

DIRECTIONAL VARIANT AND INVARIANT HEARING THRESHOLDS IN THE RAINBOW TROUT (*SALMO GAIRDNERI*)

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Summary

The gas-filled bladder, the fish middle-ear analogue, transforms sound pressure (p) into pulsations, which generate displacement waves with body-fixed orientation that stimulate the nearby labyrinths. Moreover, in addition to this indirect stimulation, the otolith organs are stimulated directly by the particle motion vector (\mathbf{v}) in line with the source. For pure tones the vector sum of both stimulations results in elliptical displacement orbits, which are nearly identical for left and right ears. We hypothesize that these orbits are centrally analysed, either by breakdown into the original, direct and indirect components, the segregation hypothesis, or by analysis of their characteristic form and orientation, the orbit hypothesis. This provides fish with spatial hearing. Analysing the orbit form and orientation would constitute an essentially monaural mechanism of directional hearing that should show strong and characteristic azimuthal anisotropies. To investigate these anisotropies we have studied the rainbow trout *Salmo gairdneri* psychophysically with respect to directional-detection and directional-masking paradigms involving heart rate conditioning. We employed superpositioning of standing waves in a large tank for total control of a probe signal and a narrow-band noise masker.

With a sinusoidal p and \mathbf{v} probe and a p and \mathbf{v} (omnidirectional) noise masker, or with a pure \mathbf{v} probe and a ('uni'directional) p noise masker, trout proved to be equally sensitive to all directions. Only when the indirect stimulation was mimicked by a \mathbf{v} stimulus, were we able to demonstrate anisotropy. This indicates that trout indeed use the orbit lengths in the detection and masking tasks. The results can be explained if binaural convergence plays a role, under the assumption that left and right orbits differ appreciably. This might be the case if the divergence in orientation between the indirect stimulations reaching the right and left labyrinths were much larger than would be expected from the geometrical relationships between the two labyrinths and the swimbladder.

Key words: directional hearing, thresholds, behaviour, modelling, trout.

Introduction

Dual stimulation of the ear

The auditory system of bony fishes is a unique development in hearing. Without a cochlea, but with three otolith systems – lagena, sacculus and utricle – and the swimbladder as a middle-ear analogue, fish hearing rivals that of many higher vertebrates in sensitivity, frequency selectivity and waveform discrimination (reviewed by e.g. Popper and Fay, 1984). A fish detects the particle motion vector (\mathbf{v}) of the impinging sound wave with its otolith systems acting together as a three-dimensional accelerometer, because the acoustically transparent fish is carried along with the wave and thus oscillates around its dense (hence practically non-moving) otoliths. Although the instantaneous orientation in space of \mathbf{v} can be determined by such an accelerometer, the \mathbf{v} -vector alternately points towards and away from the (monopole) source. In fish possessing swimbladders, the phase reference resolving this 180° ambiguity in localization is provided by the sound pressure (p). The gas-filled swimbladder transforms sound pressure into pulsations that reach the nearby labyrinths and thus also displace the hair cells relative to the stationary otoliths. The inputs due to the sound pressure and to the directly impinging particle oscillations are depicted in Fig. 1. The amplitude as well as the phase relationship between p and \mathbf{v} are determined by the distance of the sound source, whereas the direction of \mathbf{v} depends uniquely on the source direction. The dual sensitivity provides fish with spatial hearing in their three-dimensional environment, without need for the binaural intensity or time difference cues available to terrestrial vertebrates. Accordingly, fish have been shown to discriminate keenly between sound sources differing in distance, azimuth and/or elevation (Schuijf and Buwalda, 1980; Schuijf and Hawkins, 1983) and appear to be able to analyse the p – \mathbf{v} relationships to some extent (Schuijf and Buwalda, 1975; Buwalda *et al.* 1983). These results support the theory that the fish's spatial hearing abilities, like the vestibular orientation abilities mediated by the same organ system,

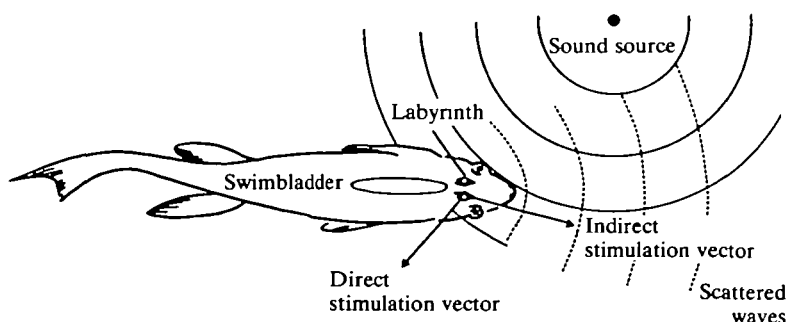


Fig. 1. Schematic representation of the direct and indirect stimulation of the otolith organs of a non-ostariophysine fish. The wave fronts and vectors are not drawn to scale. The vector of the indirect stimulation lies almost in the horizontal plane, which approximates to the plane through the centre of the swimbladder and the bilateral otolith organs.

depend on the detection of vector input. The information of the coherent pressure input will remove the ambiguity produced by the alternating direction of the acoustic vector input. The exact physiological basis, however, remains to be elucidated. As pointed out, both the 'direct' incident particle motions (in line with the source) and the p -induced swimbladder pulsations (the 'indirect' input, with body-fixed orientation) stimulate the ears. For pure tones, superposition of direct and indirect inputs results in a rotatory movement (orbit) of the hair cells with respect to the otoliths (Schuijf, 1981; De Munck and Schellart, 1987).

Elliptical displacement orbits of the hair cells

These orbits have been calculated for a monopole source (De Munck and Schellart, 1987) under the assumption that the tissues surrounding the bladder and those lying between the swimbladder and the otolith organs behave like water except for their experimentally determined damping. It is also assumed that the fish lacks special sound-transmitting structures, like the Weberian ossicles of the goldfish, which couple the swimbladder to the sacculus. A final assumption, justified for frequencies of more than 50 Hz by De Vries' (1950) measurements, is that in the external reference frame the movements of the otoliths can be neglected with respect to those of the hair cells. The calculations, yielding elliptical orbits for sinusoidal stimulation, have been made for the otolith systems of the cod and trout as a function of depth, of sound frequency, and of distance and direction of a monopole source lying in the same horizontal plane as the fish (Schellart and De Munck, 1987; Schellart and Buwalda, 1988). Fig. 2 gives an example of the results of such calculations for various fish-to-source positions. Similar sets of orbits can be obtained for the trout, for the other otolith systems of cod and trout, and for other non-ostariophysine fish. The shape and orientation of the orbits strongly depend on the source position. However, the orbits of left and right otolith organs appear to be nearly identical.

Strategies of directional hearing

There are two strategies that would allow a mechanism for extracting the positional information encoded in the orbits to be realized. One is the segregation of the p and v information, i.e. the breaking down of the rotatory stimulation into its original, constituent direct and indirect components (Schuijf, 1981; Buwalda *et al.* 1983; Rogers *et al.* 1988). This approach will be called the input segregation hypothesis. The other strategy, which will especially concern us in this report, is to analyse the end-product of the interaction between p and v , the hair cell orbits themselves: that is, to extract monaurally the orbit parameters – shape, orientation of the length axis and direction of revolution – which describe the orbit completely. These parameters together appear to define the source position uniquely, an approach called the orbit hypothesis (Schellart and de Munck, 1987). Where left and right orbits appear to be nearly identical, orbit analysis can be an essentially monaural process, provided that the macula is roughly in the same plane as the source and that the hair cells of this macula cover directional

sensitivities between 0° and 180° , or, ideally, 360° . However, performance will be poor for source directions in line with the direction of the indirect stimulation, a drawback of various models for non-ostariophysine directional hearing. A basic concept of the model is that the stimulus is mapped out on the sensory macula, thus providing a basis for a central, computational mapping of the orbit parameters. Thus, the orbit hypothesis has some parallels with generally accepted views on gravistatic perception mechanisms, but stands in contrast to recently published theories of acoustic localization in fish that partly or totally rely on binaural processing (Schuijf and Buwalda, 1980; Buwalda, 1981; Buwalda *et al.* 1983; Rogers *et al.* 1988).

Fig. 2 shows that the shape, orientation and direction of revolution of the elliptical orbits are strongly dependent on source direction and distance for distances within the near field (<3 m). It can be seen that, especially at 1.5 m, for a source at 0° and 180° with equal strengths, the orbit lengths differ markedly. For a distance of 1.5 m the long axis of the ellipses varies by a factor of 3 when the incidence angle of the source is changed from 0° to 180° . This means that the detection threshold of sound *per se* is dependent on the incidence angle. The aim

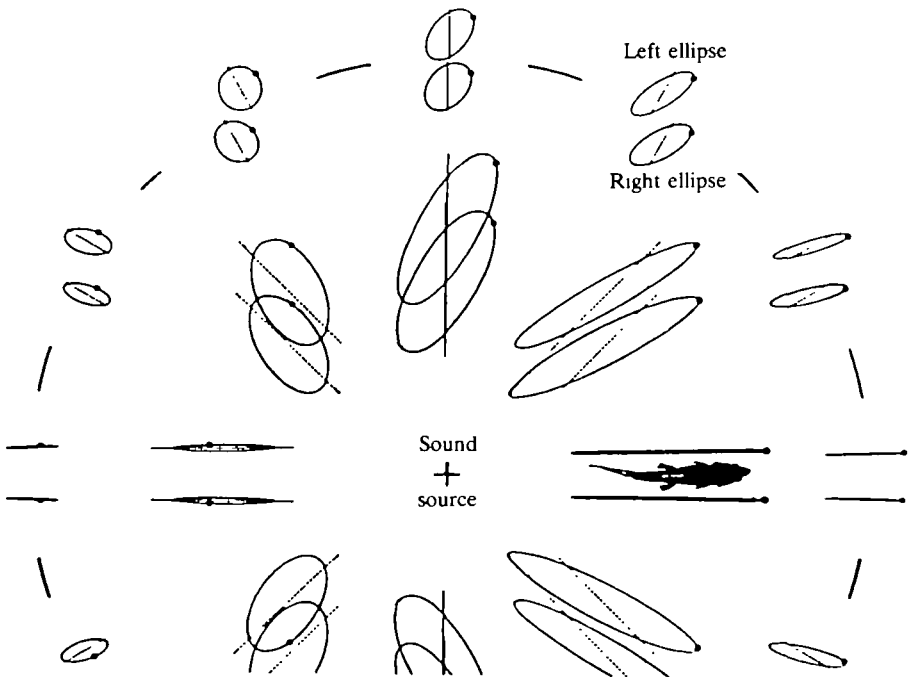


Fig. 2. Orbits of the utricular macula of a 30-cm cod. The upper and lower ellipse represent the left and right utricular orbit, respectively. Each orbit pair gives the position of the bladder of the fish relative to the source position. Left-right mirrored fish positions give the same results. The dashed line within each orbit represents the direct input. Shape and orientation change considerably as a function of fish position. The inner circle of orbit pairs represents a fish-to-source distance of 1.5 m and the outer one a distance of 3 m. (Modified after Schellart and de Munck, 1987.)

of this study is to find out whether the hearing threshold of the trout shows this dependence in accordance with the monaural orbit hypothesis, using a behavioural paradigm, and to evaluate the data in the light of the orbit hypothesis.

Materials and methods

General

The experiments were performed in a special acoustic apparatus using rainbow trout (*Salmo gairdneri*), ranging from 30 to 38 cm in length, obtained from a commercial trout farm at least a month before the experiments. The fish were kept in the laboratory in two 1000 l holding tanks with recirculating filtered tap water at about 14°C.

Fish of normal health and behaviour were fitted with twin 0.1 mm diameter trimel-insulated stainless-steel electrodes for recording the electrocardiogram (ECG). The electrodes were implanted, under MS 222 anaesthesia (0.2 g l^{-1}), by means of a blunt injection needle that carried the (180° bent) bare tips to the pericardium. The electrodes were sutured to the skin and lower jaw for anchorage and the injection needle retracted. The fish was then placed in a narrow cylindrical cage made of sound- and light-transparent material and transferred to the experimental tank. This cage was far too narrow to allow the fish to turn around, but forward swimming was possible. Aerated water was pumped continuously through the cage to keep the animal in good condition for several days. This flow increased the noise level negligibly for frequencies of more than 75 Hz. The fish was positioned in such a way as to localize its swimbladder and otolith organs in the acoustical centre of the apparatus, and allowed to recover from anaesthesia and calm down for 24 h. Depending upon its physical and motivational condition, a fish was tested for 3–6 consecutive days, after which it was returned, with electrodes removed, to the holding tanks and not used for at least another month. During its stay in the experimental tank the fish was not fed.

Psychophysical procedures

Signal detection thresholds were determined using classically conditioned slowing of the heart rate as the fish's response to the sound stimulus. The stimulus was a five times repeated 1.0 s tone burst ($f=105 \text{ Hz}$; Gaussian envelope) during a 10 s trial period. At the end of this period a mild a.c. shock (0.2 s at $2\text{--}4 \text{ mA cm}^{-2}$) was delivered through silver strip electrodes at either side of the tail. The right-hand side of Fig. 3 illustrates schematically the heart rate conditioning paradigm.

The fish was considered to have responded positively, if the maximum beat-to-beat interval measured during the 10 s trial exceeded the maximum interval during the immediately preceding 10 s pre-trial period by more than a criterion of, as a rule, 20 %. The exact criterion was determined for each fish on the basis of a series of responses to obviously superthreshold stimuli. The pre-trial included all the switching and gating procedures of the trial, but at an extremely low level of

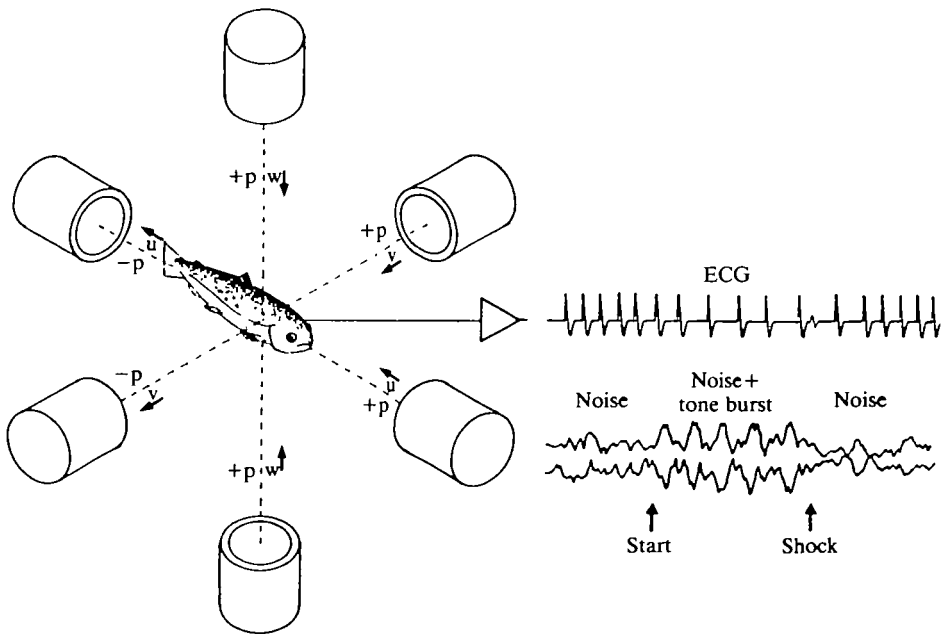


Fig. 3. Schematic representation of experimental set-up (left) and heart rate conditioning paradigm (right). The labyrinths of the fish were placed in the centre of the tank. The distance between the labyrinths of the fish and the membrane of the four horizontal sound projectors was 50 cm, and for the upper and lower vertical sound projectors the distances were 62 and 56 cm, respectively. Pressure signals are indicated by +p and -p (antiphase), displacement signals by u, v and w. The stimulus trace on the right, be it pressure or displacement, is only indicated by its envelope. The (fictitious) ECG shows an obvious rate decrease after the first tone burst.

stimulus and shock, to enable a valid comparison between the two periods and to make sure that the fish was not responding to any artefacts.

Reliable positive conditioned responses at elevated stimulus levels (i.e. >40 dB above absolute threshold and >20 dB above ambient noise level) were usually established within 10 training trials. In accordance with the staircase method of threshold approximation, the stimulus level was then lowered or increased in 3 dB steps until the fish either responded no longer or responded again. A minimum of nine such response reversals was required for obtaining a reliable 50 % detection threshold estimate (Buwalda, 1981). One threshold determination thus took 30–40 trials (training included) spaced 2–5 min apart. The fish was allowed to rest for 4–8 h between threshold determinations. Several procedures (e.g. statistical analysis of the ECG rate pattern just before and during a session) were performed to make sure of a constant level of motivation in the experimental animal.

For each animal, a complete set of data points (i.e. 6–8 thresholds 30° or 45° apart) was obtained. Depending on the fish's condition, one or two more sets could be obtained. The scatter between the data points pooled per direction had a mean s.d. of 3.2 ± 1.8 dB (mean \pm s.d., $N=36$). The reproducibility of the

threshold determinations for individual fish, i.e. the scatter between the pairs of data points, was 4.0 ± 1.8 dB (mean \pm s.d., $N=80$). The averaged thresholds (in absolute sense) of the fish had a range of 8 dB.

Acoustic methods

The acoustic apparatus has been described in detail before (Buwalda, 1981; Van den Berg, 1985). It is based on the principle of sound-field synthesis through superpositioning of standing waves in which either acoustic pressure or particle motion dominates. The use of this principle has been validated in field experiments that showed cod to be unable to discriminate between travelling waves and standing waves, as long as the amplitude and phase relationships between pressure and particle motion were sufficiently similar in both situations (Buwalda *et al.* 1983). Our experiments must fulfil this condition to obtain elliptical orbits.

By means of custom-built underwater sound projectors, standing waves were generated featuring pressure-to-motion ratios of more than +10 dB or less than -50 dB relative to the ratio characteristic of a plane travelling wave or a spreading wave very far from the source. This is the so-called far-field ratio, meaning that a sound pressure of 1.0 Pa is accompanied by a particle velocity of $6.7 \times 10^{-7} \text{ m s}^{-1}$. The frequency range of interest was 75–150 Hz. The standing pressure and displacement waves were generated by operating a pair of projectors facing each other either in phase (push–push) or in antiphase (push–pull), respectively. Three such pairs, schematically indicated in Fig. 3 (left), suspended along the *x*-, *y*- and *z*-axes of a cylindrical polyethylene tank (1.6 m in diameter and 2.1 m in height containing 4000 l of water) allowed the synthesis of the experimentally required sound fields. In these fields the phase and amplitude of the acoustic pressure and of the particle motion vector, as well as the latter's azimuthal orientation, could be controlled independently. This was done with an accuracy of better than 2° (temporal phase), 1 dB and 3° (spatial angle) in a volume at the tank's centre large enough to contain the ears and swimbladder of the fish. For a general treatment of the tank's acoustic characteristics, see Van den Berg and Schuijf (1985).

Since in our apparatus sinusoidal 105 Hz signals and narrow-band (75–150 Hz) noise stimuli were routed *via* separate pathways to the sound projectors, the pure-tone signals to be detected and the continuously presented noise maskers could be made to differ in their directional characteristics or in their pressure–motion relationships.

For the measurement of particle motion phase, amplitude and direction, an instrument was used consisting of three perpendicularly arranged accelerometers (Sensor Nederland type SM 6), mounted in an 8-cm diameter Perspex sphere. This sphere was suspended, together with the fish cage but 10 cm above it, in a vibration-isolating frame that could be lowered to the tank centre. In the sphere a small pressure-sensitive hydrophone (Bruel & Kjaer type 8103) was mounted as well. The background noise levels thus measured were about -26 dB re 1 Pa for pressure, and -143 dB or -135 dB re 1 m s^{-1} for horizontal and vertical particle velocity components, respectively, in the band 75–150 Hz.

Once a sound field had been manually balanced and adjusted to specification, all switching, gating and adjustment procedures as well as the assessment of the fish's response behaviour were under the control of a microcomputer, which allowed the automated determination of a complete set of thresholds.

Results

Directional sensitivity and directional masking

The directionality of the trout's hearing system was tested in two different ways, to reveal any anisotropies indicative of the mechanisms involved in acoustic localization.

The two approaches, that may best be characterized by the terms directional sensitivity and directional masking, both involve determining the detectability of 105 Hz signals of variable direction of incidence in a controlled noise background.

In the first and more direct approach, the signal to be detected had a composition characteristic of a sound stimulus emitted by a (monopole) source being rotated around the fish at a distance of 0.75 m. At this distance the pressure:particle velocity amplitude ratio is -10 dB re far-field value, and pressure lags 70° and 250° behind velocity when the fish is in front of or behind the sound source, respectively. For these amplitude and phase relationships, the swimbladder-radiated indirect input vector and the direct (source-oriented) input vector to the ear should, according to the model of De Munck and Schellart (1987), be nearly equally strong and either in phase (source behind) or in antiphase (source in front). This provides a good starting point for demonstrating any interaction effects.

The pressure component of this signal was produced by the vertical pair of sound projectors working push-push. The displacement part of the intended direction was generated by the two horizontal pairs (working push-pull), each pair contributing to an orthogonal component (in-phase) proportional to the sine or cosine of the desired angle of incidence.

According to the orbit hypothesis, the detectability of this signal (determined by the length of the elliptical stimulus resulting from the addition of direct and indirect input vectors) should vary in a predictable manner, with performance deteriorating sharply for more frontal source directions.

However, the determination of absolute sensitivity, if possible at all, is all but impracticable in laboratory conditions. An uncontrolled (even low) background noise level will influence in an unpredictable way the detectability for the various directions. Thresholds thus obtained might lead to invalid conclusions regarding the directional sensitivity of the fish hearing system. Therefore, the paradigm was converted into a masked detection task by the addition of a noise masker. This masker, ranging from 75 to 150 Hz and thus falling within one critical band (Hawkins and Johnstone, 1978), was generated by the two horizontal projector pairs being driven (push-pull) by independent noise generators. They thus produced uncorrelated orthogonal velocity components of equal amplitude a

$-120 \text{ dB re } 1 \text{ m s}^{-1}$ (i.e. about 23 dB above background levels). One can easily see that this procedure results in an omnidirectional noise stimulus with an equal effect on all parts of the ears, irrespective of their (horizontal) sensitivity axes. Uncorrelated pressure noise ($-7 \text{ dB re } 1 \text{ Pa}$) was added to the masker to attain a signal-to-noise ratio for pressure equal to that for displacement.

These experiments were performed on four fishes (Fig. 4). The data points appear to fit best the dashed small circle (t -test, $P > 0.95$).

The second approach for demonstrating directional effects in trout hearing is based on the directional masking effect observed in human hearing, e.g. the 'cocktail party effect'. This effect is characterized by the detectability of a signal being a function of angular separation between the signal source and any source emitting sounds masking the signal's detection. Such 'spatial windows' have also

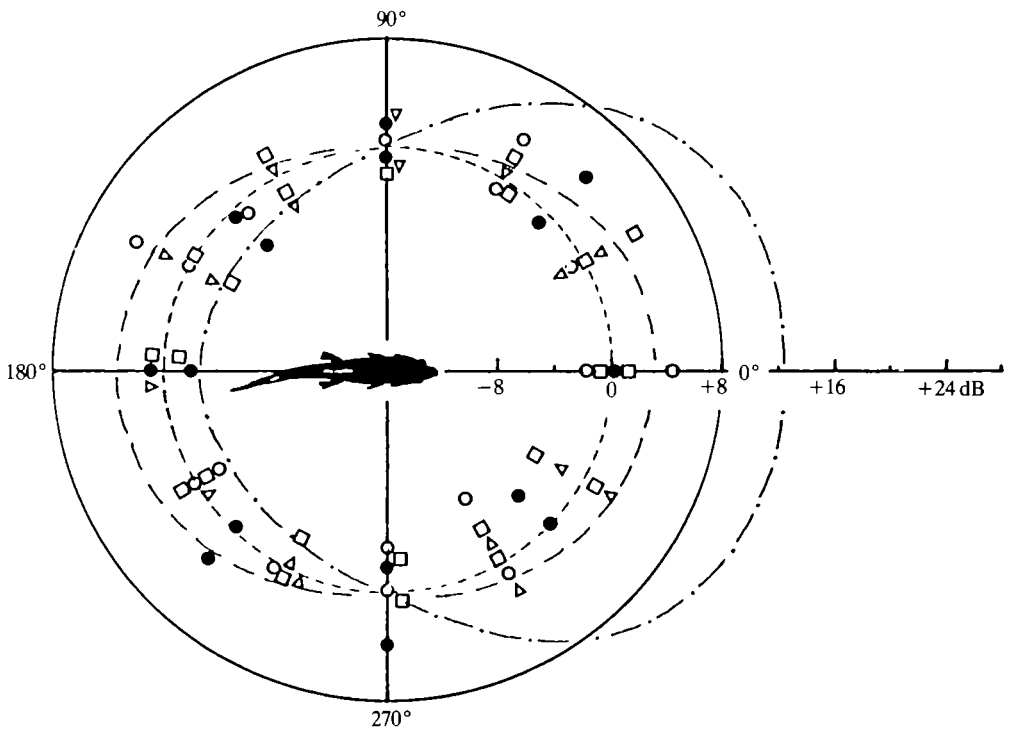


Fig. 4. Threshold intensity levels as a function of source direction in the horizontal plane, measured by motion-pressure detection experiments. The figure contains 71 data points, obtained after interpolation of the primary data and measured at angular intervals of 45° and 30° . Each type of symbol represents an individual fish. Probe signal as well as noise masker consisted of a pressure and a displacement component. The large circle indicated by the solid line was arbitrarily chosen at a relative intensity level of +8 dB. The densely dashed, small circle, representing the strength of the omnidirectional noise, is used as the reference intensity level (0 dB, i.e. approx. $-120 \text{ dB re } 1 \text{ m s}^{-1}$ or 1.5 nm displacement at 105 Hz). The coarsely dashed ellipse is the summed displacement composed of the direct and indirect signal of the noise masker. The ovoid curve (— · —) is the expected threshold curve of the trout utricle.

been demonstrated in fish hearing (Chapman and Johnstone, 1974; Sand and Hawkins, 1977).

In our approach, the directional masker and the directional signal were produced by means of standing waves. 1-octave band noise emitted by the vertical projector pair operating in the push–push mode generated a rather pure pressure noise masker. This masker, according to the orbit hypothesis, should be transformed into a noise vector input to the ears with a definite orientation determined primarily by the geometrical relationships between swimbladder and otolith organs. The magnitude of this noise vector was calculated, in accordance with De Munck and Schellart (1987), to exceed the non-correlated omnidirectional displacement noise – generated, as in the first experiment, by the horizontal projectors – by 20 dB in the rostrocaudal direction. The directional test signal of variable incidence was a pure particle motion vector stimulus generated in the same way as the displacement part of the signal used in the first experiment.

The directional masking experiment can be conceived of as being the reverse of the directional sensitivity test, with the signal strength being independent of direction and the noise masker distribution having a pronounced 20 dB anisotropy. However, in both situations a similar change in signal detectability was to be expected. According to the orbit hypothesis, the masked detection thresholds should be the same for the source in front of and that behind the fish, and 20 dB higher than that 90° right and left of the fish. The calculation yields a figure-of-eight-shaped curve. The results of the threshold determinations are depicted in Fig. 5. Owing to antisymmetry around the origin, only data obtained with source positions in the front half-plane are depicted. It is clear that, as in the detection experiment, no systematic anisotropy occurs that exceeds the 4–8 dB of inter- and intra-individual variation. The data can be fitted accurately to a semicircle that nearly coincides with the distribution of particle motion noise energy without the contribution of the swimbladder-transformed pressure noise.

Directional tests in the vertical plane

Although the biophysical orbit model of Schellart and De Munck (1987) is restricted to the horizontal plane through the swimbladder centre, anisotropies in the distribution of directional performance are to be expected in the vertical plane as well, even if they are smaller in the vertical transversal plane. Accordingly, tests of directional sensitivity and directional masking were performed with the vertical projector pair and the horizontal, longitudinal pair generating the particle motion components in signal and noise, and the remaining horizontal, lateral pair generating the sound pressure components. Two trout were tested for directional sensitivity and directional masking with simulated source positions in the median vertical plane. One trout was similarly tested with sources simulated in the transverse vertical plane. The results are not graphically displayed, because the 37 thresholds obtained were distributed in virtually the same manner as in the experiments with horizontal sources. They could be almost perfectly fitted by a

circle coinciding with the distribution of noise displacement components in the same plane.

Directional tests using simulated pressure input

The surprising lack of any anisotropy in the above experiments has led us to question the validity of our experimental design. Accordingly, the experiments were repeated, but with sound pressure components in the probe signal and noise masker used in the experiment illustrated in Fig. 4, and with the pressure component of the noise masker employed in the experiment illustrated in Fig. 5 being substituted for by particle motion. This was done to mimic – for direction, amplitude and phase – as closely as possible the ‘indirect’ vector that would have

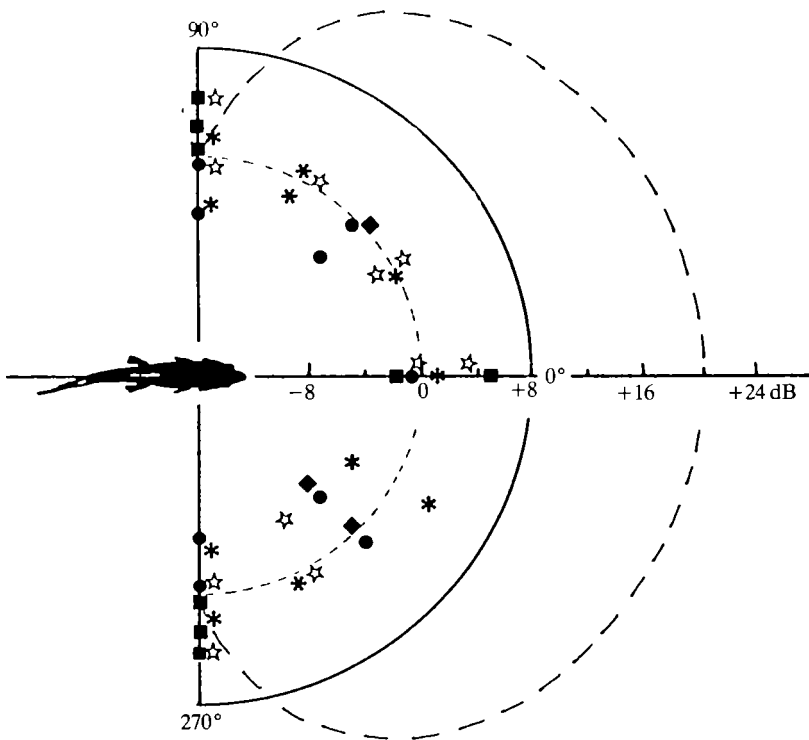


Fig. 5. Threshold intensity levels as a function of source direction measured by motion-pressure masking experiments. The figure contains 41 data points obtained from four trout. The data indicated by the filled circles were obtained from the same fish yielding the filled circles in Fig. 4. The other three types of symbols indicate three fish not used for the experiments of Fig. 4. Probe signals consisted of a displacement component only. The noise masker consisted of a strong pressure component superimposed on the 20 dB weaker omnidirectional displacement component of Fig. 4, indicated by the densely dashed, small circle. The figure-of-eight-shaped curve (dashed) is the expected threshold curve. (The data points are only plotted in the right half-plane owing to antisymmetry around the origin caused by the stimulus configuration of this experiment. So, a data point obtained at 45° , for example, also holds for 225° .)

been produced by the swimbladder's pressure-to-motion transforming action calculated according to the model of De Munck and Schellart (1987). These experiments were designated motion-motion detection experiments, and motion-motion masking experiments. To generate the appropriate probe and noise signals, the vertical projector pair was replaced by an additional horizontal projector pair (J-9 type) in line with the fish's body. This pair was used to generate the required longitudinal displacement vectors in signal and noise, mimicking the 'indirect' vector input. The other horizontal projector pairs had been rotated through 45°, and their inputs were controlled accordingly, to produce the 'direct' vector component of variable orientation in signal and noise.

The results of the directional sensitivity test and of the directional masking test are given in Fig. 6A,B. It is evident that the results do fit the expected distributions, confirming the validity of the experimental design.

Discussion

General considerations

In all recent studies concerning teleost directional hearing, pure tones have been applied as test signals. Although more or less pure tones occur under natural conditions (e.g. sound generated by swimbladder drumming muscles, crustaceans and surface-dwelling insects), generally sound is composed of several harmonics or is even aperiodic. Unfortunately, there are almost no theoretical background and experimental data about directional hearing of aperiodic sound (J.C. De Munck has calculated the hair cell displacement trajectories in response to clicks; unpublished data) and for compound harmonic signals the situation is hardly better. Non-ostariophysine hearing is restricted to a frequency range of only some octaves (excluding the frequencies to which the lateral line system is also sensitive). This means that for compound signals one harmonic is often dominant, so that the orbits are still more or less elliptical. The orbit hypothesis needs some filtering of compound signals to obtain elliptical orbits. Since (1) quantitative behavioural experiments described in the literature have nearly all been made with frequencies between 75 and 113 Hz, (2) the orbits degenerate to very flat ellipses for frequencies greater than 200 Hz, a handicap for the orbit as well as for the input segregation approach, and (3) non-ostariophysine hearing is mostly limited to 400 Hz, a test frequency of 105 Hz appeared to be a reasonable choice.

The theory of directional hearing is based on sound fields generated by monopole sources, and in behavioural experiments real or mimicked monopoles are used. Natural sound sources mostly behave as bi- and quadrupoles (Kalmijn, 1988, 1989), especially in the near field, although monopoles are present as well, such as the swimbladder and air bubbles (waterfalls and breakers). For the more distant far field, all sources behave more or less like monopoles, with a displacement component that is probably strong enough to make directional hearing feasible for distances of up to about 3 wavelengths. Because of its theoretical and practical manageability we have opted for the monopole theory. ■

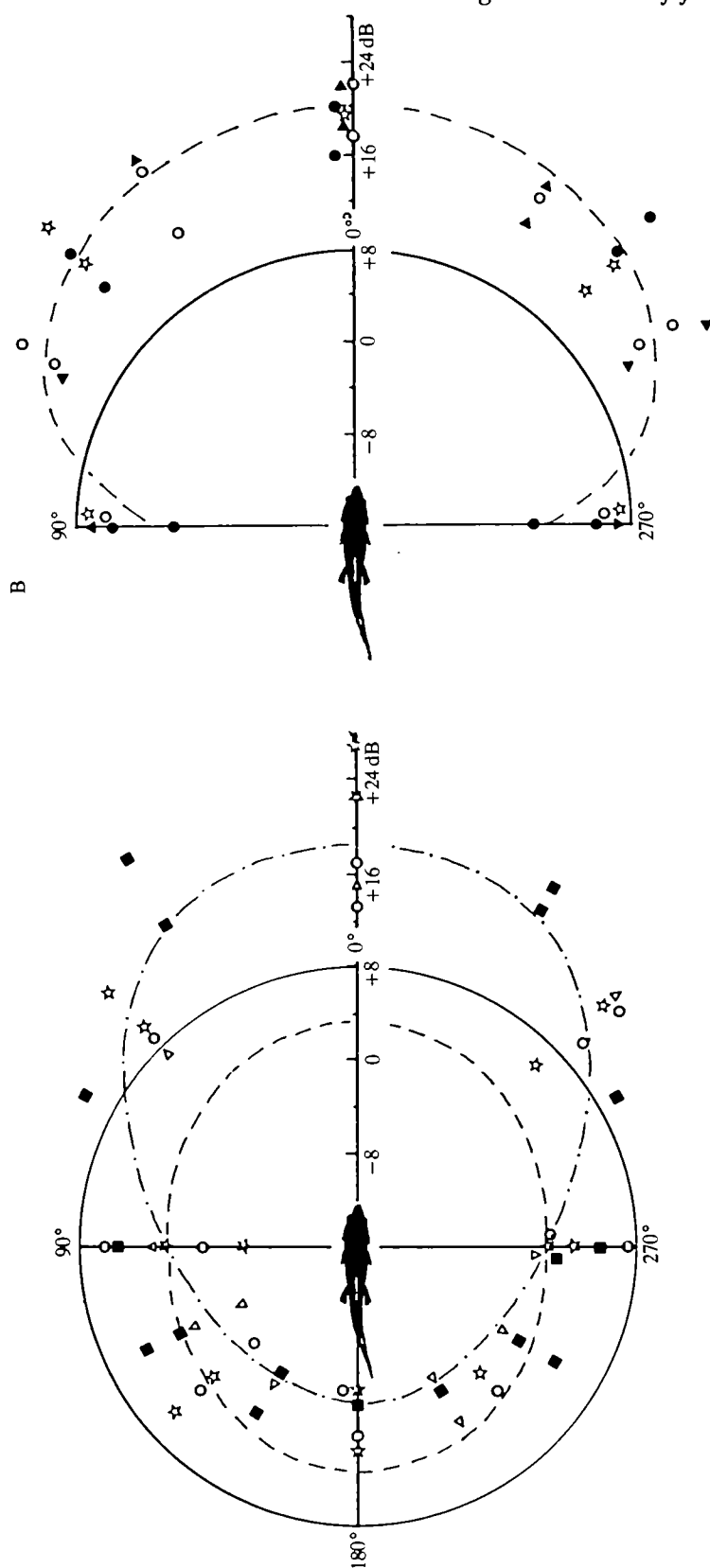


Fig. 6. (A) Directional threshold intensity in the horizontal plane, measured by motion-motion detection experiments (57 data points). These experiments were made with four fish, also used in the experiments of Figs 4 and 5. Probe signals consisted of two displacement signals, one simulating the sound source displacement and the other the displacement wave scattered by the swimbladder. The noise was composed only of omnidirectional displacement noise. The various curves have the same meaning as in Fig. 4. The data points appear to fit best the ovoid curve. (B) Directional threshold sensitivity determined by motion-motion masking experiments (four fish, 38 data points, the fish indicated by the filled triangles had not been used before). Experimental conditions as in Fig. 5, except that the pressure noise was replaced by a displacement signal along the longitudinal axis, being 20 dB stronger than the omnidirectional displacement noise.

For sound sources in the horizontal plane the utricle appears, from a theoretical point of view, to be the most suitable otolith system to enable source localization, since the differences between the orbits corresponding to the various source positions are larger than those of the sacculus and lagena (Schellart and de Munck, 1987; Schellart and Buwalda, 1988). This is due to its more appropriate position with respect to the swimbladder. Moreover, the utricle has an approximately horizontal macula and a fan-like hair cell sensitivity configuration. Thus, the utricle was the favourite otolith system for our study. A group of saccular hair cells have their sensitivity axis in the horizontal plane and roughly along the rostrocaudal axis. Unilateral comparison of the stimulation of these hair cells with those of the utricle with the same sensitivity axis provides extra information for the determination of the source direction, since the saccular hair cells obtain stronger indirect stimulation (see De Munck and Schellart, 1987). This extra information provides a way out for any theory explaining localization of sources in line with the orientation of the indirect displacement wave. For sources not in the horizontal plane, information about their elevation will be given by the sacculus and/or lagena, thus providing real three-dimensional hearing.

The input segregation hypothesis

The principal concept of the orbit hypothesis is that the fish retrieves the direction and distance of the sound source by analysis of the orbit parameters. The alternative approach, the input segregation hypothesis, is that the particle motion component (be it displacement, velocity or acceleration) is reconstructed together with the phase difference between both stimulations or, giving less information, the direction of revolution. One implementation of this strategy is peripheral segregation through local specificity for either input, based, for example, on structural adaptations ('acoustic windows') locally promoting or impeding the reception of swimbladder pulsations. This is performed by the Weberian ossicles of the ostariophysine fish, like the Cypriniformes, or the less effective tubular structure between the swimbladder and the labyrinth in herring-like fish. Another solution for peripheral segregation is based on hair cells being oriented parallel or orthogonal to the indirect input vector, thus strongly reducing or enhancing responsiveness to direct input (Buwalda, 1981). Adaptive structures are not in question, since the trout lacks them. Functional peripheral segregation has only been demonstrated so far in goldfish with its specialized swimbladder-ear link (Popper and Fay, 1984). Peripheral and consequently monaural segregation may be supplemented or even replaced by central binaural subtraction processes resulting, for instance, in the removal or segregation of the bilaterally symmetrical indirect input components. Such schemes allow for a separate central processing of v -input, of p -correlated input, and of correlation between p and v (Buwalda, 1981). The processing of v -input might involve 'binaural vector' weighing, i.e. determining the v -direction from the output ratio of binaurally symmetrically oriented otolith organs (Schuijf and Buwalda, 1980). In addition to these theoretical possibilities for the segregation of particle motion and sound

pressure, information could be recovered by the vectorial analysis of the responses of hair cells of all directional sensitivities in the otolith organs at both sides (e.g. Schuijf, 1981; Rogers *et al.* 1988). Whether some way of segregating p and v input is realized in the brain is highly uncertain. Only one study has been devoted to this problem. In the ostariophysine goldfish, results indicate that the ratio of particle motion to pressure sensitivity is higher in the medial than in the more lateral part of the torus semicircularis (Fay *et al.* 1984).

Hearing thresholds as a function of direction

The direction-dependent difference of the length of the hair cell orbits is pronounced and is a direct consequence of the vectorial addition of the direct and indirect inputs. The differences in orbit length as a function of direction are greatest for short source distances, as can be seen in Fig. 2, since at great distances indirect stimulation dominates. The influence of source direction is a manifestation of a more general phenomenon that may be termed the anisotropy of the orbit hypothesis. Simulations with the model also showed a marked anisotropy in the ability to discriminate two nearby, identical sound sources from each other (Schellart and de Munck, 1987). The direction dependence should, according to the orbit hypothesis, be shown in behavioural and central neurophysiological studies. There are no neurophysiological studies of this kind, but behavioural discrimination studies as a function of source direction have been made (e.g. Schuijf, 1975; Schuijf and Buwalda, 1975). The extent to which they are in agreement with the orbit hypothesis has been discussed elsewhere (Schellart and de Munck, 1987; Schellart and Buwalda, 1988). In brief, the orbit hypothesis in its monaural version could generally accommodate the behavioural data, unless the data concern the 0° and 180° source direction, owing to this model's poor performance for these particular directions.

The surprising outcome of Figs 4 and 5 is clearly at odds with the predictions of the orbit hypothesis in its simple monaural form. It does, however, not invalidate the concept of the orbit parameters being used for reconstructing auditory space. It would be feasible to construct a model featuring orbit analysis on a binaural basis or a monaural analysis followed by binaural interaction to restore bilateral symmetry and smooth any inherent monaural anisotropy.

The data of Fig. 6 demonstrate that hearing thresholds as a function of direction fulfil the theoretical prediction only as far as particle motion is concerned, i.e. with the role of the swimbladder eliminated. This means that this non-ostariophysine fish uses the length of the orbits in hearing tasks. On the basis of anatomical characteristics (plane of macula, configuration of hair cell sensitivity axis), the utricle is the most likely candidate to be involved in this detection and masking task. The data of Fig. 6B match the expected curve satisfactorily. At 0° and 180° the displacement noise signal, mimicking the scatter field caused by the pressure noise masker of Fig. 5, appears to determine the threshold, whereas at 90° and 270° the threshold is determined by the omnidirectional displacement noise background which is 20 dB weaker. Since both these signals are stochastic,

probability summation holds. Owing to the 20 dB difference in strength, for source directions between 0° and 67.5° , only 3 % of the combined signal is caused by the omnidirectional noise. Only when 84.3° is reached do the contributions of the mimicking signal and the omnidirectional signal become equal. In Fig. 6A it can be seen that the sensitivity at 90° and 270° can only be determined by the level of the omnidirectional noise, since the mimicking noise component, substituting for pressure noise, is oriented along the 0° – 180° axis. The data show that at 90° and 270° the detection threshold is close to the level of the omnidirectional noise. So, a signal-to-noise ratio of 1 is sufficient to reach the threshold of the detection mechanism under these stimulus conditions. In Fig. 6A this also appears to hold, as well as in Figs 4 and 5 for all directions. The data of Fig. 4 point directly to the invalidity of any straightforward superposition of the direct and indirect motion component of the test signal. The same holds for both components of the noise, since the data points clearly fit the dashed circle better than the ellipse.

The observation that the data of Figs 4 and 5 conflict with the orbit hypothesis, whereas those of Fig. 6 are in agreement with it, indicates that something unexpected happens to the indirect displacement wave along its pathway of propagation between the swimbladder wall and the otolith organs. We will try to understand this discrepancy from the point of view of the orbit hypothesis.

The concept of diverging indirect vectors

A fundamental assumption of the orbit hypothesis is that the indirect displacement wave, caused by pulsations of the swimbladder, is propagated in an undisturbed manner from the swimbladder to the otolith organs. In calculations with the orbit model the tissue between the swimbladder and the otolith organs is considered to behave acoustically like water (De Munck and Schellart, 1987). However, a theoretical and experimental validation of this assumption is hard to find. The calculated direction is approximately the same as the direction of the line connecting the otolith organ with the centre of the swimbladder (by approximation a prolate spheroid). It is possible that the angle between the medial plane and the actual direction of the indirect vector is much larger than the calculated angle. This means that the orbits on either side are clearly dissimilar with respect to orientation, shape and orbit length (Fig. 7). The latter effect will reduce the anisotropy more or less strongly, depending on how the length of the orbits of a pair are processed. To calculate the orbits of Fig. 7, it was assumed that the angle between the medial plane and the direction of the indirect vector was 45° , with the amplitude and phase unaltered. The deviating direction can be caused by transmission of the indirect particle displacement wave through the backbone (which is several millimetres away from the rostradorsal part of the swimbladder) and then through the skull. The assumption that the direction of each indirect vector diverges substantially is not specific for the orbit hypothesis. It is also a pertinent prerequisite for the various versions of the input segregation hypothesis (Schuijf, 1981; Buwalda *et al.* 1983; Rogers *et al.* 1988). Data for the frequency sensitivity of the eel (*Anguilla anguilla*) also indicate that the indirect displacement

wave does not behave in accordance with the theory of swimbladder acoustics (Jerkø *et al.* 1989).

The concept of the divergence between both bilateral indirect vectors of an otolith pair can also be applied to explain the data of the directional tests (e.g. those of Hawkins and Sand, 1977; and of Van den Berg, 1985) with sound sources in the vertical plane. It could be proposed that the elevations of the indirect vectors impinging onto two ipsilateral otolith organs, e.g. the sacculus and the lagena, are not approximately equal, as the model originally predicts from the geometry of the otolith–swimbladder system, but deviate strongly from each other. This might also be caused by channelling of the sound *via* bony structures.

Besides the predicted anisotropy as a function of source direction in the detection threshold, the orbit hypothesis predicts a strong spatial anisotropy in the ability to discriminate equal, neighbouring sound sources from each other. The strength of this anisotropy has been quantified by calculations with the orbit model (Schellart and de Munck, 1987). Qualitatively this phenomenon can easily be understood by inspecting Fig. 2. At 0° and 180° the elliptical orbits are practically linear, which seriously impedes distance discrimination and makes the two directions indistinguishable. At 45° and 135° the elliptical orbits are clearly different from each other; one is nearly four times more convex than the other. The ellipse at 90° has an intermediate shape. This means that the discrimination

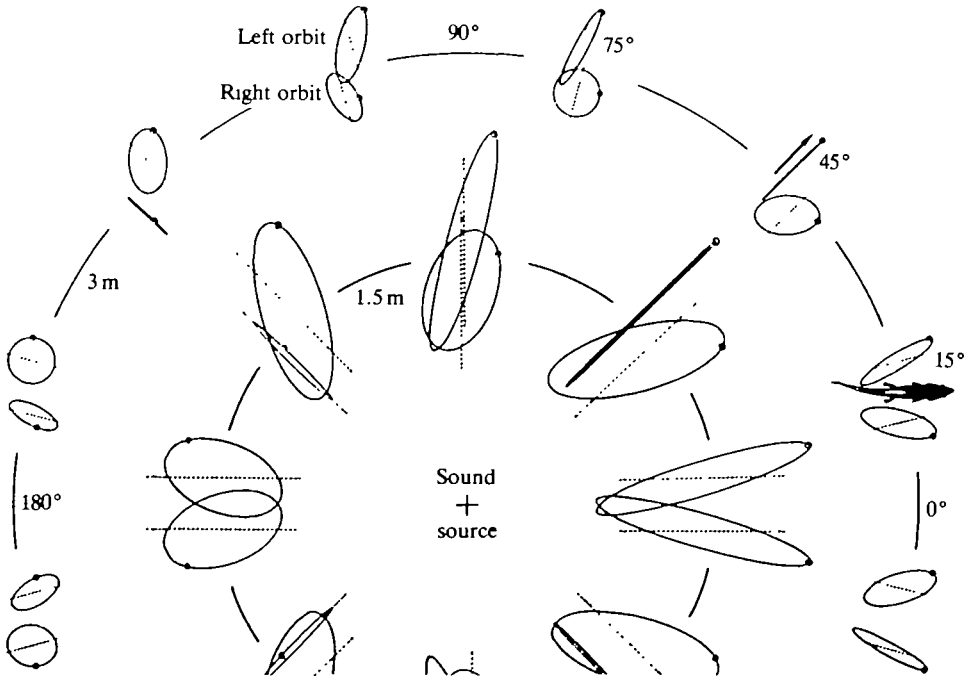


Fig. 7. Influence of the divergence of both indirect vectors on the dissimilarity between the left and right orbits of an orbit pair. The angle between the indirect vectors is 90° . For further explanation see the legend of Fig. 2 and the text.

sensitivity near 135° is larger than it is at 45° . The poor discrimination sensitivity for direction and distance at 0° and 180° is not in accordance with the data from behavioural experiments (Schuijf, 1975; Schuijf and Buwalda, 1975; Schuijf and Hawkins, 1983), even when one takes into account that extra spatial cues could not be completely excluded in these experiments (Schellart and de Munck, 1987). However, when there is a substantial divergence between the indirect vectors, at most one orbit of an orbit pair is linear (see Fig. 7), whereas at 0° and 180° neither of them is linear. This strongly increases the performance in these directions, whereas the anisotropy is seriously diminished. The results of the behavioural experiments mentioned above can now be far more easily understood. Recent behavioural experiments have shown that the direction of revolution of the elliptical orbit cannot be determined by the cod when the ratio between the short and the long axis is less than 0.25 (Van den Berg, 1985). This means that for azimuthal angles of the sound source between about $+20^\circ$ and -20° , and between 115° and 245° (with distances of less than 1.5 m and depths of less than 5 m) the 180° ambiguity, according to the original, monaural orbit hypothesis, cannot be resolved. However, for the binaural orbit hypothesis with divergence this difficulty is overcome, since for any source direction at least one of the orbits of the binaural pair has an axis ratio of more than 0.25.

In conclusion, extending the monaural orbit hypothesis with approximately parallel indirect vectors to a binaural orbit hypothesis with diverging indirect vectors greatly improves its theoretical detection and discrimination performance at 0° and 180° and greatly reduces its inherent anisotropies. However, on the basis of our experiments and present knowledge, a choice between the input segregation and binaural orbit hypothesis cannot be made.

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