

# Expansion of the Tonotopic Area in the Auditory Cortex of the Blind

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A part of the core area of the auditory cortex was examined in nine blind and 10 sighted individuals by magnetic source imaging and was found to be enlarged by a factor of 1.8 in the blind compared with the sighted humans. Moreover, the latency of the N1m component of the auditory-evoked magnetic response was significantly decreased in the blind. The development of use-dependent cortical reorganization may be a consequence of the absence of visual input in combination with enhanced

auditory activity generated by the long-term concentration by blind individuals on nonvisual cues to interact appropriately with the environment. It is consistent with and well suited to mediate the demonstrated increased ability of the blind to accurately localize acoustic sources in peripheral auditory fields and to decode speech.

**Key words:** tonotopic map; auditory cortex; reorganization; blind; MEG

Blind individuals are forced by the nature of their disability to depend on nonvisual modalities, including audition, for information about their external environment. When attention is directed to peripheral auditory space, localization of sounds has been shown to be better in blind than in sighted people (Muchnik et al., 1991; Lessard et al., 1998; Röder et al., 1999a). Data on sound localization in the frontal region (Zwiers et al., 2001) and other auditory discriminative abilities is less conclusive (Stankov and Spilsbury, 1978). Whether or not the full range of auditory perceptual ability is improved in the blind, it is nevertheless the case that sensory input over nonvisual avenues becomes of greater behavioral relevance to these individuals to enable effective interaction with the world around them.

Focused attention on behaviorally relevant stimulation over extended periods has been found to produce a substantial enlargement in the representational zones of the involved portions of the body in somatosensory cortex in research with animals (Merzenich et al., 1984; Jenkins et al., 1990) and humans (Elbert et al., 1994, 1995, 1998; Sterr et al., 1998a,b). Similarly, the primary auditory cortical fields can be dramatically refined or profoundly degraded. Use-dependent reorganization in the frequency receptive fields has been demonstrated by a number of groups (Bakin and Weinberger, 1990; Recanzone et al., 1993; Ohl and Scheich, 1996).

Increasing interest has been devoted to the phenomenon of cross-modal plasticity in blind humans, such that auditory (Kujala et al., 1992, 1995a,b, 1997; Alho et al., 1993; Rösler et al., 1993; Weeks et al., 2000) and tactile (Rösler et al., 1993; Uhl et al., 1993; Kujala et al., 1995b; Röder et al., 1996, 1997; Cohen et al.,

1997) stimuli come to be processed in visual cortex. Rauschecker et al. (1992), for instance, found in cats and mice deprived of vision from birth, a supernormal growth of facial vibrissae and an enlarged whisker representation in the somatosensory cortical barrel field. There has been little work evaluating the prediction from the use-dependent cortical reorganization literature that there would be a related but more direct effect, i.e., increased reliance on the auditory modality would give rise to alterations in the auditory areas of the brain. In one relevant experiment, Hamilton et al. (2000) found an increased prevalence of absolute pitch in blind musicians.

The present study explored changes in the auditory cortex of blind individuals as a consequence of the enhanced, visual deprivation-enforced auditory processing. An expansion of regions within the auditory cortex was expected as an indication of use-dependent cortical reorganization. Considering the evidence of the global functional organization of the auditory cortex and its topographic representation of stimulus and processing domains (Rauschecker, 1998; Schreiner, 1998; Rauschecker and Tian, 2000), the tonotopic map can be reconstructed from the auditory magnetic response to pure tones. Recently, Godey et al. (2001) validated the presently used neuromagnetic source localization of auditory-evoked fields with source localization from intracerebral-evoked potentials and demonstrated that both methods suggest that the auditory-evoked N1 may be generated from sources in the intermediate and lateral parts of the Heschl's gyrus and in the planum temporale. The present study, using magnetic source localization, explored whether the increased dependence on the auditory modality in blind individuals would result in an alteration of regions in the auditory cortex.

## MATERIALS AND METHODS

Nine blind (four male, five female; mean age, 39.4 ± 6.1; range, 27–46 years) and 10 sighted (five male, five female; mean age, 37.1 ± 6.8; range, 29–47 years) subjects participated in the study. Five of the blind subjects were blind from birth; four had become blind as adults between the ages of 16 and 30 years, with their mean duration of blindness being 8.3 ± 3.8 years. In all cases, blindness was attributable to peripheral damage of the

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visual system, and there were no additional neurological problems. All subjects were right handed, and audiological examinations indicated a normal status. Informed consent was obtained from each subject after they received a detailed explanation concerning the nature of the study.

Magnetic fields evoked by sequences of acoustic stimuli were recorded simultaneously from the right and left hemispheres using a 148-channel whole-head neuromagnetometer. For recording, subjects were placed in a supine position that was made as comfortable as possible to prevent head and body movement. The recording device (Magnes 2500; 4-D Neuroimaging, San Diego, CA) was operated within a magnetically shielded room. The magnetic sensing devices (magnetometers) were separated by 28 mm and were arranged in a uniformly distributed array on the inside surface of a helmet.

Four series of 128 tone bursts each were delivered monaurally to the right ear, at 60 dB above individually determined hearing level. For each series, stimuli had a carrier frequency of 0.5, 1, 2, or 4 kHz; the sequence of frequencies was randomized across subjects according to a fixed irregular order. Each tone burst was 500 msec in duration, with 10 msec rise and fall time with a cosine slope. Stimuli were presented through a nonmagnetic and echo-free stimulus delivery system (6.3 m in length, 16 mm inner diameter) with an almost linear frequency characteristic (deviations less than  $\pm 4$  dB in the range between 200 and 4000 Hz). The interstimulus interval varied randomly between 2.7 and 3.3 sec.

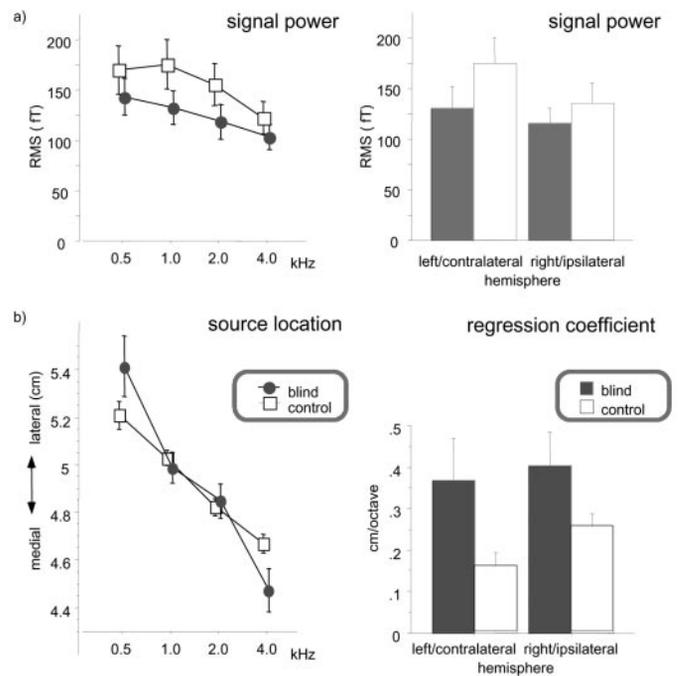
Stimulus-related epochs were recorded with a bandwidth of 1–100 Hz and sampled at 387.5 Hz. Epochs contaminated by muscle or eye blink artifacts with amplitude variations of  $>3$  pT in any channel were automatically rejected from additional analysis. The averaged evoked fields were filtered from 1 to 20 Hz and referred to a 100 msec prestimulus baseline. Source analysis followed the procedure developed by Pantev et al. (1989, 1995, 1998). Subsets of  $\sim 40$  channels centered around the source location and including the signal extrema were selected for analysis for the left or the right auditory areas, separately.

When the equivalent current dipole for a given frequency did not match one of the criteria, it was excluded from estimation of the regression line. On the contralateral side, this was the case for one sighted and two blind subjects, and, on the ipsilateral side, it was true for one sighted and three blind subjects. In four subjects (three sighted and one blind), two or more source locations did not match the criteria for a focal source, and, therefore, no regression parameters were computed. Mean residual variance was 1.6 times greater in the blind than in sighted subjects.

## RESULTS

Consistent with previous findings for sighted individuals (Pantev et al., 1988, 1989, 1995, 1998; Mäkelä, 1988), the N1m peak occurred at an earlier latency over the contralateral hemisphere than over the ipsilateral hemisphere in both groups (mean contralateral latency across all subjects,  $109.3 \pm 17.4$  msec; mean ipsilateral latency,  $119.7 \pm 14.3$  msec;  $F_{(1,15)} = 16.5$ ;  $p < 0.01$ ). In the blind subjects, N1m latencies were consistently shorter than in the sighted subjects ( $107.0 \pm 12.4$  msec for the blind and  $121.40 \pm 17.14$  msec for the sighted subjects, both hemispheres;  $F_{(1,15)} = 4.6$ ;  $p < 0.05$ ). This group difference was significant for both the contralateral (16.4 msec) and the ipsilateral (11.8 msec) hemispheres. Frequency did not have a significant effect on N1 latencies (main effect,  $p = 11$ ; interactions, all  $F$  values  $< 1$ ; all mean differences were smaller than 5 msec).

A dipolar structure for the N1m component was observed over each hemisphere and was similar in blind and sighted individuals. The global field power [root mean square (rms) across subsets of channels] and the N1m dipole moment (Q), representing the N1m source strength, showed a larger contralateral (rms,  $155.8 \pm 76.2$  fT; Q,  $37.9 \pm 29.1$  nAm) than ipsilateral magnitude (rms,  $128.5 \pm 54.6$  fT; Q,  $25.7 \pm 17.6$  nAm;  $F_{\text{rms}(1,15)} = 14.1$ ;  $p < 0.01$ ;  $F_{\text{Q}(1,15)} = 14.1$ ;  $p < 0.01$ ). On average, these measures of N1m amplitude were somewhat larger for the sighted than for the blind subjects, but the difference between blind and sighted subjects with respect to these measures of N1m magnitude did not reach significance. For the analysis of the rms, as a measure of signal power, which does not require source modeling, all subjects could be included in



**Figure 1.** The change in signal power (*a*) and source location on the mediolateral axis (*b*) is shown as a function of stimulus frequency, averaged separately for the two groups. The bar graphs on the right illustrate that the effects [smaller signal power (NS) and expanded map size ( $p < 0.01$ ) in the blind] can be observed equally in both hemispheres. The observation that the area across which the four different frequencies respond is larger in the blind whereas the signal power tends to be smaller suggests that the neuronal pool activated by a given sinusoidal tone is more specific in the blind than in sighted individuals. Error bars indicate SEs.

the analysis; there was not a significant main effect of groups ( $F_{(1,17)} = 1.5$ ;  $p = 0.24$ ). A drop of signal power with stimulation frequency (Fig. 1*a*) was present equally in both groups (main effect for frequency,  $F_{(3,51)} = 14.2$ ;  $p < 0.01$ ). Figure 1 plots the rms and the N1m source locations against the logarithms of the four standard frequencies used in this experiment for blind and sighted individuals.

The core areas of auditory cortex and adjacent regions exhibit a tonotopic arrangement in humans such that higher frequencies are represented medially and lower frequencies are represented progressively more laterally (Pantev et al., 1988, 1989). When N1m dipole locations are plotted against the logarithm of frequency (Fig. 1*b*), they can be represented (with interpolation) by a straight line (Pantev et al., 1995, 1998). The steeper the slope of this regression line, the more extended is the map of the tonotopic representation. The absolute slope of this regression line for the sighted individuals is 1.84 times steeper than for the blind individuals, indicating that the tonotopic map for blind individuals is 84% larger in the blind than in sighted ( $p = 0.001$ ) (Fig. 1*b*). As illustrated in the right panel of Figure 1*b*, this effect was present to the same extent in both hemispheres. When the two regression coefficients were averaged across hemispheres (ignoring missing values from one hemisphere), absolute coefficients were obtained for all 19 subjects; the main effect of group was  $F_{(1,17)} = 13.2$  ( $p < 0.01$ ). The effect remained significant, when only those five blind and five sighted subjects were included for whom there was a complete set of source models, i.e., a current dipole could be fitted for each frequency in each hemisphere

( $F_{(1,8)} = 9.2$ ;  $p < 0.02$ ). The averages of these subgroups were almost identical with the averages across all subjects.

## DISCUSSION

The early research on use-dependent cortical reorganization (Merzenich et al., 1984; Jenkins et al., 1990) indicated that it was the behavioral relevance of afferent input that was responsible for increases in the size of cortical representational zones associated with the reception of that input rather than simply the amount of incoming stimulation. Blind individuals do not receive more auditory stimulation than sighted individuals. However, to interact effectively with their environment, they have to rely on nonvisual, primarily auditory input to a greater extent.

Behavioral relevance as a source of use-dependent reorganization suggests the possibility that the expansion might have some value in the functional economy of the individual. It has been shown that the localization of sounds in peripheral fields (Lessard et al., 1998; Röder et al., 1999a) and other central auditory skills (Muchnik et al., 1991) are better in blind than sighted individuals. This capability should be of value in the blind, who are unable to use vision to discriminate the location of objects and potential avenues for progression. Sound localization is generally considered to be a function of binaural cues processed in the auditory cortex. However, it has been argued (Rauschecker, 1999) that there can be a second set of cues based on specific filtering of sounds by the head and pinnae that provide information concerning the spatial origin of acoustic stimuli. It is possible that the expansion of the tonotopic map in the blind might in some way be involved in providing a basis for the very subtle discriminations that would be required to improve this type of capability. For example, a larger neural network would have a higher fidelity and, consequently, as previously demonstrated, a greater speed at which temporal auditory discriminations could be made. In fact, monaural sound localization is enhanced in the blind (Lessard et al., 1998). Moreover, a more efficient encoding of verbal material (Röder et al., 2001) has been reported. This capability may also be mediated by the enlarged cortical representation given that the frequency spectrum used in the present study covers the sound spectrum of language. Finally, our findings might also explain the shorter refractory periods observed in the blind for the N1 evoked potential component (Röder et al., 1999b).

Previously, we showed in blind individuals that there is an increase and alteration in the functional organization of the area of the cortex receiving somatosensory information (Sterr et al., 1998a,b), and Pascual-Leone and Torres (1993) have shown that a similar phenomenon takes place in motor cortex. Recently, attention has also been focused on the intriguing phenomenon of cross-modal plasticity in blind individuals whereby auditory and somatosensory input comes to be processed in the visual areas in the brain (Rauschecker, 1995; Kujala et al., 2000). These areas have been deprived of their normal source of visual sensory input and might therefore otherwise be unused. We found no activity in the latency range below 120 msec that could be fitted by dipolar sources in visual areas and thus no evidence of short-latency processing of simple auditory input in visual cortex in blind people. However, the auditory map, which we determined had expanded greatly in blind individuals, is situated in the area of the brain that does carry out short-latency processing of auditory input by the nature of its built-in structural connectivity. This is fundamental to later auditory processing, which can involve regions adjacent to primary auditory cortex, as in sighted individuals, and also distant locations, as in the blind.

One plausible explanation of the expansion of auditory cortex in blind individuals found in the present study is the elaboration of a use-dependent cortical reorganization involving either an unmasking of previously silent connections and/or sprouting of new neural elements from those that previously existed. Alternate hypotheses are possible. For example, blindness could lead to reduced cell death in the cortical territory of other modalities, including auditory cortex, or to stabilization of transient connections. It also seems possible that an expanded auditory area might include a larger number of contributing neurons and hence larger dipole moments. Another possibility is that the frequency tuning of neurons might become more frequency specific with the consequence that a tone of a particular frequency would activate a smaller set of neurons; an expansion of the auditory cortex would thus be needed to house more such sets (Bakin and Weinberger, 1990). The mechanisms are not mutually exclusive, and, in some cases, they are partially overlapping; the present data do not permit determination of which were operative. It also remains questionable whether the expanded tonotopic map observed here has a causal relationship to the auditory discrimination abilities observed to be enhanced in the blind noted above.

However, the expansion of the tonotopic map observed in this experiment does supplement the picture of the way in which the brain reorganizes itself in response to blindness, possibly as a result of the blind individuals' greater attention to and reliance on nonvisual sensory avenues to maintain adequate commerce with the world around them. The expansion of the tonotopic map, the reorganization of somatosensory cortex, and cross-modal plasticity in the blind (Rösler et al., 1993; Kujala et al., 1995a, 1997; Sadato et al., 1996; Cohen et al., 1997; Sterr et al., 1998a,b) would appear to be an excellent composite example of the principle formulated by Merzenich et al. (1984) of the continual competition for cortical space. When there is increased use of a body part of type of sensory discrimination, the representational zones within the brain normally responsible for mediating those functions expand at the expense of other regions that are currently not being used to the same extent.

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