Vibration-induced auditory-cortex activation in a congenitally deaf adult

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Considerable changes take place in the number of cerebral neurons, synapses and axons during development, mainly as a result of competition between different neural activities [1–4]. Studies using animals suggest that when input from one sensory modality is deprived early in development, the affected neural structures have the potential to mediate functions for the remaining modalities [5–8]. We now show that similar potential exists in the human auditory system: vibrotactile stimuli, applied on the palm and fingers of a congenitally deaf adult, activated his auditory cortices. The recorded magnetoencephalographic (MEG) signals also indicated that the auditory cortices were able to discriminate between the applied 180 Hz and 250 Hz vibration frequencies. Our findings suggest that human cortical areas, normally subserving hearing, may process vibrotactile information in the congenitally deaf.

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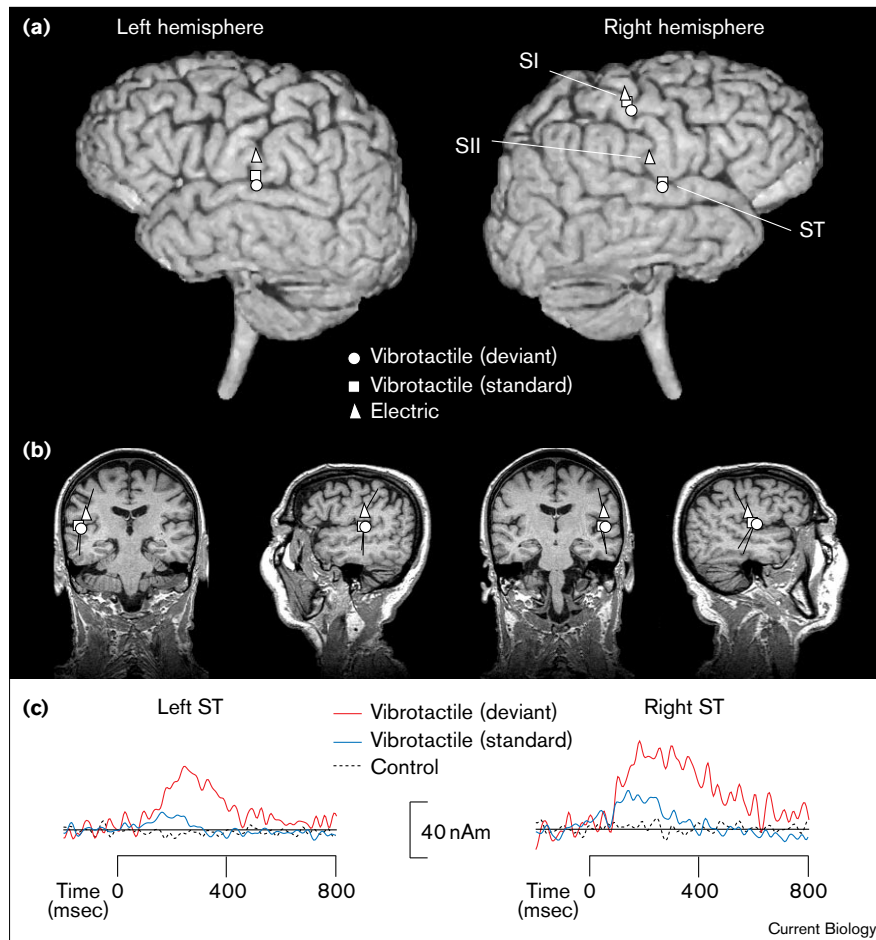
Results

We recorded magnetic signals from a congenitally deaf right-handed male (age 77 years; fluent in Finnish sign language and in lip-reading; hearing thresholds ≥ 110–120 dB hearing level (HL); 5 out of 10 siblings in the family congenitally deaf) and from six healthy right-handed control subjects (ages 26–37 years; four females). Vibrotactile stimuli were applied on the left palm and fingers of each subject by delivering 100 millisecond tones with a bass-reflex loudspeaker to a plastic blind-ended tube (diameter 38 mm) once every second. To test the reactivity of the brain to sudden stimulus changes, the randomised stimulus sequence consisted of frequent 'standard' (250 Hz, $p = 0.85$) and infrequent 'deviant' (180 Hz, $p = 0.15$) stimuli. During the measurement, each subject felt the vibrations while holding the left hand around the tube but did not hear any sounds.

Figure 1a shows magnetic-field patterns of the deaf subject following the deviant vibrotactile stimuli. The pattern suggests activation of the right-hand area in the primary somatosensory (SI) cortex about 60 milliseconds after stimulus onset. Source modelling [9] and projection of the source areas onto the anatomical magnetic resonance images (MRIs) indicated activation of the SI hand area, which was also activated by electric stimulation of the left median nerve at the wrist (see Figure 2). The vibration-induced SI signals were similar in the deaf subject and all control subjects (Figure 1b); in the group data, the SI areas activated by the vibrotactile and electric stimuli did not differ significantly from each other.

Figure 1
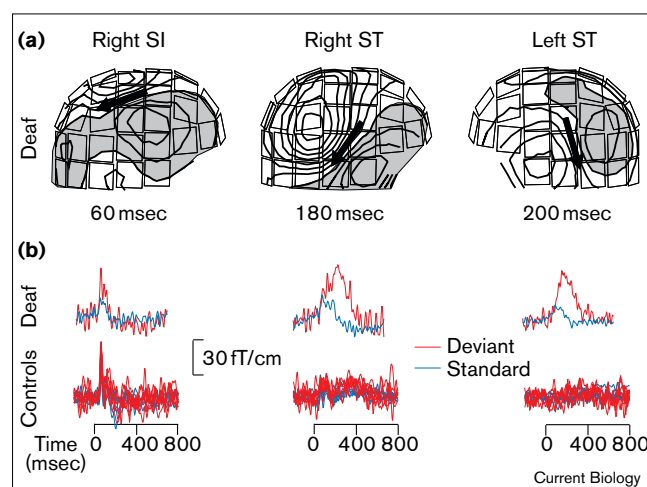
Responses to vibrotactile stimuli. **(a)** Magnetic field patterns for the deaf subject during the maximum responses to deviant vibrotactile stimuli over the right SI cortex and the right and left ST cortices. The helmet-shaped sensor array is viewed from right and left, and the patterns are based on simultaneous recordings with 122 sensors. Each sensor unit (squares in the figure) contains a pair of orthogonal planar gradiometers that measure the two orthogonal tangential derivatives of the magnetic field component normal to the helmet surface at the sensor location. These gradiometers detect the largest signal just above a local dipolar source, where the field gradient has its maximum. The two independent derivatives measured at each site also give the direction of the source current. The arrows show the sites and orientations of the sources. The separation between the isocontours is 40 femtotesla (fT). The shaded areas indicate magnetic flux emerging from the head. **(b)** Magnetic signals (averaged) in response to standard and deviant vibrotactile stimuli, shown for all subjects from channels with maximum responses over the SI cortex and over the right and left ST cortices. The responses of the six control subjects are superimposed. A minimum of 80 responses to the deviant stimuli were averaged, and about 500 responses to the standards.

Figure 2

(a) Left hemisphere — Right hemisphere — SI, SII, ST

● Vibrotactile (deviant)
■ Vibrotactile (standard)
▲ Electric

(b)

(c) Left ST — Right ST

— Vibrotactile (deviant)
— Vibrotactile (standard)
⋯ Control

40 nAm

Time 0   400   800
(msec)

Time 0   400   800
(msec)

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Cortical sites activated in the deaf subject by standard and deviant vibrotactile stimuli, and by electric stimuli (left median nerve stimulation once every 3 sec; intensity exceeding the motor threshold). **(a)** Source areas projected onto the individual brain surface (based on MRI). **(b)** Locations and orientations for the SII and ST sources in the same subject shown on coronal and sagittal slices. **(c)** Time variation of source strengths in nanoamperemeters (nAm) in the right and left ST cortices during standard and deviant vibrotactile stimuli, and when the subject did not hold his hand around the tube (control).

Only in the deaf subject, but not in the controls, was the vibration-induced SI activation followed by a strong bilateral activation of the supratemporal (ST) auditory cortices, strongest at about 200 milliseconds (Figures 1 and 2). The deviant vibrotactile stimuli produced two to three times stronger ST signals than the standards, indicating discrimination of the two vibration frequencies in the auditory cortex in a similar manner as has been shown in healthy subjects for sounds of different frequencies [10,11]. Source modelling confirmed that the activated ST area was clearly separate from the second somatosensory (SII) cortex in the upper lip of the Sylvian fissure, activated by electric stimulation of the median nerve (Figure 2), and that the directions of the ST and SII source currents were nearly opposite.

The results in the deaf subject were replicated in four separate measurement sessions, using slightly modified stimulus-delivery systems. Responses to vibrotactile stimuli agreed with activation of the ST cortex, and the strong responses to the deviant stimuli were significantly ($p < 0.005$) separated from the electrically activated SII

sources in the same hemisphere (mean vertical distance 1 cm). Potential acoustic contamination was ruled out in a control experiment, in which the deaf subject did not hold his hand around the tube while the vibrotactile stimuli were presented; in this condition, the ST cortices were not activated (Figure 2c; dashed traces).

Discussion
Our new findings indicate that the auditory cortex of a congenitally deaf adult may process vibrotactile information. Functional substitution by an anatomically distant area within the same sensory system has been shown to occur in mature as well as in immature brain [12–14], but functional reorganisation across sensory modalities has been demonstrated primarily following sensory deprivation in early stages of development [5,6,15].

In individuals who are congenitally blind, or blind from an early age, Braille reading and tactile and auditory discrimination may activate the occipital cortex [16,17], suggesting that whole functional areas may be remodelled and thus express cross-modal plasticity. More recent transcranial

magnetic-stimulation studies have shown that occipital activation by tactile stimuli in early blind subjects does have functional relevance for the performance, thus reflecting functional compensation subsequent to the loss of one sensory modality [18]. In congenitally deaf humans, the absence of competition from auditory input has marked effects on the efficacy of processing peripheral visual information [19,20].

Cross-modal plasticity could be based on multimodal innervation and competition for synaptic terminals in the developing brain [21]. When input from one sensory modality is deprived early in life, the connections from other modalities may stabilise or become unmasked. Cross-modal plasticity could also be related to reorganisation of thalamocortical connections [22]. For example, cortical sensory areas may obtain functions of other sensory systems if their input is surgically changed during early stages of development [7,8,23].

We suggest that the auditory system is well suited for the processing of vibrotactile information as auditory and vibratory stimuli are essentially similar temporal patterns. In fact, von Békésy [24] in his studies of cochlear mechanics often emphasised the similarity between skin sensations and hearing. The waveforms and the source current orientations of the discrimination responses in our deaf subject closely resembled the late auditory responses elicited by infrequent deviant tones in a monotonous sequence of standard tones (see, for example, [11]). Such responses are assumed to be specific to the auditory system and to reflect automatic detection of stimulus changes. Our results thus seem to indicate that cross-modal plasticity, subsequent to congenital deafness, can change the modality of input to the human auditory cortex.

Materials and methods

Measurements
MEG signals were recorded with a helmet-shaped 122-channel neuro-magnetometer [25]. The recording bandpass was 0.03–100 Hz with a sampling rate of 0.4 kHz. The responses were averaged on-line, time-locked to stimulus onsets. The vertical electro-oculogram was recorded simultaneously, and epochs contaminated by eye movements or blinks were rejected. Location of the head with respect to the sensors was determined by measuring the magnetic fields produced by small currents delivered to three coils attached to the scalp. Location of the coils with respect to the preauricular points and the nasion was measured with a three-dimensional digitizer to allow the alignment of the MEG and MRI coordinate systems.

Source modelling
From visual inspection of the magnetic field distributions, subsets of 16–18 channels were first selected around the signal maxima. Then the three-dimensional locations, directions and strengths of the equivalent current dipoles, best describing the measured field patterns at given response peak latencies, were obtained from least-squares fits to the measured data [9]. Only single sources accounting for > 80% of the field variance in one hemisphere at a given latency were accepted for further analysis. Note that the goodness of fit of the model drastically depends on the number of signals included in the analysis. After

identifying the single sources, the analysis period was extended to the entire measurement epoch and the strengths of the previously found sources were allowed to change as a function of time while their locations and orientations were kept fixed. The validity of this multi-dipole model was evaluated by comparing the measured signals with responses predicted by the model. This approach has been used previously (for examples, see [11,26]) and found to give reliable results (for a review, see [9]).

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