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RESEARCH ARTICLE

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Representation of sound source direction in the superior colliculus of the guinea pig in a virtual auditory environment

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Abstract The deep layers of the superior colliculus (SC) receive visual, auditory, and somatosensory input. A major function of the SC is the control of orientation movements of the eye, head, and pinna. While a topographical map for sound source direction remains elusive in primary auditory structures of mammals, such a map for azimuthal sound source directions has been reported in the deep layers of the SC. Moreover, a gradient of elevation tuning has been also seen in the SC of ferrets and cats. Here we demonstrate that a virtual auditory environment can be used to reveal azimuthal and elevational topography for auditory spatial receptive fields in neurons in the SC of guinea pigs. Individual, head-related transfer functions (HRTF) were measured in ten guinea pigs for 122 directions in the upper hemispheric field and convolved with white noise. Many neurons (39%) in the deep layers showed robust responses to these virtual sounds, and the majority of these neurons had small spatial receptive fields that were restricted to the contralateral hemifield. Best directions varied from 0° to 135° azimuth along the contralateral side and from –10° to 60° elevation. Like previous studies using free-field stimulation, a gradient of best azimuth direction was found along the rostral-caudal axis, with rear directions represented caudally and front directions rostrally. The topographical organization for best elevations had not been studied previously in the guinea pig. We found that it roughly followed the mediolateral axis, with preference for high elevations represented medially and low elevations laterally. A similar organization using free-field stimulation has been reported in the ferret.

Keywords Superior colliculus · Spatial hearing · Virtual auditory space · Guinea pig

Introduction

The mammalian superior colliculus (SC) receives visual, auditory, and somatosensory input and is involved in multi-sensory integration. The major function of the SC is the control of orientation movements such as eye, head, and pinna movements (Wurtz and Albano 1980). While there is scant evidence for the presence of a map or place code for sound source direction in primary auditory structures of mammals, such a map has been found in the deep layers of the SC. In the ferret and the cat, these neurons are arranged in two gradients of preferred direction, azimuth and elevation. This two-dimensional map of auditory "space" aligns roughly with the visual map (King and Hutchings 1987; King and Palmer 1983; Middlebrooks and Knudsen 1984). A similar map for sound source directions along the azimuth was also reported in the guinea pig (King and Palmer 1983; Withington-Wray et al. 1990). The neurons were stimulated with noise pulses via a moveable loudspeaker or with an array of loudspeakers. However, there are numerous problems associated with free-field stimulation. Head-holders, electrode microdrives, and stereotaxic benches produce acoustic reflections and distortions. Furthermore, it is difficult to control for pinna position and it is a critical parameter for internal representation of sound source incidence (cat: Young et al. 1996). For these reasons, we chose to use a virtual auditory environment to study the organization of sound source direction in the SC of guinea pigs. These virtual stimuli simulated sound directions in the azimuthal and elevational planes.

Sounds emitted by a source pass the external ears, where they are diffracted and partly shadowed off by the skull. Within the pinna/ear canal system they are further modified by resonance. Thus, spectral modifications are superimposed upon the incoming signals on their way to the eardrum which are specific with respect to the direc-

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tion and distance of the sound source relative to the head. Mathematically, these linear distortions can be described as head-related transfer functions, "HRTF." Quite recently it has become possible to present sounds via headphones that are spectrally shaped to match the effects of the directional filtering by the external ears. A virtual auditory environment can be created by filtering sounds with the individually measured HRTF (Hartung and Sterbing 1997; Wightman and Kistler 1989).

Methods

Animals

We used ten fully pigmented guinea pigs (350–700 g) of either sex. The animals were bred in the Department of Neuroethology at the University of Münster, Germany, and housed in the Department of Zoology and Neurobiology at the Ruhr University, Bochum. All animals had normal external and middle ears.

Measurements of the HRTFs

The animals were anesthetized with a ketamine/thiazine mix (100 mg/kg ketamine and 1.5 ml/kg thiazine i.m). Atropine sulfate (0.06 mg/kg) was injected subcutaneously to avoid hypersalivation. The HRTF measurement lasted less than 1 h, so that no additional applications of anesthetics were necessary. For HRTF measurement, a jaw holder was used to fix the position of the head so that the eyes and ears were in the horizontal plane. The animal was placed in the prone position on a turntable that was slightly smaller than the animal, so that no additional reflections were caused by it. This turntable was placed in the center of an anechoic room (approximately 5 m × 5 m × 5 m; absorber, G and H Isover SPS2; low-end cut-off frequency, 110 Hz). A miniature microphone (Knowles 3046) was positioned a few millimeters within the entrance of the ear canal of both ears and blocked the ear canals. Blocking is necessary for these HRTF measurements to be equivalent to such measurements made at the tympanum (Kulkarni and Colburn 1998). The HRTF measured at the tympanum can be separated into two terms: one that varies with direction of incidence, and another term that contains the nondirectional transfer function of the ear canal (Hammershøi and Møller 1996). The directional part of the HRTF can be measured at a distance of a few millimeters from the entrance of the blocked ear canal. If the sound pressure at this position matches the sound pressure of free-field stimulation, the sound pressure at the eardrum is the same as in the free field.

We measured HRTFs for 122 directions of the upper hemisphere through 11 loudspeakers that were mounted on a vertically oriented arc ranging from –10° to 90° in 10° steps. After measuring HRTFs for all the elevations for one azimuth, the table was turned clockwise in 15° steps to cover the 360° of azimuth. In order to keep the density of measured directions constant, not all elevations of each azimuth were tested. After the HRTF measurements, the animals were allowed to recover for at least 12 h.

Earphone measurement and calibration

The influence of the earphones coupled to the ear canal has to be compensated in the transfer functions before it can be used to present virtual sound sources. This was done by a measurement of the transfer function from the port of the earphone to the port of the microphone in the ear canal, and then filtering the raw HRTFs with the inverse transfer function.

The microphones were left in the same position as for the HRTF measurement, and the tips of the tubes of the custom-made earphones (transducers: Beyer DT911) were positioned at the entrance to the ear canal in the same position used to play the virtual sound sources to the animal. Direct comparison of the free-field responses at the eardrum with the virtual auditory responses revealed almost identical transfer functions. The variation was smaller than 2 dB for the entire frequency range used for stimulation, and for all tested directions. For pure tone stimulation, the transfer functions of the earphones were used for pre-equalization.

Surgery and electrophysiological experiments

For surgery and neural recordings, the guinea pigs were anesthetized with the same drug regimen used in the HRTF measurement. During the recordings, the guinea pigs metabolized the ketamine increasingly faster, so that the dose for maintaining anesthesia was increased every hour from 50 mg ketamine/kg to 100 mg ketamine/kg after approximately 6 h. This procedure kept the animal in a light anesthetic state throughout the neural recordings (breathing rate was monitored). Animals were maintained at a rectal temperature of 38°C using a heating pad. After exposing the skull, a metal bolt was fixed to the bregma with histoacryl and dental cement and used to fix the position of the head. Several holes of about 500 µm in diameter were drilled into the skull to allow microelectrode recordings from neurons in the left SC. A second hole was made in the contralateral frontal skull for a silver-wire reference electrode. The neural recordings were made in a soundproof chamber in complete darkness.

Once a single-unit response was isolated, broadband virtual sounds (frozen Gaussian noise from 200 Hz to 16 kHz, 50 ms duration, 5 ms rise/fall time) from 122 directions of the entire upper hemisphere were presented via individually calibrated earphones to the animal in a pseudorandom order. Each position was presented a total of five times. The sound pressure level before convolution with the HRTFs was 80 dB SPL (approximately 40 dB spectrum level). The sound pressure varies with sound source incidence and with frequency. Hence it is unnecessary to equalize the sound pressure level for these factors, since the same happens under free-field stimulation. Our goal was to simulate the free field as closely as possible.

In order to avoid long-term suppression effects in SC neurons (Hirsch et al. 1985), we used a long interstimulus interval (500 ms). Single-neuron activity in the deep layers of the SC was recorded with glass microelectrodes (impedance 3–10 MΩ, filled with 3 M KCl). The number of spikes for each sound source direction was tested against neighboring directions using the Kruskal-Wallis test. A neuron that failed this test would be either not acoustically responsive or omnidirectional (not found). Spatial tuning sharpness was calculated on the basis of half-maximal response. The sound source direction, which elicited the maximal spike count, was defined as "best direction." For neurons with a plateau-like receptive field, the geometric center of the receptive field was chosen as best direction.

The last penetration in each animal was made with a tungsten/iridium electrode to make electrolytic lesions (6 µA/2 min). The lesions served as benchmarks to make a 3D-reconstruction of the recording sites. Brains were fixed by immersion in buffered 8% formaldehyde solution for 3 weeks, cryoprotected with 30% sucrose, and sectioned (50 µm) with a cryostat in the transverse plane, and then stained with cresyl violet. All surgical, experimental, and euthanasia procedures were carried out in accordance with the German law for ethical treatment of animals and were approved by the district government (26.8720) and the grant application agency (DFG grant Ho 450/23–1-347).

Results

The size of the superior colliculus, without correction for curvature, was on average 4,100 µm for the rostral-caudal axis and 4,500 µm for the medial-lateral axis. However, there was considerable variability in the size of the

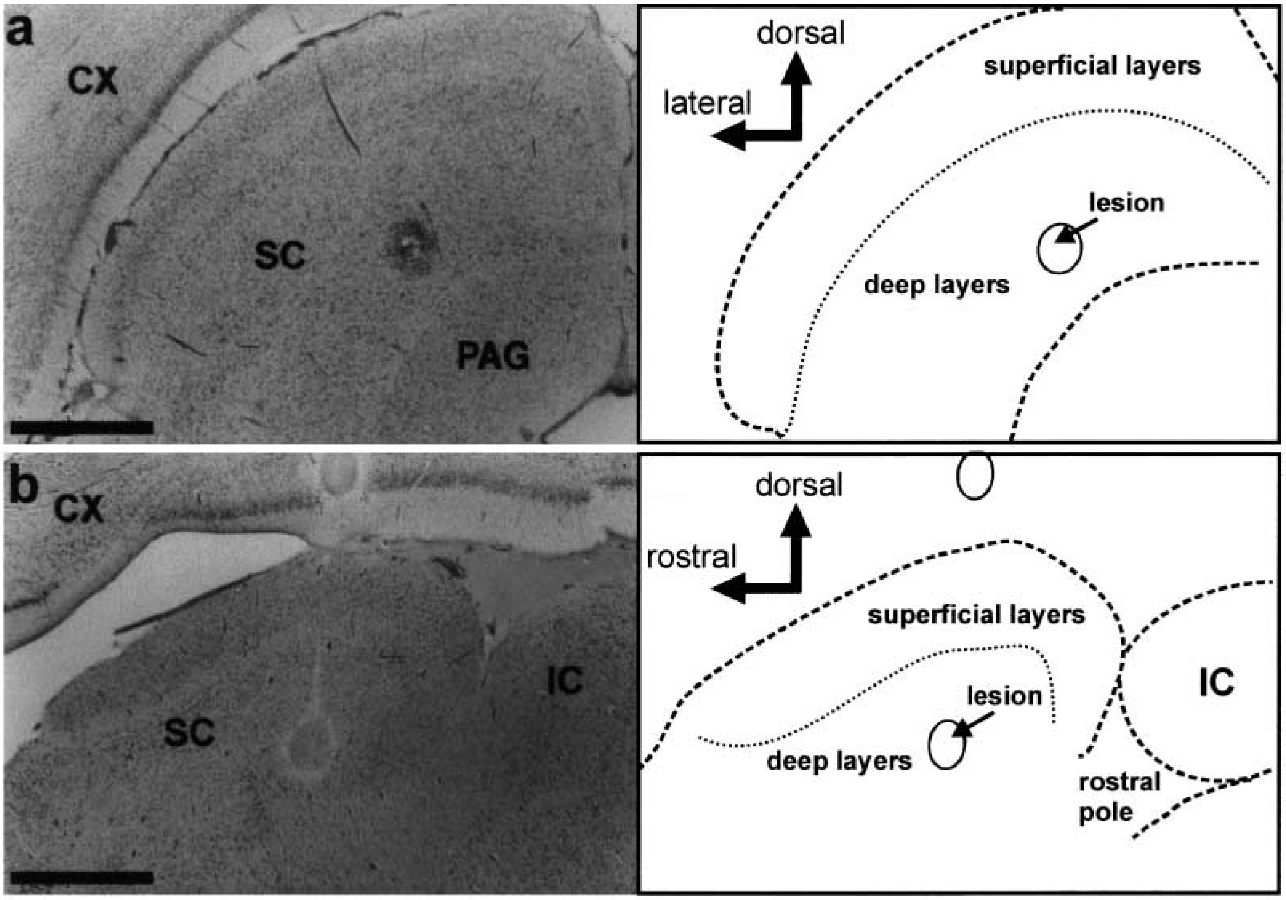


Fig. 1a, b **a** Photomicrograph of a Nissl-stained frontal section of the superior colliculus (*CX* cerebral cortex, *PAG* periaquaeductal gray, *SC* superior colliculus). **b** Parasagittal section of the SC (*IC* inferior colliculus). *Scale bar* 1 mm

SC, because the animals were from an outbred stain with a very high genetic variation. To estimate the distribution of the positions of the recording sites across animals, we normalized the positions for each animal. Figure 1 shows photomicrographs of a coronal (a) and a parasagittal (b) section of the SC. Each photomicrograph shows an electrolytic lesion.

The recording sites were scattered throughout the deep layers of the SC. We found auditory neurons in 23 out of 34 penetrations (68%) and on average we recorded from three or four neurons per penetration. All auditory neurons were located in layers 4–7. King and Palmer (1983) found auditory neurons in 71% of the SC penetrations in the guinea pig, which matches well our findings. No recordings were obtained from the extreme medial part of the SC. Recordings from extreme lateral positions were excluded because elevations lower than –10° could not be tested. Out of 200 spontaneously active neurons recorded in the deep layers, 77 (39%) were acoustically responsive and showed a preference for certain sound source directions. This percentage is smaller than described by Meredith and Stein for the cat (1986). They found that 49% of the deep layer neurons could be driven acoustically. In the present study, only 11% of the neurons were responsive to monaural presentation of tones.

Figure 2 shows six examples of neuronal response patterns seen in the SC to virtual sounds. The responses are displayed as dot rasters for each of the 122 virtual sound directions (five presentations at each direction) and sorted according to azimuth. The responses often showed an initial response that was tightly coupled to the stimulus onset response at favourable sound directions (Fig. 2a–c, e). This initial response could be the only response, which was the case for 20% of the neurons (Fig. 2b, e), or it could be followed by a patterned (22%; Fig. 2a) or non-patterned (12%; Fig. 2c) response that lasted throughout the sound duration. Most neurons (46%) only displayed a diffuse response (Fig. 2d, f). Figure 3 shows the elevation tuning of four neurons recorded along the mediolateral axis of the SC of one animal.

The median latency was 16.4 ms. The latency of 80% of the neurons (interdeciles) ranged from 7.7 to 28.8 ms (Fig. 4). Few neurons had a longer latency than 30 ms. One of them is shown in Fig. 2d.

The majority of the neurons (38%) responded with 2 spikes/50 ms virtual sound source stimulus; 27% responded with three and more action potentials. Maximal spike rate was 140 Hz (7 spikes/stimulation). The remainder of the neurons (35%) responded with 1 spike/stimulation (Fig. 5).

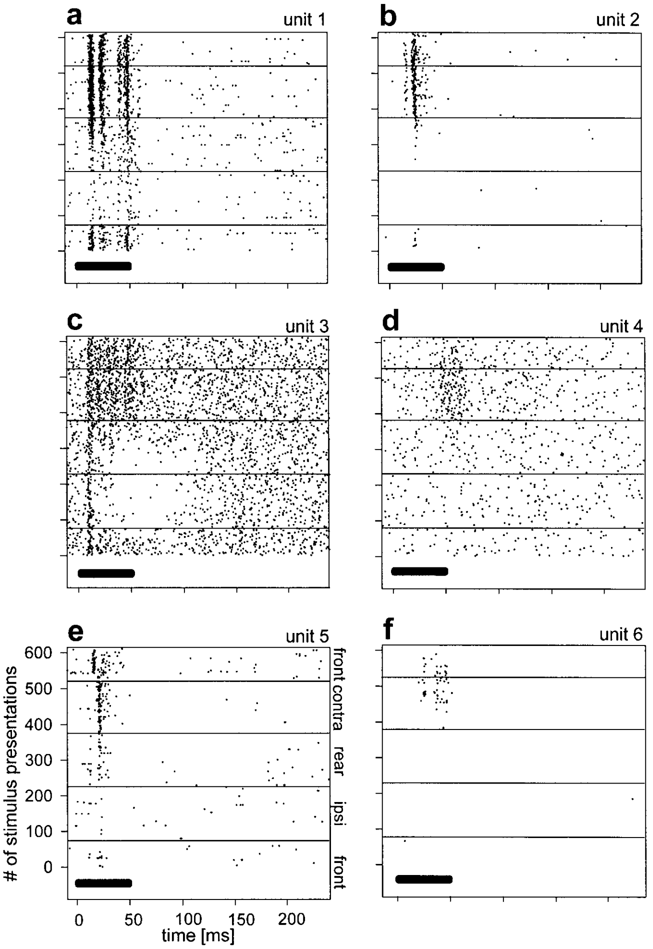


Fig. 2a–f Spike raster displays of six different single neurons in the superior colliculus. All the 610 runs (122 virtual sound source directions, 5 times each) are plotted. The *black horizontal bar* indicates the stimulus duration. The tested positions along the horizontal plane are arranged vertically. The respective space sectors are indicated on the *right side* of **e** (front, rear, ipsi, contra). Note that tested high elevations are intermingled **a** Hemifield neuron with a patterned sustained response; **b** neuron with a smaller receptive field; **c** neuron with high spontaneous activity and pronounced inhibition during stimulation from rear/ipsilateral directions; **d** neuron with a very weak, late and diffuse response; **e** this neuron shows a direction dependent first-spike latency; **f** very sparse response, only one sound source position resulted in a significant response (i.e., three of five presentations elicited a response)

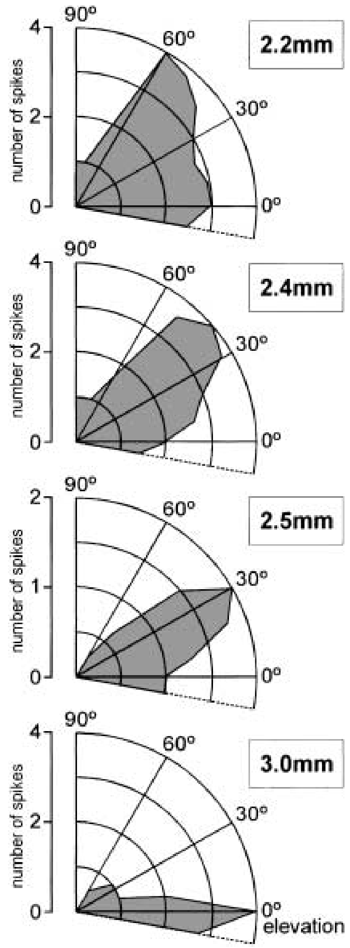


Fig. 3 Elevation tuning at best azimuth for four different single neurons recorded in one animal. The *numbers in the boxes* show the distance to the midsagittal plane

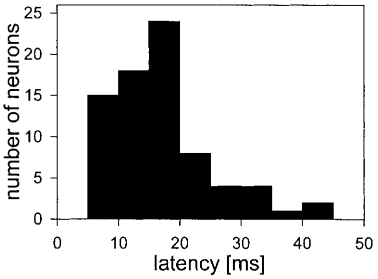


Fig. 4 Response latency of superior colliculus neurons. The median latency was 16.4 ms. Only a few neurons showed response latencies longer than 20 ms

The size of the receptive fields was calculated at half-maximal response and varied from very small (one or two sound directions; e.g., Fig. 2f) up to sound directions covering half of the sound field (180° in azimuth or –10° to 90° in elevation). The vast majority of the neurons (74%, 57/77) showed receptive fields, which were smaller than half the sound field and thus were tuned in azimuth and/or elevation. Only 18 (23%) neurons showed hemifield sensitivity. However, most hemifield neurons had unambiguous response maxima (best direction), and only a few showed constant responses within the receptive field. Only two neurons displayed two response maxima (“bilobed”) and consequently were excluded from our analysis of spatial field size and topography. Although we did not find omnidirectional neurons, 17 neurons also responded to ipsilateral sounds, but showed a much stronger response to contralateral sounds.

Spatial tuning varied from neuron to neuron. Figure 6 shows eight examples of receptive fields in the SC, recorded from different animals. The bold numbers (upper left of each panel in Fig. 6) represent the location of the

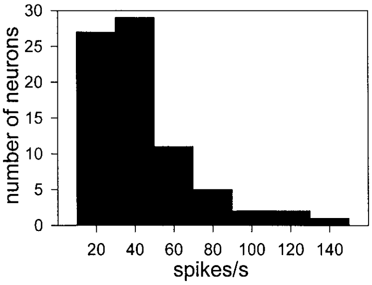
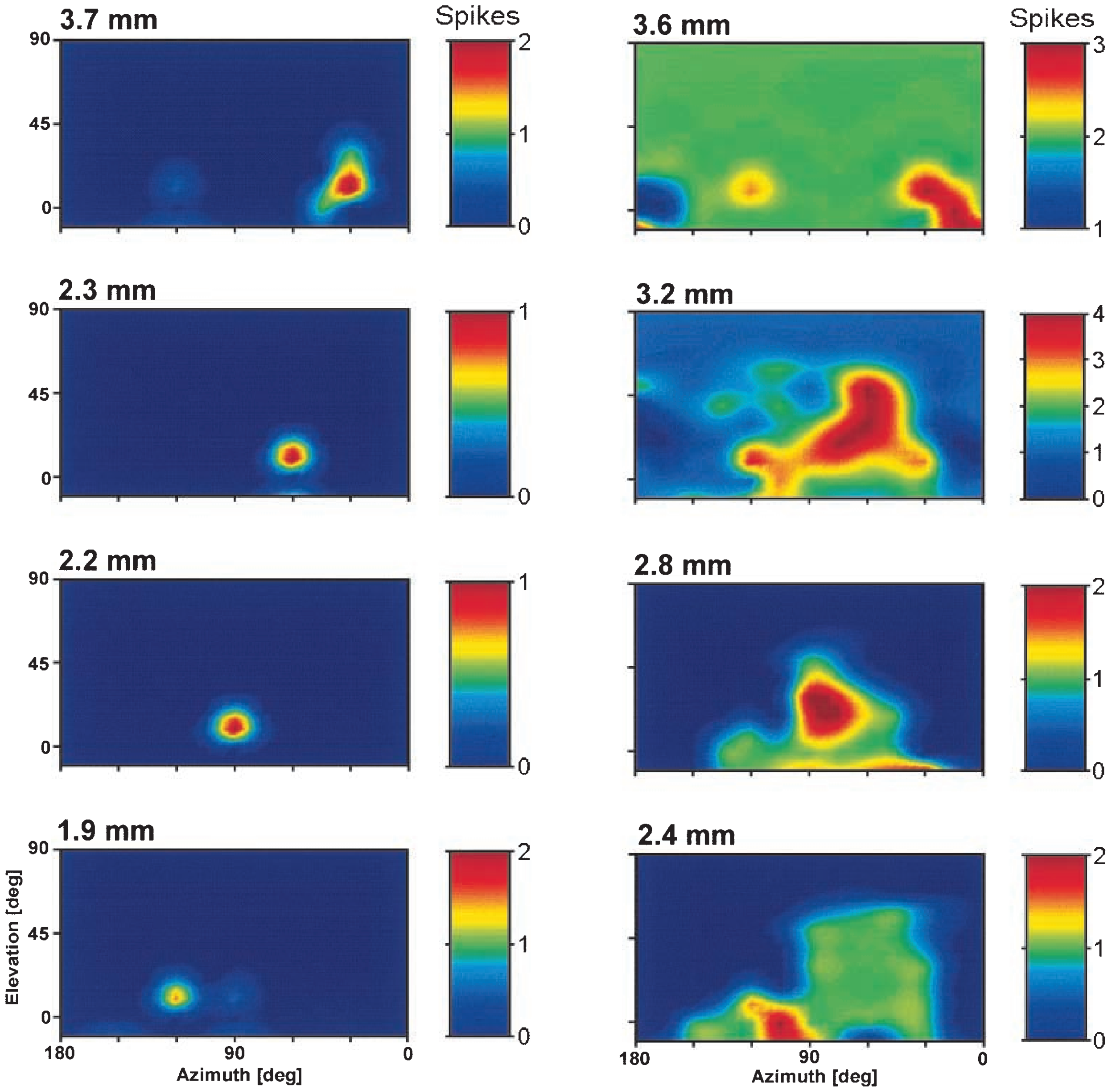


Fig. 5 Spike rates. Most neurons responded with 1 spike or 2 spikes per 50-ms stimulation time (20 Hz/40 Hz, respectively). Only a few neurons fired with spike rates higher than 100 Hz

Fig. 6 *Left*: Four neurons with very small receptive fields and their position along the caudorostral axis (distance from caudal SC pole in millimeters). *Right*: Neurons with receptive fields of intermediate size. The *colorbar* indicates median of spikes per stimulus presentation

neuron relative to its distance from the caudal pole of the SC. The receptive fields in the left column of Fig. 6 represent the smallest in our sample, while those in the right column are examples of neurons with mid-sized receptive fields. Note that in all examples, the center of the receptive fields (red in Fig. 6) shifts from right (front directions) to left (rear directions), with decreasing distance from the caudal pole of the SC.

To determine the sharpness of the SC units' tuning to virtual sound sources, we described their response areas in three-pole coordinates (left/right, front/back, up/down elevation, based on half-maximal responses; Fig. 7). In contrast to the azimuth/elevation system, this coordinate system allows a full description of the extents of the receptive fields. The problem with the azimuthal/elevation system is that neurons with same azimuthal receptive field become artifactually classified as broader with increasing elevation. In accordance with the international



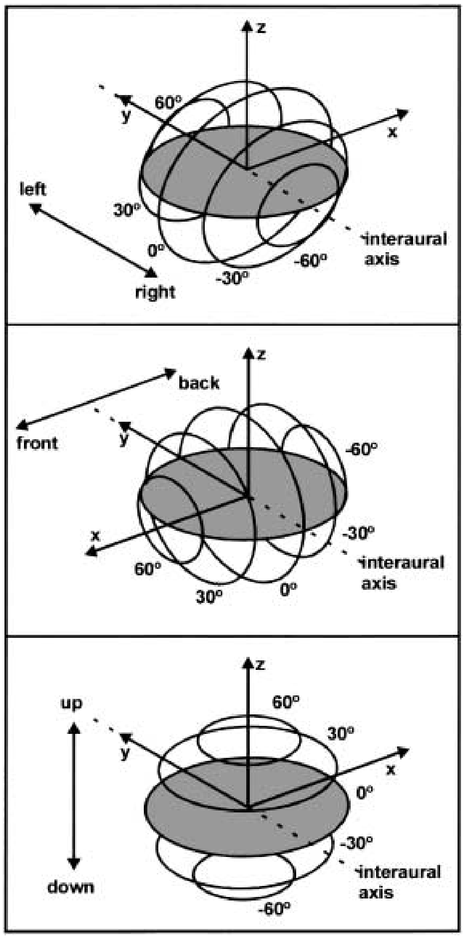


Fig. 7 The three-pole coordinate system. *Upper panel*: Left/right coordinate; *middle panel*: front/back coordinate; *lower panel*: up/down coordinate, which is identical with elevation

standards for measuring the skull, the origin of the three-pole system of coordinates is the intersection of the horizontal plane at the interaural axis, the median plane, and the frontal plane. The three planes lie at right angles to each other. The coordinate left/right is defined as the angle to the median plane, and coordinate front/back is the angle in relation to the frontal plane (see Fig. 7).

The median tuning sharpness for the left/right coordinate was 37° (interdeciles 9°–66.1°), 46.5° (interdeciles 21°–87.1°) for the front/back coordinate, and 19° (interdeciles 11°–35°) for the up/down-coordinate. Hence, the median size of the receptive fields turned out to be smaller than an octant.

Best directions varied from 135° (close to rear) to 0° azimuth (front) along the contralateral side, and from –10° to 60° elevation. Figure 8a plots best azimuthal direction for all neurons as a function of their distance from the caudal pole of the SC. Best azimuth for rear directions were represented caudally and front directions rostrally (*r*=0.64, *P*<0.001; 2nd-order fit). Low contralateral positions seemed to be overrepresented. Sixty-two percent of the neurons preferred azimuths between 60° and 90°. Only 38% showed best azimuths for frontal or rear directions. No neurons with preference for extreme rear (more than 135°) directions could be found. Most neurons (75%) preferred low elevations from 0° to 20°.

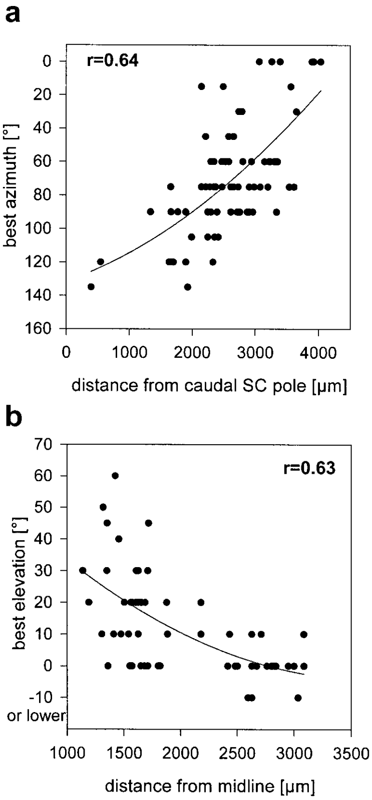


Fig. 8a, b Topographical representation of best directions. **a** Best azimuth plotted against the distance from caudal pole of the superior colliculus. **b** Best elevation plotted against the distance from midline. Note that most of the best azimuths ranged from 60° to 90°. Best elevations from 0° to 20° seemed to be overrepresented

Figure 8b plots best elevational direction of our neurons as a function of their distance from the midline. High best elevations tend to be located medially and low best elevations tend to be located laterally (*r*=0.63, *P*<0.001; 2nd-order fit).

Discussion

In the present study, for the first time, a virtual auditory environment was used to study the representation of auditory space in the SC. We demonstrated that the SC contains a map of sound source azimuth and elevation and that this representation is, in general, in accord with previous studies using sound delivered in the free field.

Comparison with studies using free-field stimulation

Representation of azimuth

Similar to our findings, King and Palmer (1983) found a representation of best azimuths from front to back

(0–158°) along the rostral-caudal axis for sounds delivered in the contralateral hemifield of the guinea pig. A similar organization was seen in the SC of the wallaby, i.e., best azimuths from 0° to 180° along the rostral caudal axis (Withington et al. 1995). In the SC of ferrets (King and Hutchings 1987), the representation of the contralateral azimuth also follows a rostral-caudal organization, but with the addition of a medial-lateral component (i.e., rostral-lateral to the caudal-medial). Additionally, there was a small representation for sounds from the ipsilateral hemifield (–20°).

Although we did not map visual receptive fields, others have reported that the visual fields roughly align with the auditory fields (King and Palmer 1983). They found that the best directions of the visual receptive fields ranged from 0° and 130° along the rostral-caudal axis. This corresponds nicely with the range of sound source directions found in our study (0–135°).

The organization of auditory receptive field in the SC of cats appears different from that observed in guinea pigs and ferrets. Middlebrooks and Knudsen (1984) found two classes of neurons: sharply and broadly tuned. Sharply tuned neurons had best azimuths in the frontal, contralateral hemifield (0–60°) and were located in the rostral portion of the SC; broadly tuned neurons had receptive fields that covered the contralateral hemifield and were found in the caudal portion of the SC.

Representation of elevation

In the present study we found a topographical representation of best elevation from low to high elevations (–10° to 60°) along the lateral-medial axis of the SC. Elevations lower than –10° could not be tested. Elevation tuning has not been reported previously in the guinea pig, but has been studied in the ferret and cat. In the ferret (King and Hutchings 1987), best elevations from –50° to 60° were represented along the caudal-lateral, rostral-medial axis. In the cat, best elevations tuning was seen only from –10° to 20°, with a lateral-medial representation (Middlebrooks and Knudsen 1984). Thus, it appears that elevation tuning in all animals is represented along the lateral-medial axis, with the guinea pig and ferret covering a much wider range than the cat.

Size of the receptive fields

The majority of neurons examined in this study had receptive fields that were smaller than the hemifield based on half-maximal neuronal activation. The median size of the receptive fields in the SC (front/back coordinate, 47°; left/right coordinate, 37°; up/down coordinate, 19°) did not significantly differ from those in the inferior colliculus and auditory cortex of the guinea pig (Hartung and Sterbing 1997; Sterbing and Hartung 1999). Similar to our findings, King and Palmer (1983) showed that the azimuth tuning was less than 45° (estimated from their plots) Furthermore, they found that spatial tuning slightly increased with sound intensity for most (63%) of the neurons, but preferred direction remained unchanged.

In the cat, neurons with spatially restricted receptive fields were first shown by Harris et al. (1980) and studied in greater detail by Middlebrooks and Knudsen (1984). Middlebrooks and Knudsen found that the size of the receptive fields (75% of the maximal response) was between 15° and 70° for neurons tuned to frontal azimuths (0–60°). Like in the guinea pig (King and Palmer 1983), the receptive field size increased slightly with sound intensity but preferred direction remained unchanged.

In the ferret (King and Hutchings 1987), the mean size of the receptive fields (based on half maximal response) was 77° for azimuth and 46° for elevation. The effects of sound intensity were mixed and sharpened spatial tuning in some neurons and broadened it for others. Again, as in previous report, sound intensity did not affect a neuron’s best position.

All studies, including ours, show that the size of the auditory receptive fields varies considerably. Neurons with small receptive fields were found intermingled with neurons with large receptive fields. The exception is the cat, where small receptive fields apparently are only found for frontal directions.

Behavioral impact

There seem to be fundamental differences between the representations of auditory space in the different species. The representations in the ferret and in the guinea pig show many similarities (topography, size of the receptive fields), while those in the cat do not. This difference may be linked to pinna mobility. The pinna of cats is highly mobile, while those of the guinea pig and ferret are not. The directionality of SC neurons is altered by changes in pinna position (Middlebrooks and Knudsen 1987). Another factor may be related to the cat’s visual field (area centralis) that over-samples frontal space. Hence, to match this overrepresentation, the auditory neurons covering the corresponding space sector show a relatively sharp spatial tuning. Nevertheless, the cat must be able to perform orientation movements toward sound sources in the back. Because the SC is regarded as source for the generation of orientation movements, the hemifield neurons described by Middlebrooks and Knudsen for the caudal SC might serve this purpose. The ferret, as a predator, also displays an overrepresentation of the area centralis in the SC, but the magnification factor is smaller than in the cat (Quevedo et al. 1996; Feldon et al. 1970). Best azimuths of the visual receptive fields range from –20° to 120° (Quevedo et al. 1996) or –10° to 110° (King and Hutchings 1987), with a slight overrepresentation of the central visual field.

The guinea pig’s eyes, in contrast, are oriented toward the side of the head and have a horizontally oriented visual streak. This animal has only a small binocular overlap (approximately 20°) in the front, but wide monocular fields on the sides. In the guinea pig, the retinal ganglion cells coding for positions close to the contralateral horizon are overrepresented, which is referred to as "visual streak" (Do-Nascimento et al. 1991). This organization corresponds with our findings that auditory receptive fields along the contralateral horizontal plane were overrepresented.

Advantages of virtual sound

We have shown that the organization of receptive fields studied with virtual sounds is similar to that measured using sounds from the free field. However, using virtual sounds to simulate auditory space has several advantages over free-field stimulation. First, it alleviates the concern of reflections created by the recording environment. Second, the monaural and binaural characteristics of a neuron can be tested, a feature not possible for free-field stimulation. Third, the binaural cues to which a neuron is sensitive can be determined, again a feature not possible in free-field stimulation. Finally, a neuron's spatial field can be tested more efficiently than for free-field stimulation.

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