Vibration Measurements of the Perch Saccular Otolith

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Summary. 1. The vertical movement of different parts of the perch saccular otolith was measured with a laser vibrometer during horizontal vibration of the fish back and forth along its long axis. Data were obtained at four different frequencies within the audible range of the fish. Vibration at these frequencies caused very little vertical movement of the skull.

2. No vertical oscillations of the otolith were detected at 20 Hz, whereas both ends of the otolith showed vertical vibrations at 40, 90 and 220 Hz. An area of minimum vertical movement appeared around the midpoint of the otolith at these frequencies, thus indicating the existence of a horizontal axis of rotation.

3. It is argued that the stimulation technique is a reasonable approximation to underwater sound exposure. The measurements thus support the idea of a coarse, peripheral frequency analysis in fish based on a frequency dependent pattern of sound induced otolith movements.

Introduction

The sacculus and the lagena are the parts of the teleost ear which are mainly involved in hearing. These structures consist of an endolymph-filled sac containing a heavy calcareous otolith in close contact with the sensory epithelium. The otoliths have a specific gravity of about 2.9 (de Vries, 1950). Due to their greater density the otoliths lag behind the motion of the sensory epithelia when the fish is vibrated in a sound field, thus creating shearing movements of the sensory hairs.

Fish lack an obvious mechanical frequency analyzer comparable to the mammalian cochlea. Behavioural studies have, nevertheless, shown fish to have a well developed ability of frequency discrimination (see Sand and Enger, 1974). Detection of only 3–4 % frequency difference has been reported for ostariophysine species. In comparison, humans are able to discriminate between tones differing about 0.2 % in frequency (within the optimal frequency range).

The mechanism for frequency discrimination in fish is not known, but there are two hypothetical possibilities: 1) Central analysis exploiting the synchronization between sound frequency and nerve impulse discharge, and 2) peripheral analysis based upon sensory units having different frequency sensitivities. Recordings from auditory neurones in fish show a clear phase locking between the afferent spikes and the sound stimuli, particularly at lower frequencies (Lowenstein and Roberts, 1951; Enger, 1963; Furukawa and Ishii, 1967). In addition, the tuning curves of single auditory nerve fibers may cover different frequency ranges (Enger, 1963; Furukawa and Ishii, 1967). The tuning of these fibers is considerably broader than those of mammals possessing a cochlea (Evans and Wilson, 1973). The data are, on the other hand, in agreement with the idea that fish may have a coarse, peripheral analyzer in addition to a central one.

Differences in the frequency sensitivity of the receptor cells may be caused by variation in size, sensory hair structure, stiffness etc. (Stylis, 1971). Such mechanisms have not been supported experimentally in either vertebrates or invertebrates. Another hypothesis has been introduced by van Bergeijk (1967), who suggested that sound stimulation might cause frequency dependent travelling waves along the fish maculae, thus creating a spatial distribution of stimulation maxima. The mechanism would be rather similar to the mechanism of frequency analysis in the cochlea. Other mechanisms based on the mechanical properties of the peripheral auditory system might, however, be responsible for a spatial distribution of stimulation maxima (Sand, 1974a):
Most teleosts have a gas filled swimbladder, and this organ may have an auditory function by acting as a pressure-movement transformer (Sand and Enger, 1973). The effective driving force acting on the inner ear in a fish exposed to pressure waves will thus be oscillations of the body originating from and traveling radial to the swimbladder, irrespective of the direction of the incident sound pressure wave. The otoliths are situated almost at the same horizontal level as the swimbladder. The otoliths should therefore oscillate in the horizontal plane when the fish is exposed to sound pressure waves. The movements of the otoliths may, however, also have a component in the vertical plane, since the asymmetrical shape and suspension of the otolith may cause rotational movements. Furthermore, a propeller effect may create torques acting on the stone due to the relative movements between the asymmetrical otolith and the surrounding liquid. A horizontal driving force could thus partly be translated into vertical otolith movements. Such a translation would be of physiological significance, since parts of the sound sensitive maculae of teleosts are situated in a vertical plane with a dorso-ventral orientation of the hair cells' sensitivity axis (Wersäll et al., 1965; Hama, 1969; Dale, 1976; Jørgensen, 1976; Popper, 1976; Enger, 1977). If the pattern of otolith movement is frequency dependent, then the part of the macula which is maximally stimulated by the otolith may change with frequency.

The present investigation was carried out to test this hypothesis. The vertical movement of different parts of the perch saccular otolith was measured during horizontal vibrations of the fish along its long axis. The measurements indicate the existence of a horizontal axis of rotation of the otolith and provide data for comparison at different frequencies. The measurements were performed using a laser vibrometer, which employs the reflected laser light to determine the vibration velocity of the reflecting surface (Michelsen and Larsen, 1978).

Materials and Methods

Preparation

The measurements were performed on six perch (Perca fluviatilis), ranging in length from 18 to 20 cm. The handling and operation of the fish has been described previously (Sand, 1974a). A fish was fixed in a holder, the skull was opened and the brain removed. The two sacculi lying in grooves in the skull floor were then exposed. The grooves are covered with the saccular membrane, which was removed in order to obtain laser reflections from the otolith surface. The reflections from the otoliths were too diffuse to give reliable measurements. Presumably, the somewhat translucent nature of the otoliths caused the light to be reflected not only from the surface, but also from inner parts of the otoliths. Fortunately, the otoliths are so heavy that we could add a small amount of white paint to their surface without a marked change in their weight. The liquid level of the saccus was therefore temporarily lowered by means of a small suction pipette, to allow the upper rim of the saccular otolith to be painted with white latex paint. After about 15 min the liquid was allowed to rise to its original level. It is not known whether this rise was caused by endolymph drained from other parts of the inner ear, or if the refilling liquid had a different source. White spots were also painted along the skull floor between the two sacculi, in order to facilitate vibration measurements of the skull itself.

The weight of the saccular otoliths used for our measurements ranged from 15 to 19 mg, and the paint added 0.5-0.7 % to these weights. The length of the otoliths was arbitrarily divided into 10 regions, which were numbered 0 to 9. The extreme anterior and posterior positions (named 0 and 9, respectively) were covered by the upper edge of the saccular groove in the skull floor. The vertical motion was measured at the eight remaining, evenly spaced points along the upper rim of the otolith.

Vibration

The vibrating table used for our measurements is a modified version of the type previously described (Sand, 1974a). The fish holder is attached to a 30 x 16 x 1.2 cm aluminum plate, which is vibrated horizontally by a coil vibrator driven by amplified signals from an oscillator (Fig. 1). The fish is clamped in air, so that no interference from water vibrations occurs. The table is freely suspended from steel brackets by steel wires (3 cm long, 0.3 mm diameter) attached at each of the four corners of the table. The movement of the table is monitored by three velocity transducers, positioned on the table in three orthogonal directions. The laser vibrometer was used to measure the vertical vibrations of the skull. At many frequencies the horizontal vibration of the fish caused vigorous vertical movements of the skull. At other frequencies, which were selected for the measurements of otolith movement, vertical movements of the skull could hardly be detected. The frequencies used (20, 40, 90 and 220 Hz) cover most of the audible frequency range in perch, which has an upper auditory frequency cut-off at about 300 Hz (Sand, 1974b). The velocity of the sinusoidal horizontal vibrations was kept constant at 630 µm/s (peak-peak) at all frequencies. This is within the physiological range.

Laser Measurements

The use of laser vibrometry for measuring the vibration velocities in hearing organs is discussed in detail elsewhere (Michelsen and Larsen, 1978). The laser vibrometer utilizes the principle of optical heterodyne detection for measuring the Doppler shift of light scattered from the surface of moving objects (Buchhave, 1975). The laser beam is divided into a measuring beam and a reference beam by a beam-splitter (Fig. 1). The measuring beam is focused on the object (here a spot of 30 µm diameter on the surface of the otolith, or, as a control, on the skull). The reflected light passes through the same lens system onto a pair of photo-sensitive diodes. The reference beam is given a 40 MHz frequency shift in a Bragg cell and is passed onto the diodes. The interaction of the two beams produces a beat frequency of 40 MHz plus the Doppler shift caused by movements of the object. A frequency tracker is used for demodulating the FM-signal, thus providing an analog signal proportional to the instantaneous velocity of the object. The apparatus can be used to detect vibrations from a fraction of a Hz to above 100 kHz.