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Source analysis reveals plasticity in the auditory cortex: Evidence for reduced hemispheric asymmetries following unilateral deafness

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H I G H L I G H T S

- Experience-related plasticity is apparent in adult humans with profound unilateral deafness, reflected by changes in dipole strength, location and orientation.
- Inconsistencies in previous studies using dipole source analysis may be explained by inadequate consideration of the effect of dipole location and orientation.
- This study provides evidence for experience-related plasticity in the adult central auditory system, and the results may help to clarify the meaning of altered dipole strengths, location and orientation parameters.

A B S T R A C T

Objective: To investigate the effect of acquired unilateral deafness on hemispheric asymmetries in adult humans using cortical auditory evoked potentials.
Methods: N1 cortical auditory evoked potentials were measured from 30 channels in 18 unilateral profoundly-deaf participants (6 right-sided and 12 left-sided deafness) and 18 audiogram-matched controls. Stimuli were 0.5-kHz and 4-kHz tones presented monaurally, and the data were analysed using global field power and dipole source analysis.
Results: There was a statistically significant difference in dipole source strength and orientation between the two groups. Similar changes (increased dipole strength and more medial orientation) were apparent after profound unilateral deafness of either ear and for both stimuli.
Conclusions: The results reveal evidence of central auditory system plasticity that is consistent with animal models having experimentally induced unilateral deafness.
Significance: The trend towards reduced hemispheric asymmetries was reflected in the dipole source model by changes in dipole strength, location and orientation. These findings may explain the inconsistencies reported in previous studies involving dipole source analysis where location and orientation have not always been considered.

1. Introduction

The central auditory system (CAS) is known to exhibit experience-related plasticity following the onset of deafness (Neuman, 2005). Evidence of auditory plasticity in mature humans has been obtained from studying individuals with unilateral deafness (Scheffler et al., 1998; Bilecen et al., 2000; Ponton et al., 2001; Langers et al., 2005; Firszt et al., 2006). In normal hearing individuals, monaural stimulation results in asymmetrical activation of the CAS, with the contralateral hemisphere producing greater activation than the ipsilateral hemisphere (Woldorff et al., 1999; Hine and Debener, 2007). This is referred to here as hemispheric asymmetry. Profound unilateral deafness leads to changes in the normal pattern of hemispheric asymmetry upon stimulation of the remaining intact ear. These changes consist primarily of an increase in the response of the hemisphere ipsilateral to the ear of stimulation, while activity in the contralateral hemisphere remains largely unchanged (Popelar et al., 1994; McAlpine et al., 1997). Therefore, monaural stimulation in individuals with unilateral deafness results in a greater overall response of the CAS and reduced hemispheric asymmetry. However, whilst data from functional magnetic resonance imaging (fMRI) studies have consistently shown these changes in humans with profound unilateral deafness (Scheffler et al., 1998; Bilecen et al., 2000; Langers et al., 2005; Firszt et al., 2006), this has not been the case in studies using magnetoencephalography (MEG) and electroencephalography (EEG). To date there has only been one published study, using

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cortical auditory evoked potentials (CAEPs), that has demonstrated experience-related plasticity in humans with late-onset profound unilateral deafness (Ponton et al., 2001). CAEPs produced using a click stimulus were measured from 15 individuals with unilateral deafness and compared with those of nine normal hearing controls. A key aspect of the methodology of this study was that the analysis was based on sensor level data, and was carried out in two stages. First, the root-mean-squared amplitude of CAEPs across groups of sensors, over each hemisphere, was compared. Second, the amplitude of the N1 obligatory CAEP across subsets of sensors was compared. Results from the first analysis showed that while the response amplitude over the contralateral hemisphere was similar between the groups of participants, the amplitude over the ipsilateral hemisphere was significantly greater in those with unilateral deafness, resulting in reduced hemispheric asymmetry. Furthermore, these changes were subsequently found to be reflected primarily by sensors in the central scalp regions. Despite this finding, most studies involving the N1 wave in CAEPs or its MEG equivalent, N1m, have not consistently shown any evidence of plasticity following unilateral deafness in adult humans (Vasama et al., 1995, 2001; Fujiki et al., 1998; Khosla et al., 2003; Hine et al., 2008; Hanss et al., 2009). The present study was therefore conducted with the aim of clarifying the reasons for the inconsistent findings in EEG/MEG studies of plasticity in adult humans with late onset profound unilateral deafness.

One explanation for these inconsistencies could be methodological factors involving the source modeling techniques most often used to characterize the response of the CAS (Vasama et al., 1995, 2001; Fujiki et al., 1998; Khosla et al., 2003; Hine et al., 2008). CAEPs such as the N1 (or N1m) are usually characterized in source models by one or more dipoles in each hemisphere. Measuring hemispheric asymmetries therefore becomes a case of comparing the strength, location and orientation of the dipoles in each hemisphere. In normal hearing individuals the contralateral dipole would be expected to have a greater strength than the ipsilateral dipole following monaural stimulation (Woldorff et al., 1999; Hine and Debener, 2007). Previous studies investigating changes in CAS activity following unilateral deafness have focused on changes in dipole strength, and have not always considered changes in orientation or location of the dipole (Vasama et al., 1995, 2001; Fujiki et al., 1998; Khosla et al., 2003; Hine et al., 2008). However, it is possible that changes in the normally observed asymmetrical CAS response may be reflected by changes in dipole strength, location, orientation or complex interactions between all three parameters in each hemisphere.

The present study therefore aimed to characterize any differences in N1 CAEPs between adults with profound unilateral deafness and a control group by measuring the degree of activation produced over each hemisphere in the N1 latency range to monaural stimulation. The analysis involved consideration of dipole strength, location and orientation since this has not been done in previous such studies. It was hypothesized that an overall increase in CAEP response amplitude would be apparent in those with unilateral deafness, reflecting an increased responsiveness of CAS neurons to stimulation of the intact ear, but that reduced hemispheric asymmetries may be reflected by changes in the relative dipole strengths, locations and orientations in each hemisphere.

2. Methods

2.1. Participants

Eighteen unilateral profoundly deaf adults (UDs) took part in the study (5 female, 13 male; mean age = 60 years old, range = 43–75 years old). Of these, 6 had right- and 12 had left-sided deafness due to translabyrinthine surgery for the removal of a unilateral acoustic neuroma. This surgery results in abrupt and complete deafness of the affected side. The duration of deafness after surgery ranged from 6 months to 7 years and all participants were right handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). Matched to each individual was a control participant (MCs) with hearing threshold levels in both ears similar to the participant's intact ear (±10 dB at 0.5-kHz and 4-kHz). The participants were also matched for sex, handedness and age (controls mean age = 58 years old, range = 42–74 years old). The mean pure tone hearing threshold levels for participants and matched controls is shown in Fig. 1. The study was approved by the Cumbria and Lancashire NHS Research Ethics Committee (08/H1016/66) and all participants gave written, informed consent.

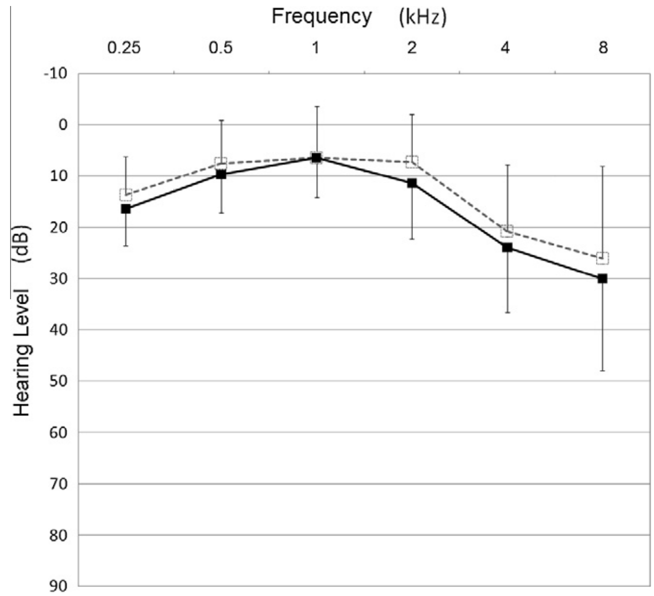

Fig. 1. Mean pure tone hearing thresholds for the test ear of unilaterally deaf (filled symbols) and matched control participants (open symbols). Error bars denote ±1 s.d.

2.2. Stimuli

Two pure tones (0.5-kHz and 4-kHz) were selected to represent low and high-frequency stimuli. These were of 80 ms duration including 10 ms onset and offset ramps, defined using the Blackmann windowing algorithm. The stimuli were generated digitally and presented via a 44.1 kHz digital-analogue converter monaurally to the intact ear of participants with unilateral deafness, and the corresponding ear in control participants. Stimuli were presented in a pseudo randomly interleaved fashion via ER-3A insert earphones. The inter-stimulus interval varied pseudo randomly between 900 and 1300 ms. Each stimulus was presented in blocks of 500 repetitions and the order of frequency of presentation was counterbalanced across participants. The presentation level was set at a sensation level (SL) of 60 dB, although three participants and their matched controls received reduced SLs of 40 dB in the 4-kHz condition due to subjective loudness discomfort. The absolute levels varied by up to 30 dB between participants. Statistical comparison of results between groups was carried out after exclusion of these three participants and their matched controls, and the pattern of results did not change. Hence, no further distinction was made in the analysis. Passive attention was maintained through watching a silent closed-caption movie for the duration of each session.