

## Mapping of sound direction in the trout lower midbrain

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### Abstract

In the trout lower midbrain 35% of the auditory neurons are directionally selective (DS). Most of these neurons have a higher directional selectivity than the sensory hair cells. DS units and non-DS units occur in vertical clusters, with the former more dorsally. The direction of preference is topographically mapped. Apparently, auditory space mapping is a common feature in the midbrain of vertebrates.

**Keywords:** Rainbow trout; Torus semicircularis; Directional hearing; Directional selectivity enhancement; Auditory space mapping; Vertical clusters

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Behavioral experiments have demonstrated that fish are able to detect the direction of an underwater sound source [1,2,18]. Terrestrial vertebrates make use of interaural time, phase and intensity differences of sound pressure to localize a sound source. However, for fish, which make use of both the pressure and kinetic components of sound, these cues are not available due to the small distance between the right and left inner ear (typically a few mm), the high velocity of sound in water (5 times that of air), and the almost identical acoustic transparency of the fish body and the surrounding water.

The fish inner ear comprises three otolith systems, each with their specific hair cell orientation pattern. A sound field causes displacement of the directionally sensitive hair cells relative to the otolith which lags the surrounding tissue because of its higher inertia. The inner ear may be considered as a single 3-D accelerometer. Since particle motion is alternatively directed towards the source and away from it, a 180° ambiguity remains. However, an additional cue is provided by the gas-filled swimbladder, a sound pressure to displacement transducer, stimulating the inner ear indirectly from a body-fixed angle. Addition of direct and indirect stimulation yields different displacement orbits depending on the location of the stimulus source. Thus, the 180° ambiguity can be

solved (and distance information can be extracted) [13, 17]. Theoretically, however, the performance of a monaural system is poor for some source directions [13]. Because the orientation of the two indirect stimulus vectors differs, the displacement orbits of the hair cells in the right and left ear will not be the same. Therefore, we expect that fish use input from both ears for auditory localization. Recent theories on this subject, either being conceptual [1,13,21], or more based upon anatomical structure [11] do not answer the question how sound source direction is actually analyzed in the fish brain.

Animals were initially anesthetized by 250 mg/l MS-222 and paralyzed with 0.15 mg Pancuronium bromide. During surgery the MS-222 concentration was reduced to 20%. Lidocaine was applied locally. Recordings started 2 h after complete removal of MS-222 [22]. Animal treatment was in accordance with the Dutch law.

We investigated the neuronal encoding of sound direction in the horizontal plane. Single-unit spike responses were recorded in the midbrain with high-impedance micropipettes from neurons of the medial nucleus in the torus semicircularis, the homologue of the inferior colliculus. This is the first nucleus along the auditory pathway with substantially binaural input [12]. Extensive auditory processing like frequency and time analysis occurs here [9,10,12]. In addition, lateral line input and especially visual information are being processed in this nucleus [14,15].

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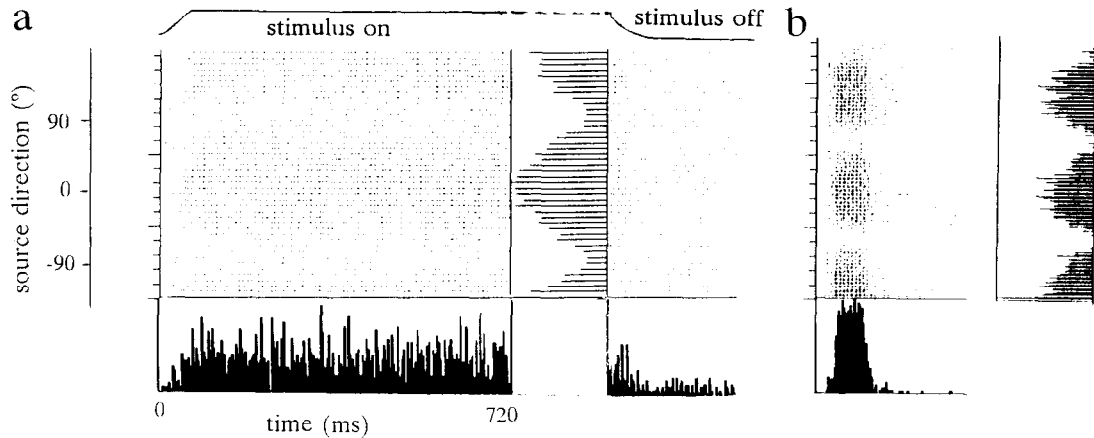


Fig. 1. Dot-displays of the spike response of (a) a tonic unit (stimulus amplitude  $1.2 \text{ mm s}^{-2}$ ) and (b) a phasic unit ( $120 \text{ mm s}^{-2}$ ) to 172 Hz tone bursts (790 ms on, 650 ms silent intervals, rectilinear motion). Time is indicated along the horizontal axis. The direction of each tone burst (rotated a few degrees anti-clockwise with respect to the preceding one) is given along the vertical axis ( $0^\circ$  is forward). The bottom histogram denotes the peristimulus time histogram and the right-hand histogram the number of spikes elicited during a single burst.

We developed a horizontal ( $x$ - $y$ ) vibrating platform with adequate mechanical features [16] on which the fish was rigidly attached. Vibrations of the skull were measured with a miniature 3-D accelerometer fixed to the skull with three small screws. The acoustic stimulus was presented as tone bursts (frequency 172 Hz; amplitude  $0.5$ – $200 \text{ mm s}^{-2}$ ).  $X$ - $y$  cross-talk caused by small movements of the fish's head with respect to the platform was compensated by adjusting the computer-generated signals driving the coils that move the platform [6].

In Fig. 1a the neuronal response to each tone burst is represented as a line of dots (spikes). Since each subsequent tone burst simulates a slightly different source direction, the right-hand histogram shows the direction dependency of the unit. The bottom histogram reveals the sustained/transient nature of the response. Units that respond with a direction dependent spike rate are said to be directionally selective (DS). The  $-3 \text{ dB}$  width of the histogram is called the directional selectivity range. By definition a cosine-shaped histogram has a directional selectivity range of  $90^\circ$  ( $-3 \text{ dB}$  points  $90^\circ$  apart). Such a cosine relationship is shown by hair cell responses [20] and by eighth nerve fibers of fish [4]. When the  $-3 \text{ dB}$  points were more than  $150^\circ$  apart or absent, a unit was considered non-DS.

In 37 trout we found 183 auditory units, generally showing the same response characteristics as reported before [10,12]. In this study, for the first time, the directional dependency of the response was investigated. It appeared that 63 units showed a direction dependency of the spike rate in the horizontal plane (Fig. 1a,b). Units for which it could not be excluded that vertical cross-talk of the horizontally driven platform had contributed to the response were not included in this analysis.

The response of DS units and non-DS units varied from purely sustained (Fig. 1a) to exclusively transient (Fig. 1b). However, 92% of the units had a transient onset

of at least twice the response strength during the second half of the tone burst. The presence of many transient units, which are rare in acoustic nuclei of the hindbrain [22], reaffirms the importance of the torus for temporal analysis.

Most DS units have a directional selectivity range  $<90^\circ$  (Fig. 2a), which usually is intensity independent. Therefore, we conclude that a suppression mechanism is involved in directional tuning of torus DS units. Units with a large directional selectivity range probably obtain excitatory input from fibers with different preferred directions. The many non-DS units that were found obtain input from fibers covering all directions.

The recording sites of auditory units were located in the upper  $800 \mu\text{m}$  of the torus (Fig. 3a). (During electrode advancement, the ventricle-torus interface is recognized by a jump of the electrode signal. This is used as a depth reference. Since identified units could be found again while withdrawing the electrode, the accuracy of the recording depth was estimated to be  $25 \mu\text{m}$ . The accuracy in the horizontal plane, determined stereotactically, was  $100 \mu\text{m}$ .) The DS units mainly occurred in the upper  $400 \mu\text{m}$ , which comprises two layers of neurons with small somata [3]. Visual units, responding to a moving object in the visual field, were predominantly found at greater depths.

Usually, several units were encountered when advancing the electrode into the torus. The fact that units of the same modality occur in vertical clusters [12] was confirmed in this study. It appeared, however, that DS and non-DS units also occur in separate clusters. All preferred directions in the population of DS units have a similar frequency of occurrence (Fig. 2b). The preferred direction of DS units found in a single electrode track shows a small (non-systematic) deviation from the mean of all DS units encountered in that track (Fig. 2c). Thus, DS units occur in clusters with the same preferred direction.

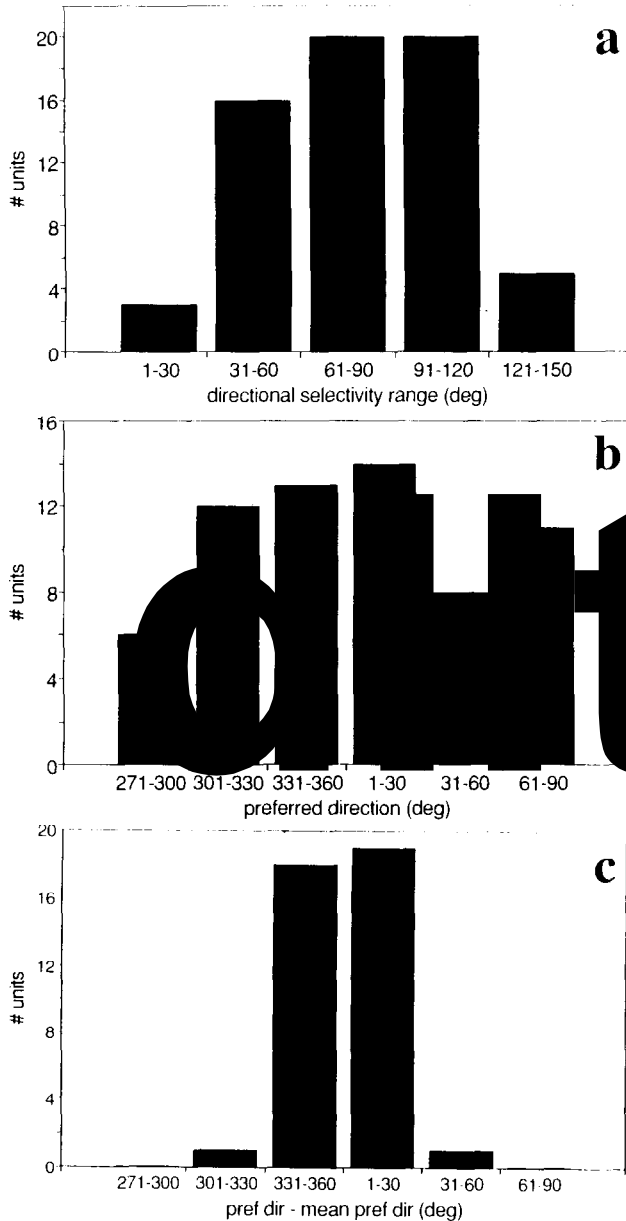


Fig. 2. (a) Directional selectivity range of DS units. The directional selectivity range was  $67 \pm 48^\circ$  (mean  $\pm$  SD). (b) Distribution of the preferred direction of all DS units (SD =  $57^\circ$ ). (c) Deviation of individual DS units from the mean preferred direction of DS units encountered in a single electrode track (SD =  $13^\circ$ ).

Fig. 3b presents the preferred directions of 24 (clusters of) DS units and the location of their recording sites (projected on the plane parallel to the torus-midbrain ventricle interface; data from 20 animals). The Dirichlet tessellation method [7] was used to decide which random combinations of two locations are neighbors. The obtained 64 pairs of neighbors yielded a mean difference of the preferred direction of  $38 \pm 26^\circ$ . When the measured preferred directions were randomly combined with the given locations, 1000 Monte Carlo realizations yielded only 14 cases with a smaller mean difference, indicating

that directional selectivity is topographically organized in the upper torus. The medial part of the torus appears to code the rostro-caudal direction ( $0^\circ$ ). In the rostro-lateral part the  $45^\circ$  direction predominates, and in the caudo-lateral part  $-45^\circ$ .

Bony fish with a similar auditory apparatus as the trout show localization behavior [1,18,19]. Our study shows that many units of the torus encode the direction of the particle motion. Therefore, it is thought that the torus plays an important role in source localization in the trout and probably in other bony fish. For airborne sound, mapping of auditory space in the midbrain has been demonstrated in birds and mammals [5,8]. Although fish, as other aquatic vertebrates, are subject to different bio-

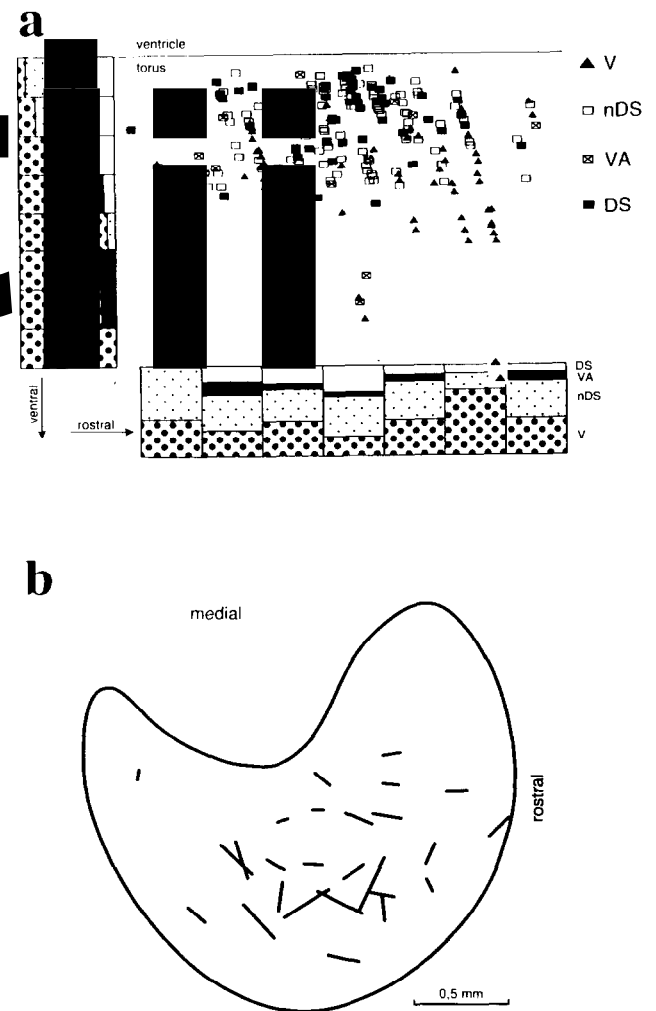


Fig. 3. Topographic organization. (a) Lateral view of the recording sites of DS and non-DS units, visual units (V) and bimodal units (VA). The histogram columns represent the normalized probability of occurrence. Binwidth: 0.33 mm along abscissa, 0.2 mm along ordinate. (b) Coding of preferred direction. The direction of preference to a rectilinear stimulus, estimated from the spike density histograms, is denoted by a line segment, the length of which is proportional to the supplement of the directional selectivity range. When in a single electrode track  $n$  DS units were found, the  $n$  preferred directions have been vectorially added and the resulting modulus was weighed with  $1/\sqrt{n}$ .

physical constraints, auditory space also appears to be mapped in the midbrain of the trout.

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