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Directional encoding by fish auditory systems

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This paper reviews and discusses several investigations of the peripheral neural code for the directional axis of acoustical particle motion in the saccule of two fishes: goldfish (*Carassius auratus*) and toadfish (*Opsanus tau*). Most saccular afferents are directional in the manner of hair cells, having a cosine-shaped directional response pattern. The saccular sensory epithelia are orientated almost vertically in a para-sagittal plane. In the horizontal plane, these epithelia are orientated obliquely with respect to the midline. Hair-cell stereocilia project perpendicularly. Thus, directional response patterns of saccular afferents tend to be orientated in azimuth parallel to the orientation of the epithelia in the head. The oblique angle of the toadfish saccule is greater than that of the goldfish, and the range of best directions in the horizontal plane for each species reflects those differing orientations. The azimuth of acoustical particle motion could be computed by comparing the relative activation of the two saccules, as is the case for the ears of most terrestrial vertebrates. The spatial patterns of saccular hair-cell orientation of most fishes thus appear to have little function in azimuthal source location, but for toadfish are probably most important for determining the elevation of monopole sources.

Keywords: teleost; saccule; hearing; sound-source localization; fish ear; single cell recording

1. INTRODUCTION

Some fishes have been shown to be able to localize sound sources in azimuth and elevation using their auditory system (e.g. Hawkins & Sand 1977; Schuijf 1975). The dominant theories of sound-source localization by fishes (e.g. Schuijf & Buwalda 1975) are founded on the detection and processing of the vector component of underwater sound: acoustic particle motion. The auditory receivers are one or more of the otolith organs (the saccule, in most species studied) that respond with great sensitivity (Fay 1984; Fay & Edds-Walton 1997) to near- and far-field acoustic particle motion in the manner of inertial accelerometers (de Vries 1950). The motion of the very dense otoliths occurs at a smaller amplitude than the surrounding tissue as sound passes through the animal. Sensory hair cells of the ears transduce this relative motion as it occurs between the otolith and the sensory epithelium. Hair cells are inherently directional receivers (Hudspeth & Corey 1977).

Hair cells are arranged on the sensory epithelium with orientation patterns that are often species or family specific (Popper & Fay 1993). The majority of saccular afferents appear to contact one or more hair cells having the same directional orientation, and different afferents have different 'best orientations', i.e. the axis of stimulation that results in maximum spike activity at a given stimulus level (Fay & Edds-Walton 1997; Edds-Walton *et al*. 1999). Thus, the axis angle of acoustic particle motion could be resolved by processing the patterns of activity across the population of primary afferents, as proposed by Schuijf (1975). For monopole sources, the axis of particle motion falls on a line between the receiving fish and the source.

Our experimental work on the question of sound-source localization in fishes has focused on the peripheral neural codes that underlie the determination of the axis angle of acoustic particle motion. This paper reviews and compares neurophysiological experiments on two species: goldfish (*Carassius auratus*) (Fay 1984) and toadfish (*Opsanus tau*) (Fay & Edds-Walton 1997). These two species differ considerably in the auditory periphery, and in their uses of sound in communication. Goldfish are 'hearing specialists', having the Weberian ossicles that mechanically link the anterior swimbladder chamber with the ears' saccule. In this way, goldfish receive sound pressure as well as acoustic particle motion. Sound-pressure sensitivity gives them great overall acoustic sensitivity and hearing in a wider bandwidth than toadfish. Goldfish are not known to produce sounds or communicate vocally, and have relatively sensitive hearing at frequencies up to 2000 Hz. Toadfish lack peripheral adaptations for sound-pressure detection, but are known to vocalize during reproductive behaviors. The male advertisement call ('boatwhistle') is one of the most intense vocalizations known among fishes (Fish 1972). In spite of these differences, both species would be expected to localize sound sources, and to do so both must encode the directional features of the underwater sound field. The experiments discussed lead to the suggestion that the azimuth of a monopole sound source may be resolved using binaural cues while source elevation may be resolved monaurally using the directional neural code arising from diverse hair-cell orientations.

2. MATERIAL AND METHODS

Extracellular recordings were made from single afferents of the saccular branches of the auditory nerve in response to

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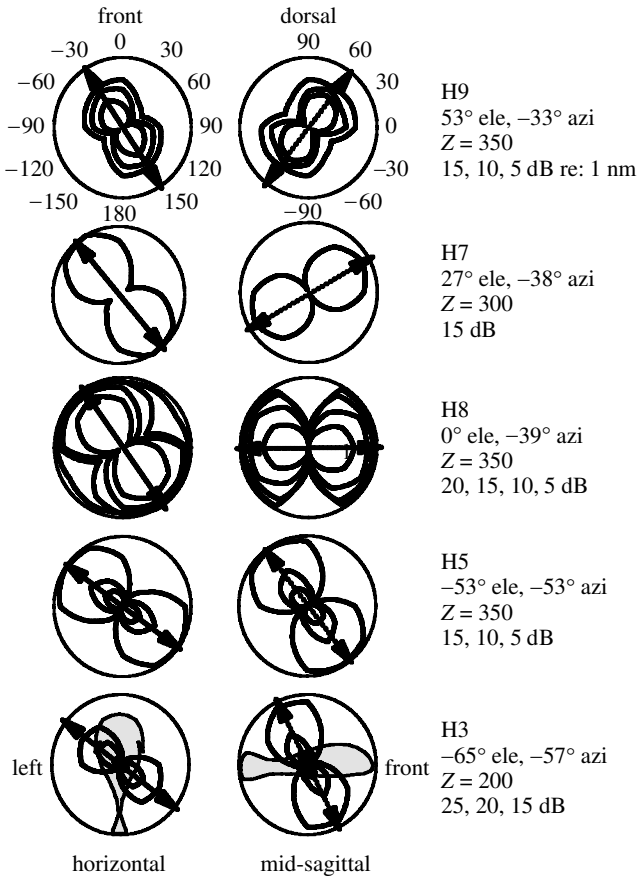

Figure 1. Directional responsiveness patterns for five saccular afferents from the left ear of a toadfish. Each is a polar plot of phase-locked spike rate (Z-statistic) as a function of stimulus axis angle, usually at several fixed displacement amplitudes (given in dB re: 1 nm). The afferent identity is given in the column on the right (e.g. H9), the most effective axis of stimulation in the mid-sagittal plane (ele) and the horizontal plane (azi) are given along with the phase-locked spike rate (Z) indicated by the maximum radius of the circular axes. The best direction in the horizontal plane (plots on left) and the mid-sagittal plane (plots on right) are shown for each afferent by the double-headed arrows, which also illustrate the 180 ambiguity inherent to these measurements. The stimulus angles are shown around each circle. To make these figures, the lines connect data points (not printed), each of which is plotted twice for clarity—once at the nominal axis angle, and once again at that angle plus 180°. The cartoon of the toadfish in the bottom panels indicates the plane represented.

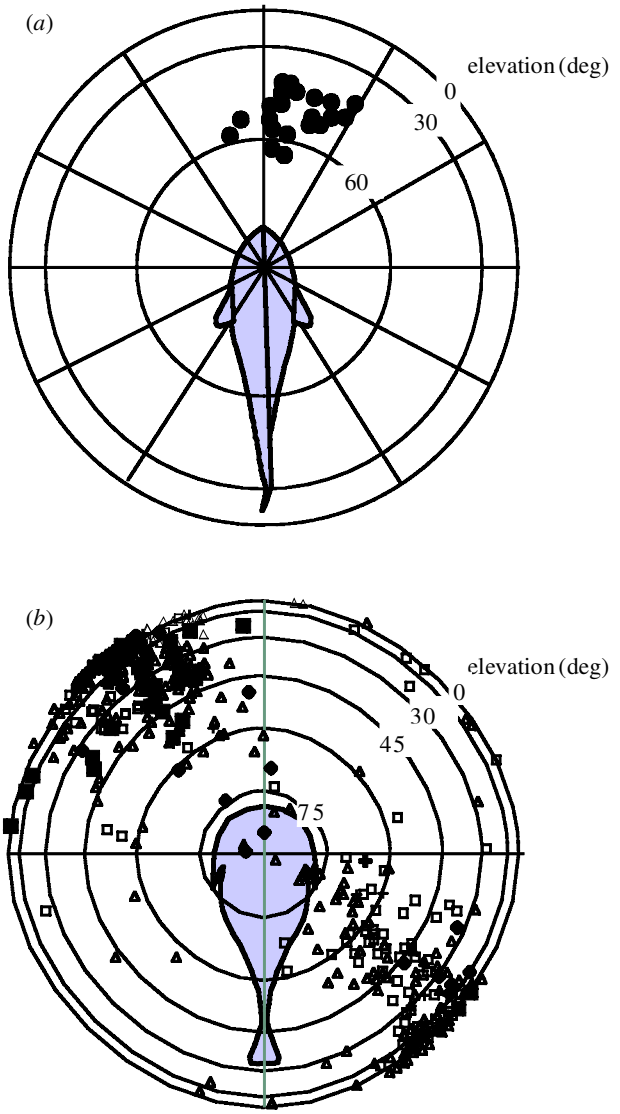

Figure 2. Representations of a globe, with the fish at the centre, showing the location on the Northern Hemisphere at which the most effective axis for each afferent penetrates the surface (see § 3). An afferent's azimuth is plotted on the circular axis as in a polar plot. Elevation is represented on the radial axis. (*a*) Twenty-one right saccular afferents from the goldfish (redrawn from Fay 1984). (*b*) Four hundred and forty-three left saccular afferents from the toadfish (redrawn from Edds-Walton *et al.* 1999). The differing symbols in (*b*) indicate data sets from different research seasons.

whole-body, linear translatory motion of low amplitude (displacements generally less than a micrometer). Stimuli were produced by a three-axis shaker system described in detail by Fay & Edds-Walton (1997). Two pairs of minishakers operated in a push–pull manner to create motion in the horizontal plane. A single shaker operated vertically. The five shakers were attached to a water-filled aluminium cylinder. Programs were created to generate sinusoids (100 Hz for toadfish and 140 Hz for goldfish) for each of the three shaker channels with the appropriate starting phases and amplitudes to create translational oscillatory movements of the cylinder along various axes in the horizontal and mid-sagittal planes of the fish. Cylinder movement was calibrated by monitoring three, orthogonally orientated accelerometers attached to the cylinder. Anaesthetized animals were attached rigidly within the cylinder by clamping the bones of the skull. For details, see Fay (1984) and Fay & Edds-Walton (1997).

When an afferent was contacted by the electrode, motional stimuli were presented sequentially at 30° intervals over a 150° range within at least the horizontal and mid-sagittal planes. Two types of directional response measurements were made. In the first (used with goldfish and toadfish), displacement thresholds were obtained by varying overall stimulus amplitude (displacement) for each of the directional stimuli using phase-locked spike rate as measured response magnitude. Phase-locked spike rate was defined as the Z-statistic ($Z = r^2N$), where r is the coefficient of synchronization, a phase-locking metric, and N is the number of spikes recorded during the stimulus presentations. A threshold was defined as the stimulus level producing a

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Z-value of 20, from which was obtained the stimulus angle at which threshold was lowest in each plane studied (details in Fay & Edds-Walton 1997).

In the second type of measurement (toadfish only), stimuli at each axis angle were presented sequentially at a given suprathreshold amplitude, and response magnitude (Z-statistic) plotted in polar coordinates as a function of stimulus axis angle (see figure 1). The axis angle producing the largest response was determined by fitting each directional responsiveness pattern with a cosine function. The phase angle of the best-fitting cosine defined the afferent's best azimuth in the horizontal plane, and the best elevation in the mid-sagittal plane. Thus, both measurement methods permitted the determination of the afferent's best orientation in azimuth and elevation.

3. RESULTS

For both goldfish and toadfish, the afferents investigated had best displacement thresholds between 0.1 nm and 1 μm, root-mean square. Figure 1 illustrates directional responsiveness functions for five afferents from the left saccule of one toadfish. These data illustrate the cosinusoidal (i.e. circular) form of most directional response patterns. On the left-hand side of figure 1, the best direction in the horizontal plane is illustrated using arrows for five afferents from the left saccule of one toadfish. Note that all best axes are near $-30°$ (and $-30° + 180 = 150°$), which approximately corresponds to the orientation of the saccular epithelium with respect to the midline of the fish. The right-hand column illustrates the diversity of best directions in the mid-sagittal plane for the same five afferents, with dashed arrows indicating the elevation of the best axis. This variation is probably caused by the various orientations of hair cells with which the afferents make contact. Thus, hair-cell orientation patterns on the saccular epithelium largely determine the range of best elevations recorded, at least for toadfish.

Figure 2 summarizes the best azimuths and elevations for the saccule of (*a*) the goldfish and (*b*) the toadfish. In these plots, the view is down onto the North Pole of a globe with a fish at its centre. Each point locates the place that an afferent's best axis pierces the globe's surface in the Northern Hemisphere. Illustrated here is the finding that the distribution of best azimuths in the horizontal plane for saccular afferents is relatively narrow: most toadfish afferents (for the left ear) tend to respond best to a stimulus axis angle of about $-25°$ to $-65°$ to the left front, while most goldfish saccular afferents (for the right ear) respond best to an azimuthal axis of about 17° to the right front. These are the approximate angles at which the saccules are orientated in the head of the respective species. Thus, the range of azimuths seems to be determined by the horizontal plane orientation of the receptor organ itself.

4. DISCUSSION

Most saccular afferents in goldfish and toadfish have directional response patterns that resemble the cosine directional response functions of individual hair cells (Hudspeth & Corey 1977). This suggests that each afferent makes synaptic contact with one or more hair cells having approximately the same directional orientation on the sensory epithelium (Edds-Walton *et al.* 1999). In the goldfish, the majority of saccular hair cells are orientated dorsally or ventrally. In the toadfish, saccular hair cells may be found at all possible orientations in the vertical plane (see references in Fay & Edds-Walton (1997)). In both species, the saccular epithelium tends to be orientated obliquely when viewed from above: the left saccule is orientated forward to the left and the right saccule is orientated forward to the right with respect to the midline of the fish. Thus, no matter what the directional orientation of the hair cells on the epithelium, azimuthal stimulation will tend to be greatest when the relative otolith movement is parallel with the epitheliar surface (i.e. along the general orientation axis of the organ in the head). The distributions of best azimuth for the saccules of both species (figure 2) are consistent with this conception. This means that the saccular organs are themselves directional in response to motional stimuli in the horizontal plane. Thus, the population of saccular afferents will respond best to motional stimuli (acoustic particle motion) that are parallel to the orientations of their saccules, and will thus respond approximately in proportion to the cosine of the angle between the organ's orientation and the axis of particle motion. Since the paired saccules are differently orientated in azimuth, there will tend to be interaural differences in overall responsiveness for monopole sound sources at different azimuths.

In some afferents response magnitude is also represented in terms of spike times; phase-locking angle is level dependent in non-spontaneous afferents (Fay & Edds-Walton 1997). There will be, in effect, azimuth-dependent interaural differences in response magnitude and time for the fish saccules, even though there are zero or minimal interaural intensity or time differences, *per se*, reaching the ears. We hypothesize that these interaural response differences are used by the brain to compute stimulus azimuth. In this model, fishes would be like most other vertebrates studied in using interaural response differences as the basis for the computation of azimuth. Thus, hair-cell orientation patterns over the surface of the otolithic epithelium are likely to be unimportant for azimuthal sound-source localization.

Hair-cell orientation patterns on the saccule appear to be useful, however, in the determination of sound-source elevation, at least for toadfish. Given the approximately vertical orientation of the saccular epithelial plane, each differently orientated hair cell will respond best to motional stimuli having a corresponding elevation. Thus, it seems possible that an animal's determination of source elevation could be made based on the profile of activity over a population of orientation-labelled saccular afferents (as originally conceived by Schuijf (1975)), but within a single ear. In humans, sound-source elevation is thought to be estimated from the spectra of impinging sounds as shaped by the head-related transfer function: a monaural computation based on the frequency filtering of the head, pinnae, and torso, and the tonotopic organization of the cochlea. The toadfish saccule is not tonotopically organized (Fay & Edds-Walton 1997), but is organized directly with respect to the elevation of the most effective particle motion axis. This means that sound localization in fishes could be based on mechanisms of

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monaural and binaural computation substantially similar to those operating in most other vertebrates, and further, that these processing strategies may have originated among the fishes. The goldfish saccule does not seem as well suited to resolve the elevation of acoustic particle motion since the hair cells are orientated similarly, and the distribution of best elevations for saccular afferents is relatively narrow (figure 2). We have suggested (Fay & Edds-Walton 1997) that the lagena could serve this function in goldfish (see also Fay 1984).

Much of the theoretical writing on sound-source localization by fishes has focused on the '180° ambiguity' problem. This occurs because the process described above does not determine which end of the resolved axis points towards the source. This important ambiguity can be solved, in principle (Schuijf 1975), by comparing the particle motion phase with the sound-pressure phase. This issue has dominated thinking about sound-source localization in fishes for over 20 years. However, ambiguities in sound-source localization have also been revealed in most studies of localization in terrestrial vertebrates. Animals that sample sound parameters at two spatial locations using the paired ears are always faced with the problem that, for example, all sources on the median plane (up–down, front–back ambiguities) produce zero interaural time and intensity differences. The solutions to these problems may include head movements (sequential sampling from different head positions), visual and other extra-auditory cues, and estimation of the most probable source location based on knowledge of the environment's general structure. The 180° ambiguity problem for fishes is but one example of the sorts of ambiguities facing all vertebrates, and it might be useful to look for its solution in the animal's behaviours and in the use of other, non-auditory information.

REFERENCES

de Vries, H. I. 1950 The mechanics of the labyrinth otoliths. *Acta Oto-Laryngol.* **38**, 262–273.

Edds-Walton, P. L., Fay, R. R. & Highstein, S. M. 1999 Dendritic arbors and central projections of physiologically characterized auditory fibers from the saccule of the toadfish, *Opsanus tau*. *J. Comp. Neurol.* **411**, 212–238.

Fay, R. R. 1984 The goldfish ear codes the axis of acoustic particle motion in three dimensions. *Science* **225**, 951–954.

Fay, R. R. & Edds-Walton, P. L. 1997 Directional response properties of saccular afferents of the toadfish, *Opsanus tau*. *Hearing Res.* **111**, 1–21.

Fish, J. F. 1972 The effect of sound playback on the toadfish. In *Behavior of marine animals*, vol. 2 (ed. H. E. Winn & B. L. Olla), pp. 386–434. New York: Plenum.

Hawkins, A. D. & Sand, O. 1977 Directional hearing in the median vertical plane by the cod. *J. Comp. Physiol.* A **122**, 1–8.

Hudspeth, A. J. & Corey, D. P. 1977 Sensitivity, polarity and conductance change in the response of vertebrate hair cells to controlled mechanical stimuli. *Proc. Natl Acad. Sci. USA* **74**, 2407–2411.

Popper, A. N. & Fay, R. R. 1993 Sound detection and processing by fish: critical review and major research questions. *Brain. Behav. Evol.* **41,** 14–38.

Schuijf, A. 1975 Directional hearing of cod (*Gadus morhua*) under approximate free field conditions. *J. Comp. Physiol.* A **98**, 307–332.

Schuijf, A. & Buwalda, R. J. A. 1975 On the mechanism of directional hearing in cod (*Gadus morhua*). *J. Comp. Physiol.* A **98**, 333–344.

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