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## **Directional encoding by fish auditory systems**

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# **Directional encoding by fish auditory systems**<br> **Directional encoding by fish auditory systems**

### **Richard R. Fay**\* **and Peggy L. Edds-Walton**

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Parmly Hearing Institute, Loyola University Chicago, 6525 North Sheridan Road, Chicago, IL 60626, USA<br>This paper reviews and discusses several investigations of the peripheral neural code for the directional<br>axis of acoust 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 *(Chyan* 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 *(Opsan* 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 dire (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-<br>sagittal plane. In the horizontal plane, these epithelia are orientated obliquely with respect to the<br>midline. Hair-c 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 t 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 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 h polique angle of the toadfish saccule is greater than that of the goldfish, and the range of best directions<br>in the horizontal plane for each species reflects those differing orientations. The azimuth of acoustical<br>particl 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 e particle motion could be computed by comparing the relative activation of the two saccules, as is the case<br>for the ears of most terrestrial vertebrates. The spatial patterns of saccular hair-cell orientation of most<br>fishes for the ears of most terrestrial vertebrates. The spatial pattern<br>fishes thus appear to have little function in azimuthal source lo<br>important for determining the elevation of monopole sources. **Keywords:** teleost; saccule; hearing; sound-sources.<br>**Keywords:** teleost; saccule; hearing; sound-source localization; fish ear; single cell recording

#### **1. INTRODUCTION**

**1. INTRODUCTION**<br>Some fishes have been shown to be able to localize sound<br>sources in azimuth and elevation using their auditory Some fishes have been shown to be able to localize sound<br>sources in azimuth and elevation using their auditory<br>system (e.g. Hawkins & Sand 1977: Schuiff 1975). The domi-Some fishes have been shown to be able to localize sound<br>sources in azimuth and elevation using their auditory<br>system (e.g. Hawkins & Sand 1977; Schuijf 1975). The domi-<br>nant theories of sound-source localization by fishes sources in azimuth and elevation using their auditory<br>system (e.g. Hawkins & Sand 1977; Schuijf 1975). The domi-<br>nant theories of sound-source localization by fishes (e.g. 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 nant theories of sound-source localization by fishes (e.g.<br>Schuijf & Buwalda 1975) are founded on the detection and<br>processing of the vector component of underwater sound:<br>acoustic particle motion. The auditory receivers a Schuijf & Buwalda 1975) are founded on the detection and<br>processing of the vector component of underwater sound:<br>acoustic particle motion. The auditory receivers are one or<br>more of the otolith organs (the saccule in most s processing of the vector component of underwater sound:<br>acoustic particle motion. The auditory receivers are one or<br>more of the otolith organs (the saccule, in most species acoustic particle motion. The auditory receivers are one or<br>more of the otolith organs (the saccule, in most species<br>studied) that respond with great sensitivity (Fay 1984; Fay<br>& Edds-Walton 1997) to near- and far-field ac more of the otolith organs (the saccule, in most species<br>studied) that respond with great sensitivity (Fay 1984; Fay<br>& Edds-Walton 1997) to near- and far-field acoustic<br>particle motion in the manner of inertial acceleromet studied) that respond with great sensitivity (Fay 1984; Fay & Edds-Walton 1997) to near- and far-field accustic<br>particle motion in the manner of inertial accelerometers<br>(de Vries 1950). The motion of the very dense otolith & Edds-Walton 1997) to near- and far-field acoustic<br>particle motion in the manner of inertial accelerometers<br>(de Vries 1950). The motion of the very dense otoliths<br>occurs at a smaller amplitude than the surrounding tissue particle motion in the manner of inertial accelerometers<br>
(de Vries 1950). The motion of the very dense otoliths<br>
occurs at a smaller amplitude than the surrounding tissue<br>
as sound passes through the animal Sensory hair c (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 occur occurs at a smaller amplitude than the surrounding tissue ivity and hearing in a wider bandwidth than toadfish.<br>
as sound passes through the animal. Sensory hair cells of Goldfish are not known to produce sounds or communi as sound passes through the animal. Sensory hair cells of<br>the ears transduce this relative motion as it occurs between<br>the otolith and the sensory epithelium. Hair cells are inher-<br>ently directional receivers (Hudspeth & C the ears transduce this relative motion as it occurs between the otolith and the sensory epithelium. Hair cells are in ently directional receivers (Hudspeth & Corey 1977). Hair cells are arranged on the sensory epithelium e otolith and the sensory epithelium. Hair cells are inher-<br>tly directional receivers (Hudspeth & Corey 1977).<br>Hair cells are arranged on the sensory epithelium with<br>jentation, patterns, that, are, often, species, or, fami

ently directional receivers (Hudspeth & Corey 1977).<br>Hair cells are arranged on the sensory epithelium with<br>orientation patterns that are often species or family Hair cells are arranged on the sensory epithelium with<br>orientation patterns that are often species or family<br>specific (Popper & Fay 1993). The majority of saccular<br>afferents appear to contact one or more hair cells having orientation patterns that are often species or family<br>specific (Popper & Fay 1993). The majority of saccular<br>afferents appear to contact one or more hair cells having<br>the same directional orientation, and different afferen specific (Popper & Fay 1993). The majority of saccular<br>afferents appear to contact one or more hair cells having<br>the same directional orientation, and different afferents<br>have different ibest orientations' i.e. the axis of afferents appear to contact one or more hair cells having<br>the same directional orientation, and different afferents<br>have different 'best orientations', i.e. the axis of stimula-<br>tion that results in maximum spike activity the same directional orientation, and different afferents<br>have different 'best orientations', i.e. the axis of stimula-<br>tion that results in maximum spike activity at a given<br>stimulus level (Fav. & Edds-Walton 1997: Eddshave 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*  $a^{l}$  1999). Thus the axis angle of acoustic part 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 p al. 1999). Thus, the axis angle of acoustic particle motion<br>could be resolved by processing the patterns of activity<br>across the population of primary afferents, as proposed<br>by Schuif (1975). For monopole sources, the axis could be resolved by processing the patterns of activity<br>across the population of primary afferents, as proposed<br>by Schuijf (1975). For monopole sources, the axis of<br>particle motion falls on a line between the receiving fi across the population of primary afferents, as proposed arising from diverse hair-cell orientations.<br>by Schuijf (1975). For monopole sources, the axis of particle motion falls on a line between the receiving fish **2. MATER** particle motion falls on a line between the receiving fish

tion that results in maximum spike activity at a given experiments discussed lead to the suggestion that the stimulus level (Fay & Edds-Walton 1997; Edds-Walton *et* azimuth of a monopole sound source may be resolved *al.* Our experimental work on the question of sound-<br>urce localization in fishes has focused on the peripheral Our experimental work on the question of sound-<br>source localization in fishes has focused on the peripheral<br>neural codes that underlie the determination of the axis Our experimental work on the question of sound-<br>source localization in fishes has focused on the peripheral<br>neural codes that underlie the determination of the axis<br>angle of acoustic particle motion. This paper reviews and source localization in fishes has focused on the peripheral<br>neural codes that underlie the determination of the axis<br>angle of acoustic particle motion. This paper reviews and<br>compares neurophysiological experiments on two neural codes that underlie the determination of the axis<br>angle of acoustic particle motion. This paper reviews and<br>compares neurophysiological experiments on two species:<br>goldfish (Carassius, auratus) (Fay, 1984), and toad angle of acoustic particle motion. This paper reviews and compares neurophysiological experiments on two species:<br>goldfish (*Carassius auratus*) (Fay 1984) and toadfish compares neurophysiological experiments on two species:<br>goldfish *(Carassius auratus)* (Fay 1984) and toadfish<br>*(Opsanus tau)* (Fay & Edds-Walton 1997). These two<br>species differ considerably in the auditory periphery and 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  $(Opsanus\_tau)$  (Fay & Edds-Walton 1997). These two species differ considerably in the auditory periphery, and in their uses of sound in communication. Goldfish are  $\Omega$  the single specialists' having the Weberian ossicles that species differ considerably in the auditory periphery, and<br>in their uses of sound in communication. Goldfish are<br>'hearing specialists', having the Weberian ossicles that<br>mechanically link the anterior swimbladder chamber in their uses of sound in communication. Goldfish are<br>
"hearing specialists", having the Weberian ossicles that<br>
mechanically link the anterior swimbladder chamber<br>
with the ears' saccule In this way goldfish receive sound 'hearing specialists', having the Weberian ossicles that<br>mechanically link the anterior swimbladder chamber<br>with the ears' saccule. In this way, goldfish receive sound<br>pressure as well as acquisite particle motion. Soundmechanically link the anterior swimbladder chamber<br>with the ears' saccule. In this way, goldfish receive sound<br>pressure as well as acoustic particle motion. Soundwith the ears' saccule. In this way, goldfish receive sound<br>pressure as well as acoustic particle motion. Sound-<br>pressure sensitivity gives them great overall acoustic sensi-<br>tivity and bearing in a wider bandwidth than to pressure as well as acoustic particle motion. Sound-<br>pressure sensitivity gives them great overall acoustic sensi-<br>tivity and hearing in a wider bandwidth than toadfish.<br>Goldfish are not known to produce sounds or communipressure sensitivity gives them great overall acoustic sensitivity and hearing in a wider bandwidth than toadfish.<br>Goldfish are not known to produce sounds or communi-<br>cate yogally, and, have relatively sensitive hearing a tivity and hearing in a wider bandwidth than toadfish.<br>Goldfish are not known to produce sounds or communicate vocally, and have relatively sensitive hearing at 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 cate vocally, and have relatively sensitive hearing at<br>frequencies up to 2000 Hz. Toadfish lack peripheral adap-<br>tations for sound-pressure detection, but are known to<br>vocalize during reproductive behaviors. The male adver 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 tations for sound-pressure detection, but are known to vocalize during reproductive behaviors. The male advervocalize during reproductive behaviors. The male advertisement call ('boatwhistle') is one of the most intense<br>vocalizations known among fishes (Fish 1972). In spite of<br>these differences both species would be expected to l tisement call ('boatwhistle') is one of the most intense<br>vocalizations known among fishes (Fish 1972). In spite of<br>these differences, both species would be expected to locavocalizations known among fishes (Fish 1972). In spite of<br>these differences, both species would be expected to loca-<br>lize sound sources, and to do so both must encode the<br>directional features of the underwater sound field. these differences, both species would be expected to loca-<br>lize sound sources, and to do so both must encode the<br>directional features of the underwater sound field. The<br>experiments discussed lead to the suggestion that the lize sound sources, and to do so both must encode the<br>directional features of the underwater sound field. The<br>experiments discussed lead to the suggestion that the<br>azimuth of a monopole sound source may be resolved 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<br>using binaural cues while source elevation may be<br>resolved monaurally using the directional neural code<br>arising from diverse baix-cell orientations using binaural cues while source eleva<br>resolved monaurally using the directional<br>arising from diverse hair-cell orientations.

#### **2. MATERIAL AND METHODS**

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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 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 ( $\zeta$ -statistic) as a function of stimulus axis angle, usually at afferents from the left ear of a toadfish. Each is a polar plot of<br>phase-locked spike rate ( $\zeta$ -statistic) as a function of stimulus<br>axis angle, usually at several fixed displacement amplitudes<br>(given in dB re: 1 nm). T phase-locked spike rate ( $\zeta$ -statistic) as a function of stimulus<br>axis angle, usually at several fixed displacement amplitudes<br>(given in dB re: 1 nm). The afferent identity is given in the<br>column on the right (e  $\alpha$ , H axis angle, usually at several fixed displacement amplitudes (given in the result in m). The afferent identity is given in the column on the right (e.g.  $H9$ ), the most effective axis of (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<br>stimulation in the mid-sagittal plane (ele) and the horizontal<br>plane (azi) are given along with the p column on the right (e.g. H9), the most effective axis of<br>stimulation in the mid-sagittal plane (ele) and the horizontal<br>plane (azi) are given along with the phase-locked spike rate<br> $(2)$  indicated by the maximum radius o stimulation in the mid-sagittal plane (ele) and the horizonta<br>plane (azi) are given along with the phase-locked spike rate<br> $(\zeta)$  indicated by the maximum radius of the circular axes.<br>The best direction in the borizontal plane (azi) are given along with the phase-locked spike rate  $(\zeta)$  indicated by the maximum radius of the circular axes.<br>The best direction in the horizontal plane (plots on left) and the mid-sagittal plane (plots on rig  $\left(\mathcal{Z}\right)$  indicated by the maximum radius of the circular axes.<br>The best direction in the horizontal plane (plots on left) and<br>the mid-sagittal plane (plots on right) are shown for each<br>afferent by the double-beaded ar The best direction in the horizontal plane (plots on left) and<br>the mid-sagittal plane (plots on right) are shown for each<br>afferent by the double-headed arrows, which also illustrate<br>the 180 ambiguity inherent to these meas afferent by the double-headed arrows, which also illustrate<br>the 180 ambiguity inherent to these measurements. The stimulus angles are shown around each circle. To make these the 180 ambiguity inherent to these measurements. The<br>stimulus angles are shown around each circle. To make these<br>figures, the lines connect data points (not printed), each of<br>which is plotted twice for clarity—once at the stimulus angles are shown around each circle. To make these<br>figures, the lines connect data points (not printed), each of<br>which is plotted twice for clarity—once at the nominal axis<br>angle, and once again at that angle plus figures, the lines connect data points (not printed), each of<br>which is plotted twice for clarity—once at the nominal axis<br>angle, and once again at that angle plus 180°. The cartoon of<br>the toadfish in the bottom panels indi which is plotted twice for clarity—once at the nominal<br>angle, and once again at that angle plus  $180^{\circ}$ . The cart<br>the toadfish in the bottom panels indicates the plane<br>represented represented.

whole-body, linear translatory motion of low amplitude (displawhole-body, linear translatory motion of low amplitude (displacements generally less than a micrometer). Stimuli were whole-body, linear translatory motion of low amplitude (displacements generally less than a micrometer). Stimuli were<br>produced by a three-axis shaker system described in detail by<br>Eq. 8. Edds Walton (1007) Two point of min cements generally less than a micrometer). Stimuli were<br>produced by a three-axis shaker system described in detail by<br>Fay & Edds-Walton (1997). Two pairs of minishakers operated in<br>a nucleus pair of minishakers operated in produced by a three-axis shaker system described in detail by<br>Fay & Edds-Walton (1997). Two pairs of minishakers operated in<br>a push-pull manner to create motion in the horizontal plane. A<br>single shaker approachd untically. a push–pull manner to create motion in the horizontal plane. A single shaker operated vertically. The five shakers were attached to a water-¢lled aluminium cylinder. Programs were created to single shaker operated vertically. The five shakers were attached<br>to a water-filled aluminium cylinder. Programs were created to<br>generate sinusoids (100 Hz for toadfish and 140 Hz for goldfish)<br>for soch of the three shaker to a water-filled aluminium cylinder. Programs were created to<br>generate sinusoids (100 Hz for toadfish and 140 Hz for goldfish)<br>for each of the three shaker channels with the appropriate<br>starting phases and amplitudes to a 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 starting phases and amplitudes to create translational oscillatory<br>movements of the cylinder along various axes in the horizontal<br>and mid-sagittal planes of the fish. Cylinder movement was cali-<br>hasted by monitoring three movements of the cylinder along various axes in the horizontal<br>and mid-sagittal planes of the fish. Cylinder movement was cali-<br>brated by monitoring three, orthogonally orientated acceler-<br>amateus attached to the cylinder. brated by monitoring three, orthogonally orientated acceler-<br>ometers attached to the cylinder. Anaesthetized animals were



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

attached rigidly within the cylinder by clamping the bones of<br>the shull. For details, see Fax (1994) and Fax & Edds Welton attached rigidly within the cylinder by clamping the bones of<br>the skull. For details, see Fay (1984) and Fay & Edds-Walton<br>(1997) (1997). the skull. For details, see Fay (1984) and Fay & Edds-Walton (1997).<br>When an afferent was contacted by the electrode, motional

(1997).<br>When an afferent was contacted by the electrode, motional<br>stimuli were presented sequentially at  $30^{\circ}$  intervals over a  $150^{\circ}$ <br>nance within at locat the horizontal and mid aggittal planes When an afferent was contacted by the electrode, motional<br>stimuli were presented sequentially at 30° intervals over a 150°<br>range within at least the horizontal and mid-sagittal planes.<br>This times of directional personse me range within at least the horizontal and mid-sagittal planes.<br>Two types of directional response measurements were made. In the first (used with goldfish and toadfish), displacement thresh-Two types of directional response measurements were made. In<br>the first (used with goldfish and toadfish), displacement thresh-<br>olds were obtained by varying overall stimulus amplitude<br>(displacement) for each of the directi the first (used with goldfish and toadfish), displacement thresh-<br>olds were obtained by varying overall stimulus amplitude<br>(displacement) for each of the directional stimuli using phase-<br>looked spile nets as measured param (displacement) for each of the directional stimuli using phase-locked spike rate as measured response magnitude. Phase-locked (displacement) for each of the directional stimuli using phase-<br>locked spike rate as measured response magnitude. Phase-locked<br>spike rate was defined as the  $\zeta$ -statistic ( $\zeta = r^2 N$ ), where *r* is the<br>seefficient of su locked spike rate as measured response magnitude. Phase-locked<br>spike rate was defined as the  $\zeta$ -statistic  $(\zeta = r^2 N)$ , where r is the<br>coefficient of synchronization, a phase-locking metric, and *N* is<br>the number of cul coefficient of synchronization, a phase-locking metric, and  $N$  is<br>the number of spikes recorded during the stimulus presentations.<br>A threshold was defined as the stimulus level producing a the number of spikes recorded during the stimulus presentations.

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*<sup>Z</sup>*-value of 20, from which was obtained the stimulus angle at  $\zeta$ -value of 20, from which was obtained the stimulus angle at which threshold was lowest in each plane studied (details in Fay  $\kappa$  Edds-Walton 1997)  $\zeta$ -value of 20, from which threshold was low<br>& Edds-Walton 1997).<br>In the second type of & Edds-Walton 1997).<br>In the second type of measurement (toadfish only), stimuli at

each axis angle were presented sequentially at a given supra-In the second type of measurement (toadfish only), stimuli at each axis angle were presented sequentially at a given supra-<br>threshold amplitude, and response magnitude ( $\zeta$ -statistic)<br>plotted in polar coordinates as a f each axis angle were presented sequentially at a given supra-<br>threshold amplitude, and response magnitude  $(\zeta$ -statistic)<br>plotted in polar coordinates as a function of stimulus axis angle<br>(see fours). The axis angle prod plotted in polar coordinates as a function of stimulus axis angle (see figure 1). The axis angle producing the largest response was plotted in polar coordinates as a function of stimulus axis angle<br>(see figure 1). The axis angle producing the largest response was<br>determined by fitting each directional responsiveness pattern<br>with a cosine function. The (see figure 1). The axis angle producing the largest response was<br>determined by fitting each directional responsiveness pattern<br>with a cosine function. The phase angle of the best-fitting cosine<br>defined the afferent's best 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 measuredefined the afferent's best azimuth in the horizontal plane, and<br>the best elevation in the mid-sagittal plane. Thus, both measure-<br>ment methods permitted the determination of the afferent's best<br>orientation in azimuth and the best elevation in the mid-sagittal planent methods permitted the determinatorientation in azimuth and elevation.

#### **3. RESULTS**

For both goldfish and toadfish, the afferents investis. RESOLTS<br>
for both goldfish and toadfish, the afferents investi-<br>
gated had best displacement thresholds between 0.1nm<br>
and 1.1m root-mean square Figure 1 illustrates direction For both goldfish and toadfish, the afferents investigated had best displacement thresholds between 0.1 nm and 1  $\mu$ m, root-mean square. Figure 1 illustrates directional responsiveness functions for five afferents from t gated had best displacement thresholds between 0.1 nm<br>and 1 µm, root-mean square. Figure 1 illustrates direc-<br>tional responsiveness functions for five afferents from the<br>left saccule of one toadfish. These data illustrate and  $1 \mu m$ , 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 direct tional responsiveness functions for five afferents from the<br>left saccule of one toadfish. These data illustrate the<br>cosinusoidal (i.e. circular) form of most directional<br>response patterns. On the left-hand side of figure 1 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 cosinusoidal (i.e. circular) form of most directional<br>response patterns. On the left-hand side of figure 1, the<br>best direction in the horizontal plane is illustrated using<br>arrows for five afferents from the left saccule of response patterns. On the left-hand side of figure 1, the<br>best direction in the horizontal plane is illustrated using<br>arrows for five afferents from the left saccule of one toad-<br>fish. Note, that, all, best, axes, are, ne best direction in the horizontal plane is illustrated using<br>arrows for five afferents from the left saccule of one toad-<br>fish. Note that all best axes are near  $-30^{\circ}$  (and<br> $-30^{\circ} + 180 = 150^{\circ}$ ), which approximately fish. Note that all best axes are near  $-30^{\circ}$  (and  $-30^{\circ} + 180 = 150^{\circ}$ ), which approximately corresponds to the orientation of the saccular epithelium with respect to the midline of the fish. The right-hand column  $-30^{\circ} + 180 = 150^{\circ}$ ), which approximately corresponds to<br>the orientation of the saccular epithelium with respect to<br>the midline of the fish. The right-hand column illustrates<br>the diversity of best directions in the mi 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 the midline of the fish. The right-hand column illustrates<br>the diversity of best directions in the mid-sagittal plane<br>for the same five afferents, with dashed arrows indicating<br>the elevation of the hest axis. This variatio the diversity of best directions in the mid-sagittal plane<br>for the same five afferents, with dashed arrows indicating<br>the elevation of the best axis. This variation is probably<br>caused by the various orientations of bair ce for the same five afferents, with dashed arrows indicating<br>the elevation of the best axis. This variation is probably<br>caused by the various orientations of hair cells with which<br>the afferents make contact. Thus, hair-cell the elevation of the best axis. This variation is probably interaural differences in response magnitude and time for<br>caused by the various orientations of hair cells with which the fish saccules, even though there are zero caused by the various orientations of hair cells with which<br>the afferents make contact. Thus, hair-cell orientation<br>patterns on the saccular epithelium largely determine the<br>range of hest elevations recorded at least for t the afferents make contact. Thus, hair-cell orientation<br>patterns on the saccular epithelium largely determine t<br>range of best elevations recorded, at least for toadfish.<br>Figure 2 summarizes the best azimuths and elevation tterns on the saccular epithelium largely determine the<br>nge of best elevations recorded, at least for toadfish.<br>Figure 2 summarizes the best azimuths and elevations<br>: the saccule of  $(a)$  the goldfish and  $(b)$  the toadfish

range of best elevations recorded, at least for toadfish.<br>Figure 2 summarizes the best azimuths and elevations<br>for the saccule of  $(a)$  the goldfish and  $(b)$  the toadfish. In<br>these plots, the view is down onto the North Po Figure 2 summarizes the best azimuths and elevations<br>for the saccule of  $(a)$  the goldfish and  $(b)$  the toadfish. In<br>these plots, the view is down onto the North Pole of a<br>globe with a fish at its centre. Each point locate these plots, the view is down onto the North Pole of a globe with a fish at its centre. Each point locates the place 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 globe with a fish at its centre. Each point locates the place<br>that an afferent's best axis pierces the globe's surface in<br>the Northern Hemisphere. Illustrated here is the finding<br>that the distribution of best azimuths in t that an afferent's best axis pierces the globe's surface in<br>the Northern Hemisphere. Illustrated here is the finding<br>that the distribution of best azimuths in the horizontal<br>plane for saccular afferents is relatively narro the Northern Hemisphere. Illustrated here is the finding<br>that the distribution of best azimuths in the horizontal<br>plane for saccular afferents is relatively narrow: most toadfish afferents (for the left ear) tend to respond best to plane for saccular afferents is relatively narrow: most<br>toadfish afferents (for the left ear) tend to respond best to<br>a stimulus axis angle of about  $-25^{\circ}$  to  $-65^{\circ}$  to the left<br>front while most goldfish saccular af toadfish afferents (for the left ear) tend to respond best to<br>a stimulus axis angle of about  $-25^{\circ}$  to  $-65^{\circ}$  to the left<br>front, while most goldfish saccular afferents (for the right<br>ear) respond best to an azimutha a stimulus axis angle of about  $-25^{\circ}$  to  $-65^{\circ}$  to the left<br>front, while most goldfish saccular afferents (for the right<br>ear) respond best to an azimuthal axis of about 17° to the<br>right front. These are the approxim front, while most goldfish saccular afferents (for the right differently orientated hair cell will respond best to ear) respond best to an azimuthal axis of about  $17^{\circ}$  to the motional stimuli having a corresponding el ear) respond best to an azimuthal axis of about 17° to the<br>right front. These are the approximate angles at which<br>the saccules are orientated in the head of the respective<br>species. Thus, the range of azimuths seems to be d right front. These are the approximate angles at which<br>the saccules are orientated in the head of the respective<br>species. Thus, the range of azimuths seems to be deter-<br>mined by the borizontal plane orientation of the rece 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 species. Thus, the range of azimuths seems to be determined by the horizontal plane orientation of the receptor organ itself.

#### **4. DISCUSSION**

4. DISCUSSION<br>Most saccular afferents in goldfish and toadfish have<br>cectional response patterns that resemble the cosine 4. **DISCUSSION**<br>Most saccular afferents in goldfish and toadfish have<br>directional response patterns that resemble the cosine<br>directional response functions of individual hair cells directional response patterns that resemble the cosine<br>directional response functions of individual hair cells directional response patterns that resemble the cosine<br>directional response functions of individual hair cells<br>(Hudspeth & Corey 1977). This suggests that each<br>afferent makes synaptic contact with one or more hair directional response functions of individual hair cells<br>
(Hudspeth & Corey 1977). This suggests that each<br>
afferent makes synaptic contact with one or more hair<br>
cells having approximately the same directional (Hudspeth & Corey 1977). This suggests that each afferent makes synaptic contact with one or more hair cells having approximately the same directional *Phil. Trans. R. Soc. Lond.* B (2000)

orientation on the sensory epithelium (Edds-Walton *et al.*<br>1999) In the goldfish the majority of saccular hair cells 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 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 possibl 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 orientaare orientated dorsally or ventrally. In the toadfish,<br>saccular hair cells may be found at all possible orienta-<br>tions in the vertical plane (see references in Fay & Edds-<br>Walton (1997)). In both species, the saccular enit 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 a tions in the vertical plane (see references in Fay & Edds-Walton (1997)). In both species, the saccular epithelium<br>tends to be orientated obliquely when viewed from above:<br>the left saccule is orientated forward to the left Walton (1997)). In both species, the saccular epithelium<br>tends to be orientated obliquely when viewed from above:<br>the left saccule is orientated forward to the left and the tends to be orientated obliquely when viewed from above:<br>the left saccule is orientated forward to the left and the<br>right saccule is orientated forward to the right with<br>respect to the midline of the fish. Thus, no matter 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 right saccule is orientated forward to the right with<br>respect to the midline of the fish. Thus, no matter what<br>the directional orientation of the hair cells on the epithe-<br>lium azimuthal stimulation will tend to be greates respect to the midline of the fish. Thus, no matter what<br>the directional orientation of the hair cells on the epithe-<br>lium, azimuthal stimulation will tend to be greatest when<br>the relative otolith movement is parallel with the directional orientation of the hair cells on the epithe-<br>lium, azimuthal stimulation will tend to be greatest when<br>the relative otolith movement is parallel with the epithe-<br>liar surface (i.e. along the general orienta lium, azimuthal stimulation will tend to be greatest when<br>the relative otolith movement is parallel with the epithe-<br>liar surface (i.e. along the general orientation axis of the<br>organ in the head). The distributions of bes the relative otolith movement is parallel with the epithe-<br>liar surface (i.e. along the general orientation axis of the<br>organ in the head). The distributions of best azimuth for<br>the saccules of both species (figure 2) are liar 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 concention. This means that the saccul organ in the head). The distributions of best azimuth for<br>the saccules of both species (figure 2) are consistent with<br>this conception. This means that the saccular organs are<br>themselves directional in response to motional the saccules of both species (figure 2) are consistent with<br>this conception. This means that the saccular organs are<br>themselves directional in response to motional stimuli in<br>the horizontal plane. Thus, the population of s this conception. This means that the saccular organs are themselves directional in response to motional stimuli in themselves directional in response to motional stimuli in<br>the horizontal plane. Thus, the population of saccular<br>afferents will respond best to motional stimuli (acoustic<br>particle motion) that are parallel to the orientati 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 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 particle motion) that are parallel to the orientations of<br>their saccules, and will thus respond approximately in<br>proportion to the cosine of the angle between the organ's<br>orientation and the axis of particle motion. Since their saccules, and will thus respond approximately in<br>proportion to the cosine of the angle between the organ's<br>orientation and the axis of particle motion. Since the<br>paired saccules are differently orientated in azimuth proportion to the cosine of the angle between the organ's<br>orientation and the axis of particle motion. Since the<br>paired saccules are differently orientated in azimuth,<br>there will tend to be interaural differences in overal 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 paired saccules are differently orientated in azimuth,<br>there will tend to be interaural differences in overall<br>responsiveness for monopole sound sources at different<br>azimuths azimuths. In some afferents for monopole sound sources at different<br>
In some afferents response magnitude is also repre-<br>
In some afferents response magnitude is also repre-

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

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

monaural and binaural computation substantially similar<br>to those operating in most other vertebrates, and further monaural and binaural computation substantially similar<br>to those operating in most other vertebrates, and further,<br>that, these, processing, strategies, may, have, originated monaural and binaural computation substantially similar<br>to those operating in most other vertebrates, and further,<br>that these processing strategies may have originated<br>among the fishes. The goldfish saccule does not seem a 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 that these processing strategies may have originated<br>among the fishes. The goldfish saccule does not seem as<br>well suited to resolve the elevation of acoustic particle<br>motion since the bair cells are orientated similarly an among the fishes. The goldfish saccule does not seem as<br>well suited to resolve the elevation of acoustic particle<br>motion since the hair cells are orientated similarly, and<br>the distribution of best elevations for saccular a well suited to resolve the elevation of acoustic particle<br>motion since the hair cells are orientated similarly, and<br>the distribution of best elevations for saccular afferents is<br>relatively narrow (figure 2) We have suggest motion since the hair cells are orientated similarly, and<br>the distribution of best elevations for saccular afferents is<br>relatively narrow (figure 2). We have suggested (Fay &<br>Edds-Walton 1997) that the lagena could serve t the distribution of best elevations for saccular afferents is<br>relatively narrow (figure 2). We have suggested (Fay &<br>Edds-Walton 1997) that the lagena could serve this func-<br>tion in goldfish (see also Fay 1984) relatively narrow (figure 2). We ha<br>Edds-Walton 1997) that the lagena c<br>tion in goldfish (see also Fay 1984).<br>Much of the theoretical writing of Edds-Walton 1997) that the lagena could serve this func-<br>tion in goldfish (see also Fay 1984).<br>Much of the theoretical writing on sound-source local-

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

in the animal's behaviours and in the use of other, nonauditory information.

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