows the response of the model for a given acceleration as a function of frequency. The model indicates a working range of otolith organs reaching from zero to the upper frequency limit of hearing.

The tradition of relating fish audiograms to sound pressure has led to misinterpretations concerning optimal frequency ranges and hearing capabilities, since the shape of the audiogram greatly depends on the acoustic parameter to which thresholds are related. Figure 1*c* shows a hypothetical fish audiogram related to particle displacement, sound pressure (or particle velocity) and particle acceleration. When thresholds are related to particle acceleration, which is the relevant stimulus parameter at very low frequencies, the apparent drop in sensitivity towards low frequencies disappears.

The presence of a gas-filled swim-bladder makes the situation more complex. When a volume of gas in water is exposed to pressure changes, it will display larger volume pulsations than a comparable volume of water, due to its higher compressibility. Upon exposure to sound, the surface of the swim-bladder may thus show larger motion amplitudes than the water particles in the absence of a gas-filled bladder. These amplified motions may then be transmitted to the inner ear, providing an auditory gain to the fish, and making the fish as a whole sensitive to sound pressure. However, this gain is frequency dependent, and the swim-bladder pulsations exceed the free field particle motions only above a certain frequency (Sand & Hawkins 1973), which will depend on both swim-bladder volume and depth. In any case, even fishes possessing a swim-bladder will be insensitive to sound pressure in the infrasound range.

2. BEHAVIOURAL EXPERIMENTS

To test the infrasound sensitivity in fishes, we used either an acoustic tube or a closed chamber suspended in a swing. In the first case the whole water mass in the tube, including the fish, is accelerated by vibrators operating 180° out of

*Author for correspondence (olav.sand@bio.uio.no).

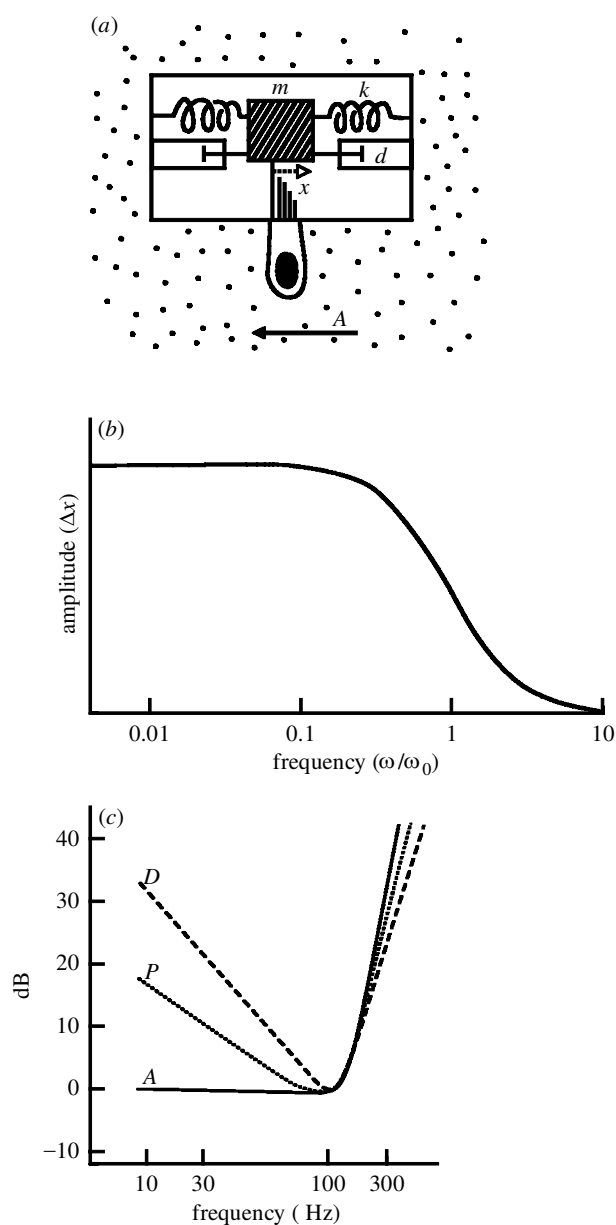


Figure 1. (a) Model of an otolith organ as a simple harmonic oscillator. m , effective otolith mass; k , spring force per unit of displacement; d , frictional force per unit of velocity; x , displacement of the otolith relative to the hair cells; A , peak acceleration of the fish. (b) Hair bundle displacement of a critically damped model system for a given acceleration as a function of frequency, presented as the ratio between the stimulus frequency (ω) and the natural frequency (ω_0) of the system (modified from Kalmijn 1989). (c) Hypothetical fish audiogram related to particle displacement (D), sound pressure or particle velocity (P) and particle acceleration (A).

phase and connected to rubber membranes at each end of the tube (Sand & Karlsten 1986; Karlsten 1992a). In the latter case, the fish is enclosed in a water-filled chamber suspended by four steel strings, and the whole chamber, including the water and the fish, is vibrated (Karlsten 1992b). Both these methods simulate the kinetic component of infrasound stimulation in the field.

The infrasound thresholds were obtained using the traditional cardiac conditioning technique. By giving the

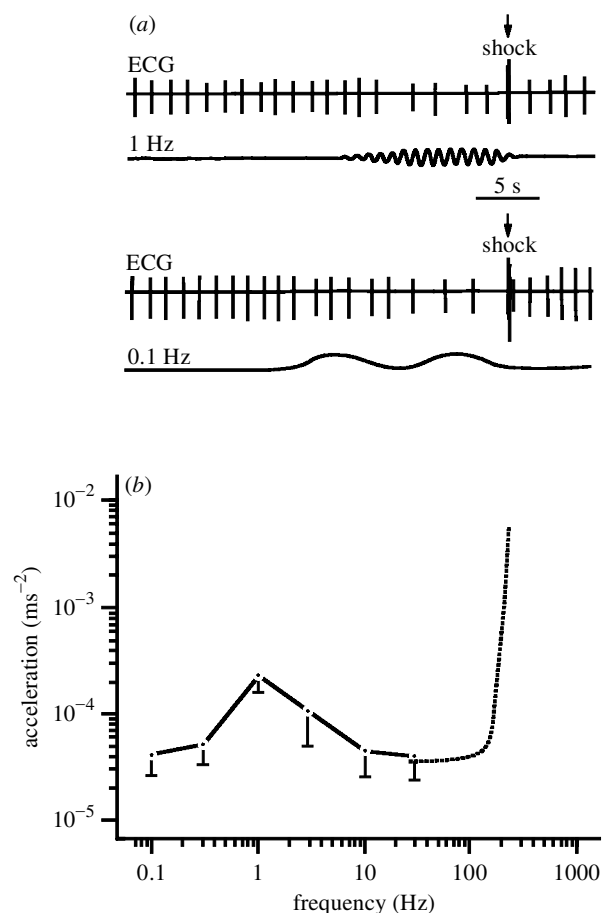


Figure 2. (a) Conditioned cardiac response (slowing of the heart rate) in Atlantic cod to 1 Hz (upper panel) and 0.1 Hz (lower panel) infrasound. The lower trace in each panel presents the particle displacement. An electric shock was given at the end of each stimulus (from Sand & Karlsten 1986). (b) Infrasound thresholds for plaice (mean values s.d., $n = 6$) compared with the previously reported audiogram for this species (from Karlsten (1992a), dotted line from Chapman & Sand (1974)).

fish a weak electric shock at the termination of the stimulus, the fish was trained to give a fright response, in the form of bradycardia or reduced heart rate, when the sound was presented. The actual thresholds were then determined using the staircase method.

The first species we tested was the Atlantic cod (*Gadus morhua*), and figure 2a presents positive bradycardia responses to 1 and 0.1 Hz tones. The threshold at 0.1 Hz was about 10^{-5} m s^{-2} , which represents a sensitivity to linear acceleration about 10 000 times higher than in humans. We later tested the plaice (*Pleuronectes platessa*), which is a flatfish, and the freshwater perch (*Perca fluviatilis*). Figure 2b compares the infrasound thresholds in the plaice with the previously known audiogram for this species. The added thresholds extend the audiogram with eight octaves. The reason for the elevated thresholds at 1 and 3 Hz may be masking, possibly due to respiratory movements.

The infrasound sensitivity observed in these experiments is dependent on the otolith organs and not the lateral line. The mass of the lateral line cupulae is close to that of the surrounding water, and no relative movements deflecting the sensory hair bundles will occur when the

fish and the surrounding water are accelerated in a sound field (Sand 1981). This was confirmed in experiments where the lateral line organs in the perch were blocked by cobalt ions in the external water. Both Co^{2+} and several other heavy metal ions reversibly inhibit the mechanosensitivity of the hair cells. The more exposed lateral line hair cells are effectively blocked by Co^{2+} in the water, while the enclosed hair cells of the otolith organs are not impaired by such treatment (Karlsen & Sand 1987). The infrasound thresholds in the perch were not affected by blocking the lateral line mechanosensitivity by Co^{2+} (Karlsen 1992a), confirming that the otolith organs are the sensory system involved in the observed infrasound detection.

3. POSSIBLE IMPLICATIONS OF THE HIGH INFRASOUND SENSITIVITY IN FISHES

The acute sensitivity to infrasound, or linear acceleration, in fishes may provide a wide range of information about the environment. A fish may, for instance, use the infrasound sensitivity to detect moving objects in its surroundings. This hypothesis is based on recordings made by Kalmijn (1989) of the hydrodynamic noise produced by swimming goldfishes. The major acceleration components of the noise was in the infrasound range below 10–20 Hz. Infrasound sensitivity in fishes may thus be important in, for instance, courtship and prey–predator interactions. Juvenile salmonids display strong avoidance reactions to infrasound (Knudsen *et al.* 1992), and it is reasonable to suggest that such behaviour has evolved as a protection against predators. Infrasound has been used as an effective acoustic barrier for descending Atlantic salmon (*Salmo salar*) smolts (Knudsen *et al.* 1994). We have recently shown that also descending European silver eels (*Anguilla anguilla*) are deflected by intense infrasound (Sand *et al.* 2000).

Close range detection of the hydrodynamic noise produced by moving objects may involve both the inner ear and the lateral line. However, the two systems may convey different types of information to the fish. Enger *et al.* (1989) have shown that although the predatory bluegill (*Lepomis macrochirus*) detects the presence of a goldfish by inner ear sensation in absolute darkness, an intact lateral line system is essential for launching the final strike. The division of labour between the lateral line and the inner ear in extracting information about local, low-frequency sources of hydrodynamic noise is an interesting topic that needs further clarification.

The ambient noise in the sea increases towards lower frequencies, and the spectral slope is particularly steep in the infrasound range (Urlick 1974). Among the suggested sources of the high level of ambient infrasound are turbulence along the edges of ocean currents and seismic motion of the ocean floor. Due to continental drift, the sea floor will have areas of particularly high seismic activity, such as, for instance, the Mid-Atlantic Ridge. The infrasound noise will propagate long distances with little energy loss, being reflected from the continents and causing a directional pattern of infrasound in the oceans. In coastal waters several additional sources of infrasound are important. A highly speculative hypothesis, which

has not been tested experimentally, is the idea that migratory fishes may use the infrasound pattern in the ocean for orientation and navigation.

It is also an interesting possibility that the otolith organs detect water movements due to surface waves. If the total water depth is large compared with the wavelength, the wave-generated particle movements are circular and decreasing exponentially in amplitude with depth. However, when the total depth is less than half the wavelength, the presence of the sea floor will distort the particle movements and slow the wave speed. The particle movements are then elliptical below the surface, approaching linear movements close to the bottom. The effect of the bottom on the wave speed causes the wavefront to bend (refract) towards the shallower area. Wave trains travel long distances across the oceans beyond the weather systems acting as wave generators, and wavelengths of several hundred metres are common. Wave interactions with the bottom may thus occur even in fairly deep water. It is therefore feasible that the high acceleration sensitivity allows pelagic fishes to detect the presence of shelves associated with distant land by subtle changes in the wave pattern as the total water depth decreases. The wave refraction may provide directional cues regarding the position of the land formations. Again, this speculative hypothesis has not been experimentally tested.

The emerging picture is that fishes might be living in a complex acoustic and hydrodynamic landscape, with distinct landmarks and information about distant structures, rather than in a homogeneous three-dimensional medium. The otolith organs detect the gross features causing whole body acceleration of the fish, while the lateral line organs detect local discontinuities and disturbances caused by extremely close sources. In the latter cases both the inner ear and the lateral line organs may be stimulated.

Another speculative hypothesis lacking verification is the possible use of the high sensitivity to linear acceleration for inertial navigation. This method is based on accurate measurements of acceleration, followed by integrations with respect to time to obtain velocity and distance. The remarkable ability of ballistic missiles to hit prescribed targets depends upon inertial guidance. It seems unlikely that fishes would depend on inertial navigation for long periods. However, such navigation could be very useful during shorter periods when adequate external information is lacking. The possibility of inertial guidance in animals has previously been pointed out several times. Harden Jones (1984) has for instance suggested that migrating plaice in the North Sea are using inertial guidance based on the semicircular canals to maintain a surprisingly stable heading in mid-water in the absence of visual and tactile cues. However, the acceleration sensitivity of the inner ear otolith organs may be sufficient to account for these observations. The centripetal acceleration experienced by a fish that is deflected off its original bearing and starts swimming in a circle, is the square of the swimming speed divided by the radius of the circle. Assuming an acceleration sensitivity better than 10^{-4} m s^{-2} and a swimming speed of 0.5 m s^{-1} , the detection limit will be a circular motion with a diameter of more than 5 km.

A special case of inertial guidance is the possibility of detecting the relative speed and direction of layered ocean currents. This could be achieved when a fish is cruising at constant swimming speed from one layer to another with a different current velocity. During the passage through the transition zone between the layers the fish may then experience a detectable acceleration, conveying information about the differences in current velocity. If it takes between 1 and 10 s to go from one layer to the next, the fish may detect differences in current speed of less than 1 mm s^{-1} . It has been proposed that homing salmon may use such a mechanism to determine the direction of currents housing olfactory information about the home river (Westerberg 1982; Døving *et al.* 1985).

Sensitivity to infrasound, or low-frequency linear acceleration, may be an important sensory ability not only in fishes, but also in several other aquatic animal groups. Thus both cephalopods (Packard *et al.* 1990) and crustaceans (Heuch & Karlsen 1997) have been shown to possess acute infrasound sensitivity.

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