DETECTION OF INFRASOUND BY THE ATLANTIC COD

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SUMMARY

Below about 50 kHz the level of ambient noise in the sea increases continuously towards lower frequencies. In the infrasound range the spectral slope is particularly steep. This low-frequency noise may propagate long distances with little attenuation, causing a directional pattern of infrasound in the sea. Using a standing-wave acoustic tube, we have studied the sensitivity of cod to infrasound down to 0·1 Hz by means of the cardiac conditioning technique. The threshold values, measured as particle acceleration, showed a steady decline towards lower frequencies below 10 Hz, reaching a value close to 10^{-5} m s^{-2} at 0·1 Hz. The spectrum level at 0·1 Hz in the sea ranges between 120 and 180 dB (re 1 μPa), with corresponding particle accelerations from less than 10^{-6} to more than 10^{-4} m s^{-2}. The sensitivity of cod is thus sufficient to detect the highest levels of ambient infrasound, and we put forward the hypothesis that fish may utilize information about the infrasound pattern in the sea for orientation during migration, probably in addition to an array of other sensory inputs.

INTRODUCTION

The otolith organs of the inner ear are responsible for sound detection in teleosts. These organs are acceleration detectors, showing highly directional responses to vibration (Sand, 1974; Hawkins & Horner, 1981; Fay, 1984) in addition to detecting gravitation or acceleration due to movements of the animal. This constitutes the basis for an acute directional hearing, which in teleosts occurs in both azimuth and elevation (Hawkins & Sand, 1977; Buwalda, Schuijf & Hawkins, 1983). Below about 50 kHz the level of ambient noise in the sea increases continuously towards lower frequencies (Urick, 1967). In the infrasound range below 10 Hz the spectral slope is particularly steep; about 12 dB per octave in the range 1–10 Hz and about 20 dB per octave below 0·1 Hz (Nichols, 1981). Among the suggested sources of this high level of infrasound are turbulence due to ocean currents and seismic motions of the ocean floor (Wenz, 1962; Urick, 1974). Unstable areas, like the Mid-Atlantic Ridge, may be particularly important sound sources in this frequency range. This low-frequency noise may propagate long distances with little attenuation, causing a pattern of infrasound in the sea with regional variation in the directional characteristics. The sensitivity of fish to infrasound has not been tested in any species. Several species of fish, including the Atlantic cod (*Gadus morhua*), exhibit regular and extensive migrations (Harden Jones, 1968; Smith, 1985). As a first step to investigate the
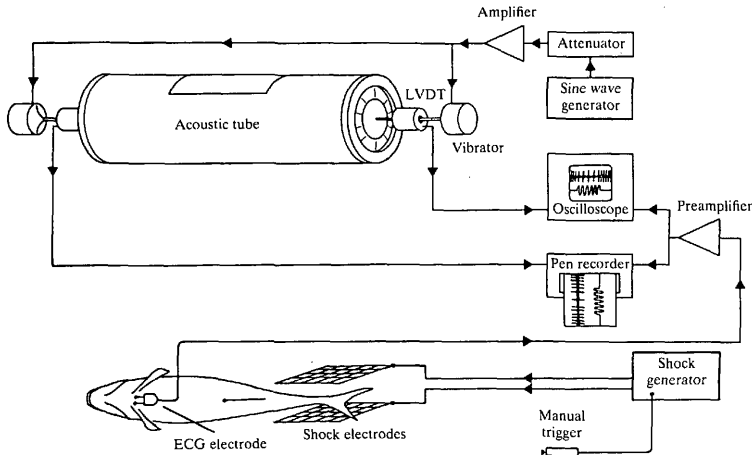
Fig. 1. The experimental arrangement for testing infrasound sensitivity in cod. The fish was positioned centrally in an acoustic tube, and stimuli were delivered by oscillating the pistons at each end 180° out of phase. See text for further details. LVDT, electro-mechanical transducer.

possibility that ambient infrasound in the sea may be used as a cue for orientation during migration, we have studied the sensitivity of cod to infrasound down to 0·1 Hz. The acute sensitivity we report for this species enables cod to detect the louder infrasound sources in the sea.

MATERIALS AND METHODS

Stimulus

The experimental arrangement is shown in Fig. 1. The fish was confined in a plastic (PVC) netting cage positioned centrally in a modified version of an acoustic tube previously described (Sand, 1981). The cage was free to move with the water column in the tube. Aerated sea water was slowly circulated through the tube, which was fitted with a piston vulcanized to a rubber membrane at each end. The pistons were driven by vibrators (Derritron, VP-2MM) which usually operated 180° out of phase, causing uniform particle movements throughout the length of the tank (Hawkins & MacLennan, 1976). The particle movements in the tank in this mode were measured by incorporating an electromechanical transducer (LVDT) as part of the axis between the piston and the vibrator. The validity of this method was assessed by separate measurements using a velocity hydrophone with a lower frequency limit of 10 Hz (Sand, 1981). At this frequency the movements of the axis reflected the particle movements centrally in the tank with an error of less than 10 % when the pistons worked at a phase difference of 180°. Particle motion in this report is presented as root-mean-square acceleration. To avoid interference with the

boundary zone close to the tube wall, a central position of the netting cage was secured by extending each of its end walls beyond the 8 cm diameter of the cage to form a flange loosely fitting the 12 cm inner diameter of the tube. The longitudinal position of the cage was secured with loose rubber bands.

The force needed to vibrate the water column in the tube is composed of acceleration, friction and spring forces. The mechanics of our system cause the friction force to be small compared to the spring force (tension in the membranes and the suspension system of the vibrators). For a given vibration amplitude the acceleration force decreases with decreasing frequency, and for the lowest frequencies tested in the present experiments, the spring force therefore dominates. This force is directly proportional to the displacement, which thus closely follows the waveform of the current through the vibrators. To avoid on-transients, the rise time of the stimuli covered several cycles for frequencies of 1 Hz and above (Fig. 2A). However, at lower frequencies this procedure would require very long stimulus periods. The stimuli at 0·3 Hz and 0·1 Hz were therefore restricted to 5 and 2 cycles, respectively, and the waveform of the stimulus was modified to reduce the necessity of a prolonged rise time. It is not possible strictly to attribute a single frequency to a stimulus consisting of a limited number of cycles. For instance, one cycle of a symmetrical sine wave displacement initiated at a phase of zero crossing, where
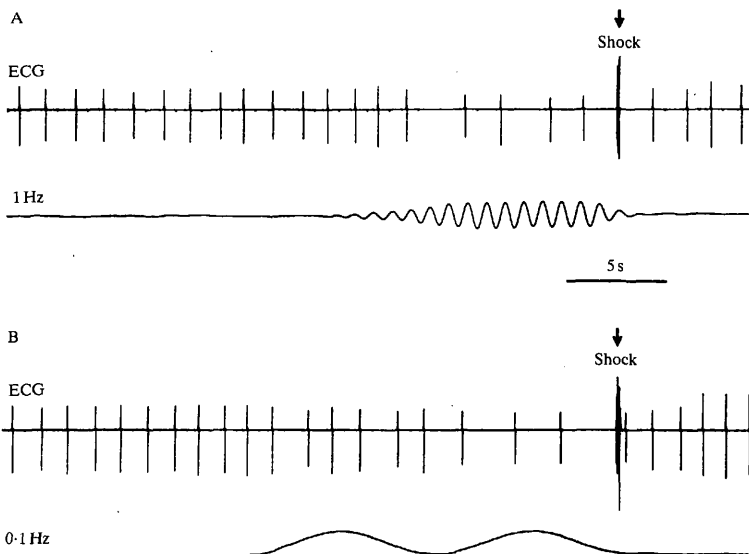

Fig. 2. Conditioned cardiac response (slowing of the heart rate) to 1 Hz (A) and 0·1 Hz (B) infrasound. The lower trace in each example is a record of the piston displacements. An electric shock was given at the end of each stimulus.

the velocity has its peak value, causes a short-lasting acceleration on-transient far exceeding the peak acceleration during a corresponding continuous sine wave vibration. To obtain a better approximation of a single frequency stimulus, the sine wave current to the vibrators was therefore d.c.-shifted one peak value, and the stimulus was initiated at zero current. The full amplitude sine wave vibrations were then entered directly at a phase of peak displacement, where the velocity is zero (Fig. 2B). This method gave an average d.c. displacement shift during a stimulus cycle, but both the velocity and acceleration followed a normal sine wave pattern symmetrically around the zero line. There were no over-shooting on-transients, although the acceleration started at its peak value.

Conditioning

The sensitivity to low-frequency sound was examined by means of the cardiac conditioning technique (Chapman & Hawkins, 1973). The Atlantic cod (31–34 cm long) were caught in creels at shallow depths and kept in captivity for at least 2 weeks before the experiments. Cardiac electrodes were attached to the fish during MS 222 anaesthesia, and the animals were allowed to recover for at least 12 h before training began. The stimulus was presented for 10–20 s, and a mild electric shock (4 V a.c.) to the tail region was given at the end of the stimulus period. The conditioned response, which consisted of a pronounced slowing of the heart rate (Fig. 2), was initially established employing high stimulus levels. The threshold level was then determined using the staircase technique. Close to threshold the stimulus was varied in 3-dB steps. Usually 5–7 steps were included in each threshold determination. The threshold was calculated as the stimulus level giving 50 % probability for a positive response (Dixon, 1965). The electrocardiogram was continuously recorded by a pen recorder during a test session. The response was considered positive if any of the heart beat intervals during the stimulus exceeded the longest of the 20 preceding intervals by at least 10 %. The heart rate of an undisturbed fish was fairly regular before the testing started. However, after the first couple of threshold determinations the fish could periodically show false positive responses in the absence of stimulation. During such periods the testing was halted. Each fish was tested for 2–3 days, and for a given frequency the final threshold was taken as the average value of 2–3 threshold determinations on consecutive days. The difference between these values was within 5 dB.

RESULTS AND DISCUSSION

A total of 11 cod were tested. All of these were easily conditioned to 3 or 10 Hz, whereas only six individuals were trainable to lower frequencies. One possible explanation for this irregularity may be that the lowest frequencies are inherently less frightening to the fish, which makes negative conditioning less efficient. The threshold values, measured as particle acceleration, declined towards lower frequencies below 10 Hz, reaching a value close to $10^{-5} \, \mathrm{m \, s^{-2}}$ at 0·1 Hz (Fig. 3). We were not able to measure the background acceleration noise in the tube at these
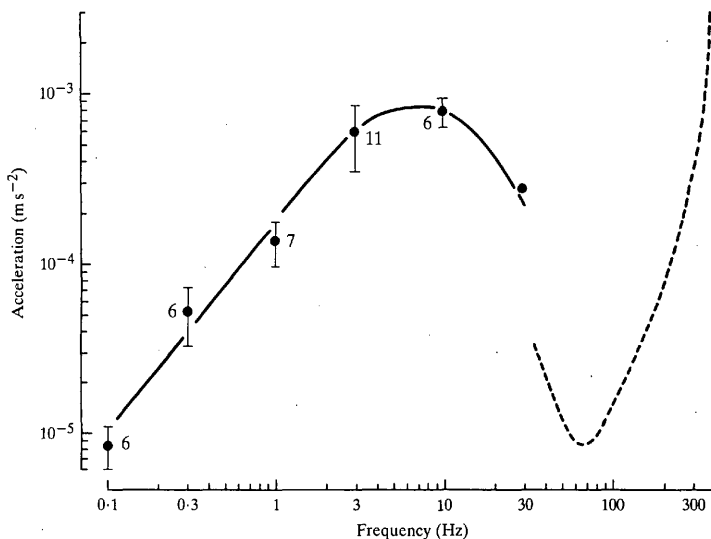
Fig. 3. Infrasound thresholds presented as mean values ± S.D. for the frequency range 0·1–10 Hz. The number of fish tested at each frequency is indicated on the figure. Only one specimen was tested at 30 Hz. The broken curve gives the available data on the motion sensitivity of the otolith organs in cod for frequencies above 30 Hz (recalculated from Chapman & Hawkins, 1973).

frequencies. However, the vertical vibrations of the laboratory floor measured in 1/3 octave bands were between 10^{-6} m s^{-2} and 10^{-5} m s^{-2} in the frequency range 0·3–10 Hz. Above 10 Hz the vibration noise increased rapidly, reaching 2×10^{-4} m s^{-2} at 30 Hz, and thresholds above this frequency were therefore not measured.

In addition to the vectorial direct input to the ear from the particle acceleration of the incident sound wave, there is an indirect motional input due to swimbladder pulsations induced by the incident sound pressure, although the end organ is still sensitive to particle motion (Sand & Enger, 1973). Taking this effect of the swimbladder into account, Chapman & Hawkins (1973) have estimated the actual displacement thresholds for the otolith organs in cod for frequencies between 30 and 470 Hz. These values have been recalculated to acceleration and are included in Fig. 3 as the broken curve. It can be seen that the acceleration threshold at 0·1 Hz is comparable to the lowest thresholds in this frequency range. At 30 Hz our threshold was about 20 dB above the corresponding value estimated from the data given by Chapman & Hawkins (1973). This indicates that our thresholds might be masked by the background noise in the tube. The degree of masking at the different frequencies was not studied in the present experiments. The shape of the presented infrasound audiogram might therefore in part have been determined by the background noise.

The biologically important result of our study is thus the generally high sensitivity to infrasound, rather than the detailed shape of the presented audiogram.

Below a certain frequency, the swimbladder will not improve the hearing sensitivity, since the reradiated motions of the swimbladder will be less than the free field particle motions (Sand & Hawkins, 1973). In the acoustic far-field this lower frequency limit can be estimated to be about 15–20 Hz in the cod (Chapman & Hawkins, 1973). In the present experiments the fish were clearly responding to particle motion and not to sound pressure. Switching the vibrators to operate in phase causes increased sound pressure and reduced particle movements in the tube centre (Hawkins & MacLennan, 1976; Sand, 1981), and such a procedure inevitably led to negative responses at stimulus levels close to threshold. At 10 Hz the ratio between the sound pressure in the tube centre at these two test situations was about 30 dB.

The lateral line organs have been suggested to function as low-frequency sound detectors at distances of more than several body lengths from the source (Suckling & Suckling, 1964; Weiss, 1969; Offutt, 1974; Horch & Salmon, 1973). However, the cupulae of these organs have a density close to that of the surroundings, and no relative movements to stimulate the hair cells will therefore occur during acceleration in a sound field at some distance from the source. In a previous study multiunit activity from the lateral line nerve in the roach (*Rutilus rutilus*) has been recorded in the same acoustic tube as used in the present experiments. The lateral line was then shown to be insensitive to water vibrations created by driving the loudspeakers 180° out of phase (Sand, 1981). We therefore believe the otolith organs to be responsible for the reported infrasound thresholds. However, blocking of the lateral line should be performed in future experiments in order to explore this question.

In humans the threshold for detection of 0·06–0·5 Hz linear oscillations or sustained linear acceleration is about $10^{-1}\,\mathrm{m\,s^{-2}}$ (Benson, 1978), which is 10^4 times above the threshold in cod at 0·1 Hz. However, the sensitivity of cod to infrasound compares well with the electrophysiologically determined seismic sensitivity in frogs, which display threshold values down to $10^{-5}\,\mathrm{m\,s^{-2}}$ (Lewis, 1984).

The available information on ambient infrasound in the sea is sparse. At shallow depths, spectrum levels above 180 dB re 1 μPa at 0·1 Hz have been reported, whereas the levels at depths of several hundred metres range between 120 and 150 dB (Schneider, Farrell & Brannian, 1964; Nichols, 1981). The corresponding particle accelerations at 0·1 Hz, estimated from these sound pressure levels, range from less than $10^{-6}\,\mathrm{m\,s^{-2}}$ to more than $10^{-4}\,\mathrm{m\,s^{-2}}$. The sensitivity in cod is therefore clearly sufficient to detect the loudest infrasound sources in the sea, and we put forward the hypothesis that fish may utilize information about the infrasound pattern in the sea for orientation during migration. Migrating fish probably depend upon an array of different sensory input for successful navigation and orientation (Harden Jones, 1968; Smith, 1985). The possibility that infrasound may be important in this respect has previously not been considered, although atmospheric infrasound has been suggested to provide clues for navigation in birds (Yodlowski, Kreithen & Keeton, 1977; Kreithen & Quine, 1979). However, it should be stated that the possible use of

infrasound detection for orientation in fish is presently a highly speculative hypo-thesis. We have no information about the actual infrasound levels along the route of migrating cod or other fish species. It is also likely that a moving school of fish produces low-frequency sounds which could mask the detection of ambient infra-sound. Future studies should be undertaken to measure the infrasound levels in the relevant areas. To clarify if the ambient infrasound may provide significant information to the fish, the behaviour in the normal habitat during interference with the natural infrasound, without exceeding normal levels, should be studied.

Apart from the possible use for orientation, high sensitivity to low-frequency sounds below a few Hz may be important for prey detection (A. J. Kalmijn, O. Sand & P. S. Enger, unpublished data). The high sensitivity to linear acceleration in cod is also interesting regarding the possible use of inertial navigation. This method is based on accurate measurement of acceleration, followed by integrations with respect to time to obtain velocity and distance. The remarkable ability of ballistic missiles to hit predescribed targets depends upon inertial guidance. In spite of the lack of compelling evidence, the potential use of this system in animals has been pointed out several times (see Barlow, 1964). It seems unlikely that migrating fish should depend on inertial navigation for long periods. However, such navigation could be very useful during shorter periods when adequate external information is lacking.

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