

# Comparing the Effects of Auditory Deprivation and Sign Language within the Auditory and Visual Cortex

Ione Fine<sup>1</sup>, Eva M. Finney<sup>2</sup>, Geoffrey M. Boynton<sup>3</sup>,  
and Karen R. Dobkins<sup>2</sup>

## Abstract

■ To investigate neural plasticity resulting from early auditory deprivation and use of American Sign Language, we measured responses to visual stimuli in deaf signers, hearing signers, and hearing nonsigners using functional magnetic resonance imaging. We examined “compensatory hypertrophy” (changes in the responsivity/size of visual cortical areas) and “cross-modal plasticity” (changes in auditory cortex responses to visual stimuli). We measured the volume of early visual areas (V1, V2, V3, V4, and MT+). We also measured the amplitude of responses within these areas, and within the auditory cortex, to a peripheral visual motion stimulus that was attended or ignored. We found no major differences between deaf and hearing subjects in the size or responsivity of early visual areas. In contrast, within the *auditory cortex*, motion stimuli evoked significant responses in deaf subjects, but not in

hearing subjects, in a region of the right auditory cortex corresponding to Brodmann’s areas 41, 42, and 22. This hemispheric selectivity may be due to a predisposition for the right auditory cortex to process motion; earlier studies report a right hemisphere bias for auditory motion in hearing subjects. Visual responses within the auditory cortex of deaf subjects were stronger for attended than ignored stimuli, suggesting top-down processes. Hearing signers did not show visual responses in the auditory cortex, indicating that cross-modal plasticity can be attributed to auditory deprivation rather than sign language experience. The largest effects of auditory deprivation occurred within the auditory cortex rather than the visual cortex, suggesting that the absence of normal input is necessary for large-scale cortical reorganization to occur. ■

## INTRODUCTION

The study of deaf and blind individuals provides a unique opportunity to examine the perceptual and neural consequences of modality-specific sensory deprivation in humans (see Bavelier & Neville, 2002; Kujala, Alho, & Näätänen, 2000 for reviews). It has been suggested that auditory deprivation in deaf subjects might lead to two different types of neural plasticity: “compensatory hypertrophy,” in which intact sensory modalities show a compensatory increase in size or function, and “cross-modal plasticity,” in which regions of cortex normally devoted to audition respond to other sensory modalities. Although there exists a relatively large animal literature demonstrating neural plasticity within the visual and auditory cortex (Pallas, Razak, & Moore, 2002; Sur, Angelucci, & Sharma, 1999; Rauschecker, 1995; Sur, Pallas, & Roe, 1990; Rebillard,

Carrier, Rebillard, & Pujol, 1977), surprisingly, few studies have investigated neural plasticity in deaf humans.

One of the earliest reports of neural plasticity in deaf subjects came from visually evoked potential (VEP) studies, which demonstrated larger responses in deaf, as compared to hearing, subjects within both temporal and occipital brain areas (Neville & Lawson, 1987; Neville, Schmidt, & Kutas, 1983). The enhanced visual responses observed within the occipital cortex supported the existence of compensatory hypertrophy within deaf subjects. However, the enhanced visual responses observed within the temporal cortex could have been mediated either by cross-modal plasticity (if these visual responses originated in auditory regions of the temporal cortex) or by compensatory hypertrophy (if these visual responses originated in visual areas known to reside in the temporal cortex). The low spatial resolution of VEP could not distinguish between these two possibilities.

More recent evidence for neural plasticity in deaf subjects has come from fMRI studies by Bavelier, Brozinsky, et al. (2001) and Bavelier, Tomann, et al. (2000). These researchers compared the responsivity and size of motion area MT+ between deaf and hearing subjects.

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<sup>1</sup>University of Southern California, Los Angeles, <sup>2</sup>University of California, San Diego, La Jolla, <sup>3</sup>Salk Institute for Biological Studies, La Jolla

They also compared the effects of visual spatial attention between deaf and hearing subjects. Although the overall size and responsiveness of motion area MT+ was not found to differ between deaf and hearing subjects, MT+ appeared to be larger in the left (LH) versus right hemisphere (RH) of deaf subjects, whereas the opposite asymmetry was found in hearing subjects. This result provides a neural correlate for the perceptual finding that deaf subjects exhibit a right visual field (RVF) advantage for motion processing (Bosworth & Dobkins, 2002a; Neville & Lawson, 1987).

Bavelier, Brozinsky, et al. (2001) and Bavelier, Tomann, et al. (2000) also demonstrated enhanced visual motion responses within a polysensory area in the posterior superior temporal sulcus of deaf subjects. Finally, attentional effects in MT+ were found to be larger for peripheral versus central stimuli in deaf subjects, whereas the opposite asymmetry was found in hearing subjects. These results are consistent with results from perceptual and VEP experiments showing enhanced attentional abilities in deaf subjects, particularly in the periphery (Bosworth & Dobkins, 2002a; Rettenbach, Diller, & Sireteanu, 1999; Stivalet, Moreno, Richard, Barraud, & Raphel, 1998; Reynolds, 1993; Loke & Song, 1991; Neville & Lawson, 1987; Parasnis & Samar, 1985).

With regard to cross-modal plasticity, a few studies have demonstrated responses to visual images of sign language within auditory regions in deaf subjects (MacSweeney et al., 2002; Petitto et al., 2000; Nishimura et al., 1999), however, these responses may have been due to the linguistic, rather than the visual, nature of the stimuli. One magnetoencephalography (MEG) study demonstrated tactile responses within the auditory cortex of deaf subjects (Levanen, Jousmaki, & Hari, 1998, and see Levanen, Uutela, Salenius, & Hari, 2001 for a behavioral correlate). Recently, we used functional magnetic resonance imaging (fMRI) to demonstrate responses to purely visual stimuli within deaf subjects' auditory cortices (Finney, Fine, & Dobkins, 2001).

In this article, we compare the size of visual areas, and responses to visual motion within the auditory and visual cortex of deaf and hearing subjects (note that some of the data reported here overlap with earlier reported work; Finney, Fine, et al., 2001). Our first goal was to investigate cross-modal plasticity and compensatory hypertrophy within the same set of subjects. Our second goal was to determine whether deaf and hearing subjects differ in their sensory processing (Bosworth & Dobkins, 1999; Bross, 1979), in their allocation of attention or both. We therefore used a pair of tasks that allowed us to measure responses to both attended and ignored motion stimuli. Our third goal was to determine whether increased visual responsiveness in deaf subjects (in either the auditory or visual cortex) is driven by auditory deprivation or experience with sign language. We therefore included hearing children of deaf adults as a comparison group. These subjects are hearing, but

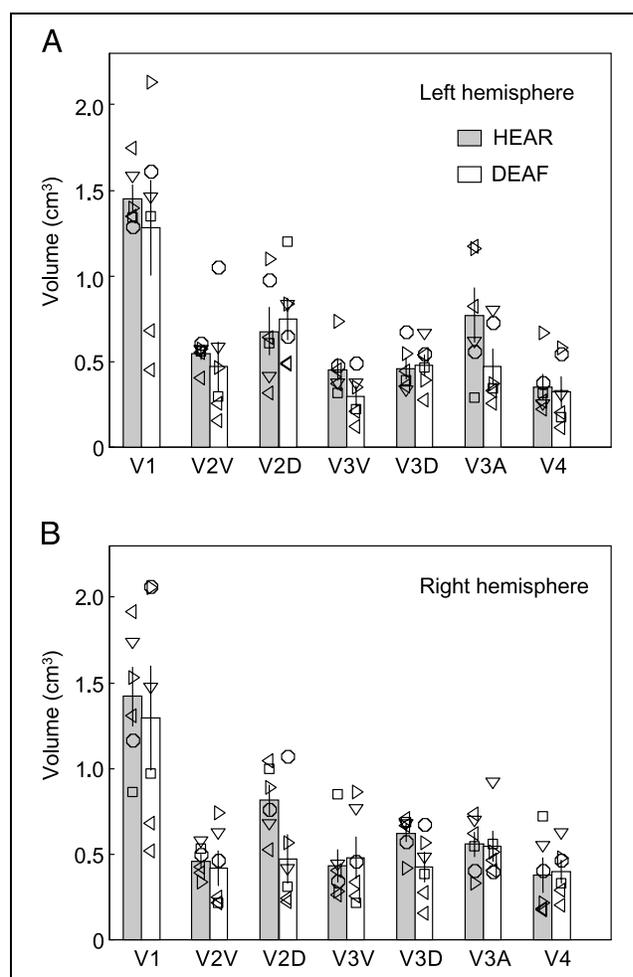
have had similar sign language experience to the deaf subjects in our study.

## RESULTS

### Size and Responsiveness of Visual Areas: Compensatory Hypertrophy

#### Size of Visual Areas

We began by measuring the size of areas V1, V2, V3, V3A, and V4 (which were defined using standard retinotopic mapping and cortical flattening fMRI techniques, see below) separately for the LH and RH. As shown in Figure 1, we found no significant differences in the size of visual areas or between ventral and dorsal areas between deaf and hearing subjects, in either hemisphere (two-factor ANOVA, Subject group  $\times$  Visual area,  $p > .05$ ,



**Figure 1.** Group mean volumes (estimated volume of gray matter, cm<sup>3</sup>) of early retinotopic areas in the LH (A) and RH (B) of hearing subjects (gray bars) and deaf (white bars) subjects. Error bars represent one standard error of the mean. The individual symbols represent visual area sizes for individual hearing and deaf subjects. Ventral (V2V, V3V) and dorsal areas (V2D, V3D) are represented separately.

Bonferroni corrected for multiple comparisons). Nor did we observe any significant difference in the amount of cortex devoted to the fovea and the periphery between deaf and hearing subjects, a finding consistent with previous reports (R. F. Dougherty & B. A. Wandell, personal communication).

However, it is possible that population differences in the size of visual areas exist between deaf and hearing subjects, but that these differences are masked by our low sample size. The size of early visual areas in hearing (and presumably deaf) subjects is known to be highly variable. For example, the size of V1 can vary by as much as a factor of 3 (Dougherty et al., 2003; Duncan & Boynton, 2003). Monte Carlo simulations based on the variability between seven individuals reported by Dougherty et al. (2003) allowed us to estimate that we would have required at least a 17–35% difference (depending on the particular visual area) between deaf and hearing subjects to observe a significant difference in the sizes of areas V1–V3 (either for the overall size of these visual areas across both hemispheres, or for just one of the two hemispheres in isolation). Similarly, to find significant differences in lateralization would have required differences on the order of 12–19% (i.e., a 19% increase in the size of the LH and a corresponding 19% decrease in the size of the RH). Note that these bootstrap estimates are only based on seven subjects, so should be treated with caution.

Volumetric results obtained from area MT+ are shown in Figure 2, separately for the LH and RH. Because the determined size of MT+ depends heavily on the correlation threshold that is chosen, we calculated volume as a function of the correlation threshold. As expected, MT+ volume varied monotonically with correlation threshold. More importantly, as can be seen from the overlapping error bars, there was no significant difference between deaf and hearing in the size of area

MT+ (in either the LH or RH) at any correlation threshold.

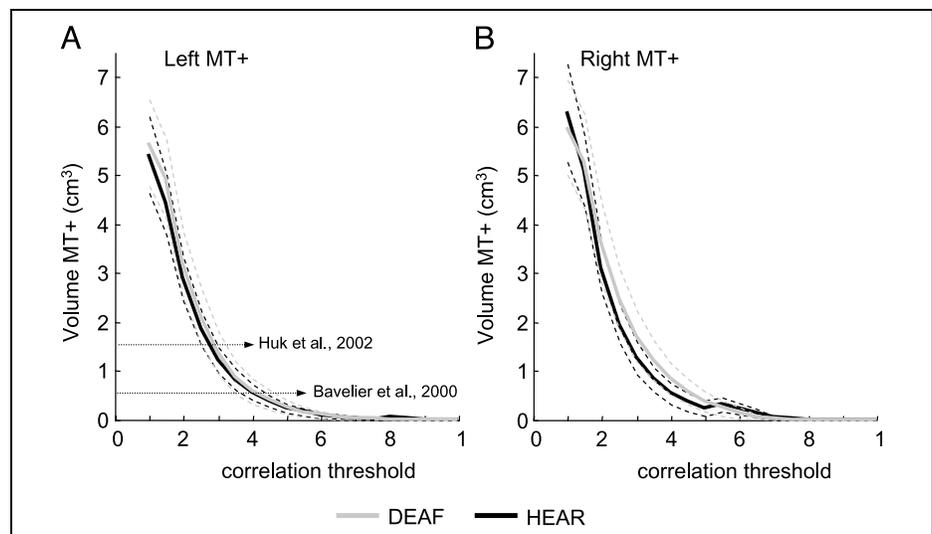
### Visual Responses to Motion Stimuli in Visual Cortex

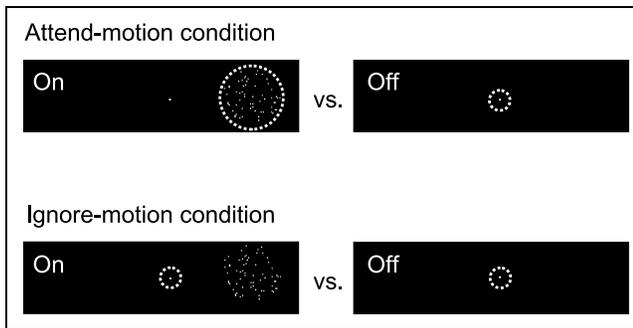
We then measured responses within these visual areas (and the auditory cortex; see below) to a lateralized visual stimulus consisting of a field of moving dots presented within a circular aperture that was eccentric to a fixation spot (see Figure 3). During each run, the motion stimulus was cycled “on” and “off” in 16-sec epochs. On alternate runs, the stimulus was presented in either the RVF or the left visual field (LVF). To study the effects of attention on visual motion responses, two attentional conditions were used (see Figure 3). In the “attend-motion” condition, subjects attended to the peripheral motion stimulus during the “on” phase and to the fixation spot during the “off” phase. In the “ignore-motion” condition, subjects attended to the fixation spot, regardless of whether or not the moving dots were present.

Response amplitudes elicited by the lateralized motion stimulus within the different visual areas (V1, V2, V3, V4, and MT+) are presented in Figure 4, separately for the LH and RH. Shown are contralateral responses (i.e., LH responses elicited by RVF stimuli, and RH responses elicited by LVF stimuli) for the “attend-motion” condition. Data for ipsilateral responses and the ignore-motion condition are described below and in Table 1.

We found no significant difference in activation between deaf and hearing subjects for any visual area, within either hemisphere. This was true in both the “attend-motion” and the “ignore-motion” condition (three-factor ANOVA, Subject group × Visual area × Attention condition,  $p > .05$ , Bonferroni corrected for multiple comparisons). The lack of any difference in responsivity between deaf and hearing subjects shown here is further corroborated by the data obtained using

**Figure 2.** Group mean volumes ( $\text{cm}^3$ ) of MT+ as a function of the correlation threshold in the LH (A) and RH (B) of hearing subjects (black lines) and deaf subjects (gray lines). Dotted lines represent one standard error of the mean. Horizontal dashed lines show the reported size of area MT+ from two previous fMRI studies (see Discussion for details).



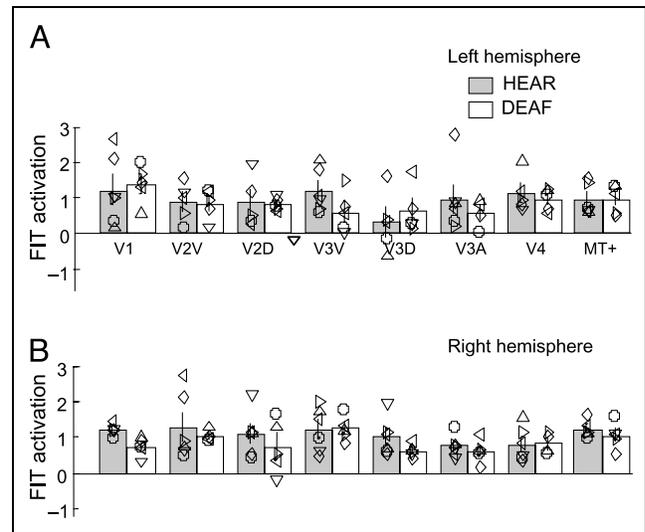


**Figure 3.** The stimulus and tasks used to measure visual responses to moving dots within visual and auditory cortex. In both the attend-motion and the ignore-motion conditions, the block design alternated between the presence (on) and absence (off) of a moving dot stimulus (10° diameter), centered 15° eccentric to fixation. A central fixation spot remained present throughout the scanning session. The stimulus was in the RVF (shown here) or LVF throughout the entire scan. Attention was controlled by having the subjects detect irregular dimming events of either the fixation spot or the moving dot field (represented as a dashed line). In the attend-motion condition, subjects' attention was directed towards the fixation spot during the off period, and to the moving dot field when it was present during the on period. In the ignore-motion condition, subjects' attention was directed towards the central fixation spot throughout the entire scan.

retinotopic stimuli (used to define all visual areas except MT+). When we compared the amplitude of responses to retinotopic stimuli, we again found no differences in activation between deaf and hearing subjects for any visual area.

#### Visual Motion Responses in Visual Cortex: Contralateral versus Ipsilateral

Like previous fMRI studies (Tootell, Mendola, Hadjikhani, Liu, & Dale, 1998; Engel, Rumelhart, et al., 1994;



**Figure 4.** Group mean activity (FIT values) of different visual areas elicited by the lateralized motion stimulus (Figure 3) within the LH (A) and RH (B) of hearing subjects (gray bars) and deaf subjects (white bars). Data are shown for the attend-motion condition and only for contralateral responses. The individual symbols represent visual responses for individual hearing and deaf subjects. Where hearing and deaf subjects differ, these differences seem to be driven by outlier subjects, and may be due to noise. Error bars represent one standard error of the mean. Ventral (V2V, V3V) and dorsal areas (V2D, V3D) are represented separately.

Sereno, McDonald, & Allman, 1994), we found that contralateral responses produced by the lateralized motion stimulus within the visual cortex were significantly larger than ipsilateral responses (i.e., LVF stimuli activated RH more than LH, and RVF activated LH more than RH). Across all visual areas, contralateral responses were larger than ipsilateral responses, in both hearing and deaf subjects. For example, in the “attend-motion” condition, mean functional intensity value (FIT) contra-

**Table 1.** Group Mean Responses to Lateralized Visual Motion Stimuli in Areas V1, MT+, and the Auditory ROI

		Hemispheric Asymmetries					
		Lateralization Effects (Attend-motion Condition)		Contralateral Stimuli, (Attend-motion Condition)		Attention (Contralateral Stimuli)	
		Contralateral	Ipsilateral	LH	RH	Attend-motion	Ignore-motion
V1	hear	1.01 ± 0.19	0.18 ± 0.05	0.88 ± 0.34	1.17 ± 0.07	1.01 ± 0.19	0.82 ± 0.12
	deaf	1.05 ± 0.16	0.04 ± 0.07	1.34 ± 0.24	0.76 ± 0.11	1.05 ± 0.16	1.02 ± 0.11
MT+	hear	0.94 ± 0.11	0.31 ± 0.07	0.77 ± 0.16	1.16 ± 0.07	0.94 ± 0.11	0.79 ± 0.12
	deaf	0.99 ± 0.12	0.41 ± 0.15	0.92 ± 0.17	1.07 ± 0.17	0.99 ± 0.12	0.77 ± 0.10
Auditory	hear	-0.55 ± 0.65	-0.07 ± 0.57	n/a	n/a	-0.31 ± 0.42	0.33 ± 0.40
	deaf	2.6 ± 0.42	1.93 ± 0.81	n/a	n/a	2.26 ± 0.45	0.91 ± 0.66

Presented are ipsilateral versus contralateral, LH versus RH, and attend-motion versus ignore-motion responses for deaf and hearing subjects. Standard errors of the means are included. *Lateralization effects* = responses (averaged across both hemispheres) for contralateral and ipsilateral stimuli. *Hemispheric asymmetries* = responses (to contralateral stimuli) for left and right hemispheres. *Attention* = responses (averaged across both hemispheres) for *attend-motion* and *ignore-motion* conditions.

lateral and ipsilateral responses within area MT+ of hearing subjects were 0.94 and 0.31, respectively. Similarly, in deaf subjects, contralateral and ipsilateral responses were 0.99 and 0.41, respectively. Deaf subjects tended to show slightly more ipsilateral activity than hearing subjects, however, the difference was not significant (two-factor ANOVA, Subject group  $\times$  Visual area,  $p > .05$ , Bonferroni corrected for multiple comparisons). See Table 1 for contralateral and ipsilateral responses within area V1 and MT+.

*Visual Motion Responses in Visual Cortex: Hemispheric Asymmetries*

Although we did not find differences between deaf and hearing subjects in either the size or responsivity of visual areas within either the LH or RH, it was nonetheless possible that the two groups might exhibit different hemispheric asymmetries. Past psychophysical (Bosworth & Dobkins, 1999, 2002b; Neville & Lawson, 1987) and fMRI (Bavelier, Brozinsky, et al., 2001) studies have suggested that motion processing may be LH dominant in deaf people. Bavelier and colleagues previously reported that deaf subjects exhibit greater activity in left MT+ than in right MT+, whereas hearing subjects exhibit the opposite pattern of activity. The direction of our results in MT+ followed this same pattern, although differences in lateralization did not reach significance in any area (two-factor ANOVA, Subject group  $\times$  Visual area,  $p > .05$ , Bonferroni corrected for multiple comparisons). Specifically, within area MT+ of deaf subjects, mean responses in the LH and RH were 0.92 and 1.07, respectively, indicating a 16% RH advantage, whereas in hearing subjects, mean responses in the LH and RH were 0.77 and 1.16, respectively, resulting in a larger 51% RH advantage. In terms of size of visual areas (V1–V4 and MT+), no differences in hemispheric asymmetries between deaf and hearing subjects were observed.

*Visual Motion Responses in Visual Cortex: Attentional Effects*

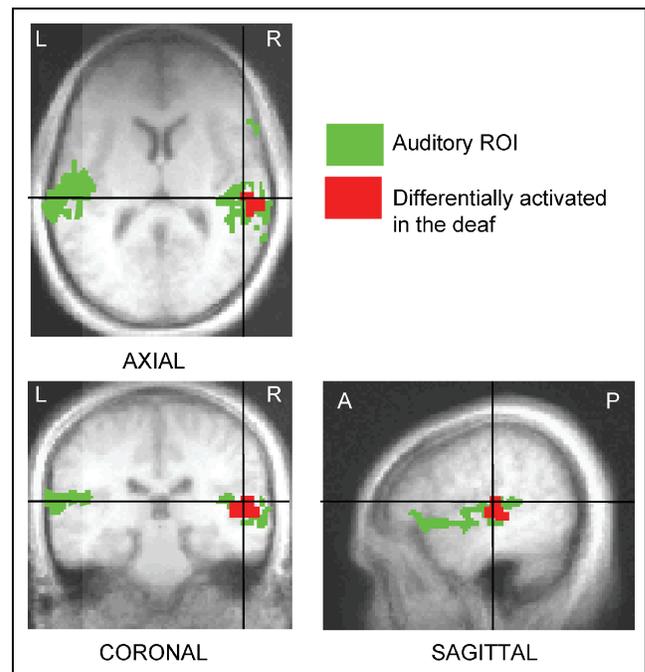
In past psychophysical (Bosworth & Dobkins, 2002b) and fMRI (Bavelier, Brozinsky, et al., 2001; Bavelier, Tomann, et al., 2000) studies, it has been suggested that visual attention to moving stimuli in the periphery is enhanced in deaf subjects. Consistent with previous fMRI studies in hearing subjects (Gandhi, Heeger, & Boynton, 1999; Rees, Frith, & Lavie, 1997) and single-unit studies in macaques (Cook & Maunsell, 2002; Seidemann & Newsome, 1999; Treue & Maunsell, 1999) investigating the effects of spatial attention on responses to visual motion, significant attentional effects were observed in both our deaf and hearing subjects. Responses were larger in the “attend-motion” than in the “ignore-motion” condition, within every visual area tested. Similar to Bavelier and colleagues, we did ob-

serve a trend for deaf subjects to show greater attentional modulation in motion area MT+, but this effect was not significant (three-factor ANOVA, Subject group  $\times$  Visual area  $\times$  Attention condition,  $p > .05$ , Bonferroni corrected for multiple comparisons; see Table 1).

**Responses to Visual Motion Stimuli in the Auditory Cortex: Cross-Modal Plasticity**

We defined auditory regions of interest (ROIs) in hearing subjects based on regions that responded in phase with on–off auditory stimuli across all hearing subjects. Clustering and significance criteria were deliberately generous so that auditory ROIs included primary, secondary, and association auditory areas. We then projected these auditory ROIs onto an average structural image resulting from combining reference anatomies across both deaf and hearing subjects, and measured responses within these auditory ROIs to the lateralized motion stimulus of Figure 3.

For the “attend-motion” condition, the results of our analyses of visual motion responses within the auditory cortex are presented in Figure 5. Shown are three slices



**Figure 5.** Anatomical scans (axial, coronal, and sagittal) averaged across all deaf and hearing subjects and transformed into standard Talairach and Tournoux coordinates. L = left; R = right; A = anterior; P = posterior. Shown are auditory ROIs (green) and the area within the ROIs showing greater activity in deaf as compared to hearing subjects (red) in response to “attend-motion” visual stimuli. Crosshairs indicate the locations of the orthogonal planes of section shown, and highlight a voxel within the area of main effect that maps to Brodmann’s area 41 (primary auditory cortex, T&T coordinates:  $x = 52, y = -25, z = 12$ ). Color bar at the right indicates the functional intensity (FIT) value, or magnitude of activation. Adapted from Finney, Fine, et al. (2001).

of a subject-averaged MRI brain image, with auditory ROIs shaded in green. The results of a two-factor ANOVA (Subject group  $\times$  Visual field,  $p < .05$ , Bonferroni corrected for multiple comparisons) yielded a main effect of subject group. Specifically, within a  $0.95\text{-cm}^3$  region of the right auditory ROI, visually evoked activity was significantly greater in deaf, as compared to hearing, subjects (Figure 5, *red*, combined voxel threshold and cluster volume criterion protects ROI-wise  $p < 0.05$ ). There was no main effect of visual field or interaction between visual field and subject group within this region. Although differences between deaf and hearing subjects were also observed in the left auditory ROI, the region of effect was extremely small ( $0.054\text{ cm}^3$ ) and did not survive stringent statistical standards for safeguarding against false positives (see Methods). Based on Talairach and Tournoux (T&T) (1988) coordinates, the region of main effect in the RH included Brodmann's areas 42 and 22 (secondary and association auditory areas, respectively), which encompasses the planum temporale. In addition, several voxels ( $0.22\text{ cm}^3$ ,  $\sim 23\%$  of the total region of effect) fell within area 41 (primary auditory cortex), which encompasses the medial portion of Heschl's gyrus. A cross-check of these coordinates against probabilistic atlases confirmed that our region of effect included both the primary auditory cortex (Rademacher et al., 2001; Penhune, Zatorre, MacDonald, & Evans, 1996) and the planum temporale (Westbury, Zatorre, & Evans, 1999). However, due to the large amount of intersubject variability in the primary auditory cortex (Penhune et al., 1996) and our small sample size, however, we cannot say with absolute certainty that the primary auditory cortex is activated (see Table 2 for coordinates and locations for all voxels within this region of effect).

For the ignore-motion condition, the results of our analyses also revealed a region of the right auditory ROI where visually evoked activity was significantly greater in deaf, as compared to hearing, subjects ( $p < .05$ ). This region was smaller than ( $0.54\text{ cm}^3$ ) and a subregion of that observed in the attend-motion condition, and mapped onto area 42, secondary auditory areas.

We then measured the mean FIT within the region of main effect defined using the attend-motion condition. To determine whether differences between deaf signers and hearing nonsigners were a result of the deaf subjects' auditory deprivation or their American Sign Language (ASL) experience, we included data from hearing signers (children of deaf adults [CODAs]). The results for the "attend-motion" condition are presented in Figure 6 (white bars). As would be expected, hearing subjects did not exhibit significant visual responses within this region of the auditory cortex as a whole ( $-0.31 \pm 0.42$ ,  $p = .76$ ), suggesting that the majority of our region of main effect fell within unimodal areas. In contrast to hearing subjects, deaf subjects exhibited significant visual activity in the attend-motion condition

**Table 2.** Coordinates and Locations for All Voxels within the Auditory Region of Effect

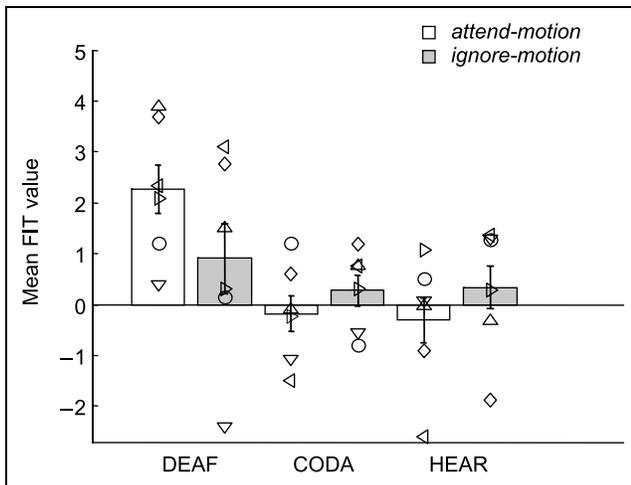
<i>x</i>	<i>y</i>	<i>z</i>	<i>BA</i>	<i>Location</i>
Auditory cluster				
62	-28	18→21	40	Postcentral Gyrus
56	-31	16→18	42	Superior Temporal Gyrus
62	-28→-31	13→15	42	Superior Temporal Gyrus
56	-31	13→15 <sup>a</sup>	42	Superior Temporal Gyrus
59	-31	13→15 <sup>a</sup>	42	Superior Temporal Gyrus
56	-35	13→15 <sup>a</sup>	42	Superior Temporal Gyrus
57→59	-28	12		Superior Temporal Gyrus/WM
56	-25	12	41	Superior Temporal Gyrus
51→53	-25	10→12	41	Transverse Temporal Gyrus/Heschl's Gyrus
56→59	-25→-28	7→9		Superior Temporal Gyrus/WM
52	-25	8	41	Superior Temporal Gyrus
56	-21	8	41	Superior Temporal Gyrus
46	-22	8		Superior Temporal Gyrus/WM
63	-29	8	42	Superior Temporal Gyrus
59	-31	8	42	Superior Temporal Gyrus
56	-28	4	22	Superior Temporal Gyrus
53→59	-25→-26	4		Superior Temporal Gyrus/WM
56	-31	4	22	Middle Temporal Gyrus
46→53	-22→-29	4		Superior Temporal Gyrus/WM
49	-28	1	22	Superior Temporal Gyrus
56→59	-28→-31	1	21	Middle Temporal Gyrus (17 voxels)
49	-31	1	21	

WM = white matter.

<sup>a</sup>Voxels also differing between deaf and hearing groups for the ignore condition.

within this region ( $2.26 \pm 0.45$ ,  $p = .00019$ ). The amount of activity is approximately a third of that produced in this same region for music in hearing subjects. Like hearing subjects, CODA subjects did not exhibit significant activity within this region ( $-0.18 \pm 0.33$ ,  $p = .71$ ).

One possible confound in these results is that we necessarily measured the effects of visual activation in the auditory cortex over and above baseline activation produced by the auditory noise of the scanner. This



**Figure 6.** Group mean activity (FIT values) within the area of main effect in the auditory cortex (Figure 5, red) for deaf, CODA, and hearing subjects. The individual symbols represent visual responses for individual hearing and deaf subjects. Visual stimuli produced significant activation in deaf subjects only. White bars represent activity for “attend-motion,” gray bars represent activity for the “ignore-motion” condition. Error bars represent one standard error of the mean.

baseline activation would (for obvious reasons) be expected to be lower in deaf subjects. With this in mind, the relatively smaller visual responses measured in the auditory cortex of hearing subjects could potentially be attributable to baseline activity saturating their responses. We do not believe this can explain our results for several reasons. First, although responses in early sensory areas show compressive nonlinearities with intensity (Boynton, Demb, Glover, & Heeger, 1999), they do not fully saturate, thus allowing for an increment in response even for high baseline stimulus intensities. If the auditory cortex acts in a similar fashion, we should have still been able to observe visual responses in the auditory cortex of hearing subjects (had they existed). Second, we found hearing subjects’ responses to auditory stimuli (both music and white noise) to be quite robust, suggesting that any saturation of auditory cortex responsiveness due to scanner noise was relatively limited.

#### *Visual Motion Responses in the Auditory Cortex: Ipsilateral versus Contralateral Responses*

Although the results of a two-factor ANOVA (Subject group  $\times$  Visual field,  $p < .05$ , Bonferroni corrected for multiple comparisons) revealed no effects of visual field (see above), it was nonetheless possible that, when analyzing deaf data *alone*, effects of visual field might be revealed. We found some evidence for lateralization, but lateralization was weaker than for visual cortex: contralateral responses in auditory cortex (2.6) were 1.35-fold larger than ipsilateral (1.93) responses, and the difference between the two was not significant

(see Table 1). Note that this is the same analysis as was carried out for the visual cortex, but was restricted to the RH as there was no significant difference in responsiveness between deaf and hearing subjects in the LH.

#### *Visual Motion Responses in the Auditory Cortex: Hemispheric Asymmetries*

Because significant differences between deaf and hearing subjects were only observed within the right auditory cortex, we were unable to compare responses between the two hemispheres. However, this result clearly indicates that there is a RH asymmetry for visual motion processing within the auditory cortex of deaf subjects.

#### *Visual Motion Responses in the Auditory Cortex: Attentional Effects*

As described above, in both the “attend-motion” and “ignore-motion” conditions, there was a region in the right auditory cortex that yielded visual responses in deaf, but not hearing, subjects. However, the size of this region was nearly double in the “attend-motion” condition, indicating that visual motion responses in the auditory cortex of deaf subjects are more extensive when stimuli are attended.

A second way of investigating the effects of attention on responses to visual motion within the auditory cortex is to compare the amount of activation produced by the “attend-motion” versus “ignore-motion” condition within a designated region of the auditory cortex. We did this by restricting our analysis to the region that yielded significant group differences in the “attend-motion” condition (Figure 5, red). Mean FIT activations obtained for both the attend-motion (white bars, Finney, Fine, et al., 2001) and the “ignore-motion” (gray bars) condition are presented in Figure 6. Within this ROI, deaf subjects’ responses to ignored stimuli (FIT = 0.91) were substantially smaller than those elicited by attended stimuli (FIT = 2.26), and this 2.4-fold difference was marginally significant ( $p = .051$ ). Interestingly, this attention effect in the auditory cortex of deaf subjects is similar in magnitude to the effect of attention in the visual areas of these same subjects.

For the “ignore-motion” condition, we found no significant difference in responsiveness between deaf and hearing subjects ( $p > .05$ ), nor was the response in deaf subjects significantly above zero in the ROI defined by the attend-motion condition ( $p > .05$ ). This lack of significant activity in the ignore condition is not surprising as this analysis included voxels that were not part of the region of main effect determined for the ignore condition (see above).

Within the region that yielded significantly greater activity in deaf than in hearing subjects in the “ignore-motion” condition, both deaf (FIT = 3.71,  $p < .05$ ) and

hearing ( $FIT = 1.57, p < .05$ ) subjects showed significant responses to the ignore-motion stimulus. As noted above, this small subregion mapped onto secondary auditory areas (area 42). This is consistent with recent data suggesting that in hearing subjects area 42 will respond to at least certain kinds of visual input, such as a silent lip-reading task (Calvert et al., 1997).

These measures comparing activation in the “attend-motion” versus “ignore-motion” condition are qualitatively consistent with differences in the size of the regions of main effect observed between the two conditions. Both analyses indicate that visual responses within the auditory cortex are driven by both sensory and attentional processes.

## DISCUSSION

In sum, we did not find significantly larger or more responsive visual areas in deaf, as compared to hearing, subjects. Nor did we see any significant differences in attentional modulation between deaf and hearing in the visual cortex. These data suggest that compensatory hypertrophy within the visual cortex as a consequence of auditory deprivation may be fairly limited. It is of course possible that the particular stimuli we employed (bilateral retinotopic stimuli without a task, and lateralized motion stimuli covering a relatively small field of view) were not ideal for revealing differences between deaf and hearing subjects, or that differences were masked by large individual variability within groups. It is also quite likely that differences between deaf and hearing subjects exist at higher levels of processing, such as the posterior parietal cortex (McCullough, Emmorey, & Sereno, 2005; Bavelier, Brozinsky, et al., 2001) which we did not examine. We did find visual responses in the auditory cortex of deaf, but not hearing, subjects, which appear to be due to auditory deprivation rather than experience with sign language, as hearing signers (CODAs) did not show the same effect. This cross-modal plasticity is restricted to the RH, with a weak preference for the contralateral (i.e., *left*) visual field. The fact that visual responses in the auditory cortex of deaf subjects were present for ignored stimuli suggests a low-level sensory component. However, because the effects were stronger with attention, this suggests that top-down processes play an important role in cross-modal plasticity. Although we found no significant differences in the visual cortex between deaf and hearing subjects, we did observe a small nonsignificant trend towards larger attentional effects in the visual cortex of deaf subjects than hearing subjects, as reported by Bavelier, Brozinsky, et al. (2001) and Bavelier, Tomann, et al. (2000). Bavelier et al. also reported an asymmetry in the extent of activity in area MT+ for deaf and hearing subjects. For deaf subjects, the region of activity in area MT+ (for a full-field moving dot stimulus) in the LH was larger than that in the RH, whereas hearing subjects

showed the opposite asymmetry. These fMRI results are consistent with psychophysical results showing an RVF (i.e., LH) advantage for motion processing in both deaf and hearing signers (Bosworth & Dobkins, 1999; Neville & Lawson, 1987). This asymmetry is thought to be due to sign language, as both psychophysical (Bosworth & Dobkins, 2002a) and fMRI (Bavelier, Brozinsky, et al., 2001) results have demonstrated the same LH advantage for motion processing in hearing signers (CODAs). It is supposed that motion processing, which is an integral part of sign language comprehension, may be recruited to the left (language) hemisphere of the brain. In the current study, the results from our *size* measures of MT+ revealed no significant differences in lateralization between deaf and hearing subjects. In terms of *responsivity*, our results were in the same direction as Bavelier et al., although this effect was not significant. There are several possible reasons why the current study may not have observed significant differences between deaf and hearing subjects in MT+. First, our study contained fewer subjects than that of Bavelier et al., although the amount of relevant scanning time was comparable across the two studies. The effects reported by Bavelier et al. were fairly small compared to the variability in the data across subjects, suggesting that effects of compensatory hypertrophy may not be particularly large compared to variability between subjects. Second, there were differences between the tasks used in the two studies. In our motion task, the moving dots appeared on one side of the visual field within a block and the dot field was relatively restricted in size ( $10^\circ$  diameter), so attention never had to be allocated within a subset of the motion stimulus. In contrast, Bavelier et al. used a full-field motion stimulus and subjects were asked to perform a task in either the center or periphery of the stimulus. Their task may therefore have revealed differences in how deaf and hearing subjects allocate attention differentially between RVFs and LVFs, and between the fovea and the periphery. A third difference between the two studies is that we analyzed our MT+ volumes using a range of correlation thresholds (between .1 and .4), whereas Bavelier and colleagues used a very stringent method for defining MT+. Their technique resulted in MT+ volumes of  $0.4\text{--}0.6\text{ cm}^3$ , substantially smaller than those recently reported using retinotopic techniques for defining MT+. For example, Huk, Dougherty, and Heeger (2002) report an average size of  $1.5\text{ cm}^3$  for MT+ (see Figure 2). Thus, it may be that differences between deaf and hearing subjects are restricted to a subregion within MT+.

In contrast with our lack of evidence for compensatory hypertrophy within the visual cortex, we found clear cross-modal effects within the auditory cortex of deaf subjects. This effect appears to be due to deafness rather than experience with ASL because hearing signers showed no response to visual stimuli within the region of main effect in the auditory cortex. Unimodal areas

were clearly included within the region that saw cross-modal responses to the attend-motion condition, as we saw no evidence of activation to purely visual stimuli within the full attend-motion ROI in either hearing or CODA subjects. Still, it is interesting that some of the areas where we found visual activation in deaf subjects may play a role in visual language processing in hearing as well as deaf subjects. Brodmann's areas 42 and 22 are activated in deaf subjects in response to visual images of sign language (MacSweeney et al., 2002; Petitto et al., 2000; Nishimura et al., 1999). These responses to sign language have been shown to be larger in deaf signers as compared to hearing signers (i.e., CODAs) (MacSweeney et al., 2002), which is consistent with auditory deprivation playing an important role in mediating visual responses in the auditory cortex of deaf subjects. In addition, in hearing subjects, these same areas are activated during a silent lip-reading task (Calvert et al., 1997), suggesting that these areas might be predisposed to process visual aspects of language, even in hearing subjects.

In the present study, the use of purely visual (nonlinguistic) stimuli demonstrates that these areas of the auditory cortex are also recruited for basic visual processing in deaf subjects. This recruitment for visual function may explain why despite significant changes in white matter, deaf subjects do not show a reduction in gray matter volume within the primary auditory cortex (Emmorey, Allen, Bruss, Schenker, & Damasio, 2003). Interestingly, Bavelier, Brozinsky, et al. (2001) also reported significant activation to visual motion stimuli in the right (as well as the left) posterior superior temporal sulcus of deaf subjects, with the maximum activation in a location only slightly anterior ( $x = 56, y = 40, z = 8$ ) to our main effect. Although we found evidence for recruitment of the primary auditory cortex (A1), our result should be interpreted with some caution given our small sample size and the large amount of intersubject variability known to exist in this area (Penhune et al., 1996). Nonetheless, the fact that we found significant differences between deaf and hearing subjects in the auditory cortex, but not in the visual cortex, suggests that the cross-modal effects of deafness are more powerful than the effects of compensatory hypertrophy.

One possible explanation for why we found only small differences in visual processing within the visual cortex between deaf and hearing subjects is that the visual cortex is already performing a demanding host of visual functions. In fact, one could argue that a reorganization of the visual cortex in response to auditory deprivation could potentially undermine the ability of the visual cortex to perform more basic (low-level) visual functions. If such constraints in fact exist, we might expect minimal reorganization within early visual areas (performing basic visual functions, like motion and form processing), as we found in the current study. By contrast, there might be more substantial reorganization

in higher-level visual areas, for example, within the ventral occipital cortex, which is known to be strongly dependent on an individual's visual experience (Gauthier, Behrmann, & Tarr, 1999; Kobatake, Wang, & Tanaka, 1998). In fact, a recent fMRI study has demonstrated that higher-level areas of the brain involved in recognizing the emotional and linguistic content of faces (in the superior temporal sulcus and the fusiform gyrus) are reorganized in deaf signers as compared to hearing nonsigners (McCullough et al., 2005).

Interestingly, the visual motion responses we observed in deaf subjects' auditory cortex appeared predominantly in the RH. Corroborating this result, we recently employed MEG to obtain responses to visual motion stimuli in deaf and hearing subjects, and found greater activation of deaf subjects' right, as compared to left, auditory cortex (Finney, Clementz, Hickok, & Dobkins, 2003). Because both the MEG and the current fMRI study employed moving stimuli, this hemispheric asymmetry may simply reflect a predisposition for motion processing in the right auditory cortex. This possibility is suggested by the finding that in hearing subjects, the right auditory cortex (specifically the planum temporale) is specialized for processing auditory motion (Ducommun, Michel, et al., 2004; Ducommun, Murray, et al., 2002; Baumgart, Gaschler-Markefski, Woldorff, Heinze, & Scheich, 1999). Thus, the right auditory cortex in deaf subjects, devoid of its normal auditory input, may come to serve visual motion processing. Remarkably, the reciprocal result has recently been reported in blind subjects. Here, responses to moving auditory stimuli are observed predominantly in the right visual cortex of the blind (Weeks et al., 2000), again suggesting a predisposition towards motion processing in the RH.

Results from animal studies suggest that the cross-modal responses observed within the auditory cortex of deaf subjects may be established very early in development. Specifically, labeling studies in cats have demonstrated exuberant projections during infancy from the visual thalamus (i.e., the lateral geniculate nucleus) to the primary auditory cortex (Catalano & Shatz, 1998; Ghosh & Shatz, 1992). Normally, these visual projections to the auditory cortex get pruned away over the course of development. In the case of auditory deprivation, however, the lack of functional auditory input to the auditory cortex may result in the stabilization of visual input to this area (Sur et al., 1999). Recently, Pallas et al. (2002) have demonstrated direct projections from the visual thalamus to the primary auditory cortex in early-deafened ferrets, leaving open the possibility of such projections in deaf individuals.

Another possible source of visual responses in the auditory cortex is input from visual cortical areas such as V1 or V2. Projections from visual area V2 to the auditory cortex have recently been reported in adult monkeys (Schroeder, 2004) and it is possible that these projections might be more pervasive in infant

monkeys. Analogously, projections from A1 to V1 have been demonstrated in both kittens (Dehay, Kennedy, & Bullier, 1988; Innocenti, Berbel, & Clarke, 1988; Clarke & Innocenti, 1986) and adult monkeys (Falchier, Clavagnier, Barone, & Kennedy, 2002).

The cross-modal responses that we observed in deaf subjects were strongly modulated by attention, suggesting the influence of top-down processes. Many previous fMRI studies in hearing subjects have shown that directing attention to a visual stimulus increases responses within the primary and secondary visual cortex (Gandhi et al., 1999; Martinez et al., 1999; Somers, Dale, Seiffert, & Tootell, 1999; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997). Analogously, directing attention to an auditory stimulus increases responses in the auditory cortex (Jancke, Mirzazade, & Shah, 1999; Grady et al., 1997; Pugh et al., 1996). The attentional modulation that we found in early visual areas was similar in magnitude to that found in these previous studies. Interestingly, the attentional modulation of visual responses within the auditory cortex of deaf subjects was as strong as that observed in area MT+ and stronger than that observed in area V1 (see Table 1). These attentional effects in the auditory cortex are therefore likely to be due to input from visual areas that are themselves modulated by attention. This input could arise either from the visual cortex or visual thalamus, given recent evidence for attentional effects as early as the visual thalamus (O'Connor, Fukui, Pinsk, & Kastner, 2002). However, it is also plausible that at least some of the attentional modulation of visual responses may be generated within the auditory cortex itself (Grady et al., 1997; Woldorff et al., 1993).

Although these differences between deaf and hearing subjects within the auditory cortex are clearly dependent on attention, it is not simply the case that responses in deaf subjects are being more strongly modulated by attention, regardless of the sensory domain. We did not see significant differences in attentional modulation between deaf and hearing subjects in the visual cortex, and we see no response to visual stimuli within the auditory cortex in our hearing subjects.

In conclusion, in our study we found that auditory deprivation has larger effects on the auditory cortex, than on the visual cortex, and seemed to be driven by auditory deprivation rather than sign language. This suggests that plasticity as a result of abnormal sensory experience may be more limited within modalities in which the normal sensory input has not been removed. This is consistent with our finding that the cross-modal plasticity observed within the auditory cortex of deaf subjects seems to be driven by auditory deprivation rather than experience with ASL. Finally, although some visual activation of the auditory cortex occurs in the absence of attention, suggestive of a low-level sensory component, these cross-modal effects were much stron-

ger with attention, suggesting that these effects are driven substantially by top-down processes.

## METHODS

### Participants

Eighteen subjects participated in the experiment. Six were deaf signers of ASL, all of whom had an 80 dB loss or greater in both ears. Of these, four were congenitally deaf, one was deaf since birth due to medications, and one became deaf at age 2 from unknown causes. All deaf subjects used ASL as their primary language and were exposed to ASL between birth and 3 years, either because they had one or two deaf signing parents or because they attended a school where sign language was used. Six subjects were hearing signers (CODAs), who had normal hearing but who have experience and fluency with ASL similar to that of deaf signers. Six subjects had normal hearing, spoke only English, and had no exposure to ASL beyond fingerspelling.

All subjects had normal or corrected-to-normal vision, were right-handed, and reported no neurological abnormalities. Deaf and hearing signers were recruited from the San Diego deaf community. Hearing nonsigners were recruited from the student population at University of California, San Diego. All subjects gave informed consent before participation, and all protocols were conducted in compliance with the University of California at San Diego's Institutional Review Board. The mean ages of the three subject groups were: deaf,  $27.0 \pm 5.7$  years; CODAs,  $23.5 \pm 6.3$  years; and hearing,  $26.8 \pm 2.6$  years. There was no significant difference in age across groups [ $F(2,38) = 0.68, p = .51$ ], and each group contained three men and three women.

### Data Acquisition

fMRI images were acquired using a low-bandwidth echo-planar imaging sequence on a 1.5-T Siemens Vision MR scanner equipped with a standard clinical whole head coil and a surface coil. Subjects' heads were kept still during scanning using both foam padding and a bite bar, to minimize motion artifacts. Only a few scans showed significant motion artifacts and were excluded from later analysis. During each session, high-resolution anatomical images were also acquired at  $1 \times 1 \times 1$  mm using a standard T1-weighted, gradient-echo pulse sequence. These anatomical images were used to align all functional data across multiple scanning sessions to a subject's reference volume, allowing identification of predefined ROIs within each session. The reference volume was a high-resolution ( $1 \times 1 \times 1$  mm) anatomical volume of the brain obtained using a standard head coil and an MPRAGE pulse sequence, and was usually obtained in a separate 18-min scan at the end of the retinotopic mapping session.

Three separate scanning sessions were carried out, each on a different day. Hearing subjects participated in *Sessions 1–3*. Deaf subjects participated in *Sessions 2–3*. CODAs participated in *Session 3* (see Table 3 for details on scanning protocols in each session).

Visual stimuli were viewed on a back-projection screen (viewed through a mirror, resulting in an effective viewing distance of 18 cm) and subjects were instructed to maintain fixation on a small central square throughout every scan. Auditory stimuli were delivered through a sound-insulated pneumatic headset. Note that background scanner noise was present throughout every scan.

### *Session 1. Auditory Stimuli*

Auditory stimuli were employed for the purpose of obtaining ROIs within the auditory cortex. The auditory stimulus consisted of classical music which was cycled “on” and “off” in 20-sec epochs (40-sec period for 4.5 cycles). Subjects were instructed to attend to the music, but there was no associated task. In five of our hearing subjects, we also obtained an auditory ROI using a “white-noise” stimulus (also see Table 3) (the sixth subject was unable to participate in the white noise experiments for medical reasons).

### *Session 2. Visual Stimuli: Mapping Visual Areas*

Several different visual areas were defined for the purpose of investigating potential differences in the size or responsiveness of areas between deaf and hearing subjects. Visual areas V1, V2, V3, V3A, and V4 were defined using standard retinotopic mapping and cortical flattening fMRI techniques (Engel, Glover, & Wandell, 1997;

DeYoe et al., 1996; Sereno et al., 1994). Three different types of visual stimuli were presented. (1) A slowly rotating black and white flickering checkerboard wedge was used to measure the polar angle component of the retinotopic map. (2) A black and white flickering checkerboard ring that slowly expanded from the fixation point into the periphery was used to measure the radial component of the retinotopic map. (3) Alternating vertical and horizontal flickering wedges were used to define the horizontal and vertical meridians within the retinotopic map. Each of these stimuli subtended 30° vertically and 30° horizontally, and covered all the visual field apart from a small (1°) fixation square. The period of each of these stimuli was 40 sec, and the stimulus was repeated for six cycles. Each retinotopic session lasted approximately an hour and generally included seven scans. Occasionally one of two repeated scans was omitted due to time constraints (see Table 3).

Area MT+, which is likely to include the human analogue of macaque areas MT/MST (Tootell, Reppas, et al., 1995; Zeki, 1980), was defined using a “MT reference stimulus,” which consisted of a full-field (30° in diameter) of dots (0.5° radius), that alternated between moving (at 20°/sec, radially, inward and outward) and stationary in 20-sec epochs (40-sec period for 6 cycles). Two MT+ reference scans were obtained per subject, Area MT+ was defined by localizing a contiguous group of voxels with a time series that correlated with the motion phase of the MT reference stimulus (Watson et al., 1993).

### *Session 3. Visual Motion Stimuli: Measuring Responses in Visual and Auditory Cortex*

The visual stimulus used to measure visual sensory and attentional responses within the auditory and visual

**Table 3.** Details of the Three Scanning Sessions

<i>Session</i>	<i>Scans</i>	<i>Parameters</i>
(1) Auditory	6 music (also 4 auditory white-noise scans carried out in a separate session)	whole head coil; 188 sec; 47 temporal frames; TR = 4 sec, flip angle = 90°, 28 coronal slices; 3 × 3 × 6 (coronal) mm resolution, FOV = 192 mm; first two temporal frames discarded
(2) Mapping visual areas	2 rotating wedges 1 expanding ring 2 horizontal wedges 2 vertical wedges 2 MT+ reference	small surface coil; 244 sec; 122 temporal frames; TR = 2 sec, flip angle = 90°, 28 coronal slices; 3 × 3 × 3 mm resolution, FOV = 192 mm; first two temporal frames discarded
(3) Visual motion	2 attend-motion LVF 2 attend-motion RVF 2 ignore-motion LVF 2 ignore-motion RVF	large surface coil; 288 sec; 72 temporal frames; TR = 4 sec, flip angle = 90°, 28 coronal slices; 3 × 3 × 6 (coronal) mm resolution, FOV = 192 mm; first four temporal frames discarded

cortex consisted of a field of moving dots (dot density = 2.7%) presented within a 10° diameter circular aperture, centered 15° eccentric to a fixation spot (see Figure 3). We used moving dots because the majority of psychophysical and fMRI results showing differences between hearing and deaf observers have used similar stimuli (Bosworth & Dobkins, 1999, 2002a, 2002b; Bavelier, Tomann, et al., 2000). Each moving dot had a diameter of 0.2°, a luminance of 590 cd/m<sup>2</sup> (placed on a black background, <1 cd/m<sup>2</sup>), and appeared at a random location for three to four frames before disappearing and reappearing in another random location within the aperture. The dots moved coherently (87% coherence) at a speed of 7°/sec, with the direction of motion alternating between leftward and rightward every 2 sec. Subjects were instructed to maintain fixation on a small central square (590 cd/m<sup>2</sup>) throughout all conditions. During each run, the motion stimulus was cycled “on” and “off” in 16-sec epochs (32-sec period for 8.5 cycles). On alternate runs, the stimulus was presented in either the RVF or LVF.

We used two attentional conditions (see Figure 3) designed to compare how differences between deaf and hearing subjects are modulated by attention. The physical stimuli were almost identical in both conditions, with only the focus of attention and the location of the brief dimming events changing between the two. In the “attend-motion” condition, the peripheral motion stimulus dimmed during the “on” phase, the fixation spot dimmed during the “off” phase, and subjects were required to respond with a button press to each dimming event. Subjects’ attention therefore switched between the peripheral motion stimulus and the stationary fixation spot. In the “ignore-motion” condition, the fixation spot dimmed during *both* the “on” and “off” phase (the motion stimulus never dimmed) and subjects were again required to respond to each dimming event. Subjects’ attention therefore remained focused on the fixation spot, regardless of whether or not the moving dots were present. In total, each subject was tested twice under four different conditions (in separate blocks): *attend-motion LVF*, *attend-motion RVF*, *ignore-motion LVF*, and *ignore-motion RVF*.

In both the “attend-motion” and “ignore-motion” conditions, stimuli dimmed to 240 cd/m<sup>2</sup> for a duration of 420 msec on a random schedule (on average, 11.3 times/min). Subjects were considered to have detected the dimming if they responded within 2 sec of the dimming event. On a few sessions, responses from the button box could not be recorded. Subjects were nonetheless told that their responses were being recorded, and were given identical instructions as for the other subjects. The difficulty of the dimming task was set so as to maintain a constant level of difficulty, regardless of whether the fixation spot or the moving dots were dimmed. We found no significant difference in perform-

ance (in terms of percent correct and reaction times) across deaf, hearing, and CODA groups within either the “attend-motion” or “ignore-motion” conditions, or for LVF or RVF presentations ( $p > .05$  for all conditions). Differences in neural activity observed between subject groups are therefore not attributable to differences in general arousal. The mean percent correct across all groups was 93% and the mean reaction time was 0.62 sec (also see Table 3).

## Data Analyses

Data analyses were conducted using both in-house (Heeger, Boynton, Demb, Seidemann, & Newsome, 1999) and MCW AFNI software (Cox, 1996). In both cases, datasets were corrected for subject movement with a 3-D registration algorithm based on realignment of images with a reference image, and linear trends were removed. Images were spatially smoothed with a Gaussian kernel of variable width (depending on the stimulus and area). fMRI intensity values were then correlated with a reference function derived from the time course of the stimulus presentation. fMRI response was quantified as the phase and amplitude of the sinusoid that best fit the average time series of voxel responses averaged across a given cortical ROI and projected onto a unit vector with an angle representing the hemodynamic delay (Boynton, Engel, Glover, & Heeger, 1996). Magnitude of activation was calculated as the “functional intensity plus threshold” (FIT) coefficient, which consists of a functional intensity measure (the amplitude of the fMRI signal relative to the reference function) and a threshold value (the correlation coefficient,  $r$ , reflecting how closely the activation in a given voxel correlates with the stimulus reference function). For analyses within the visual cortex, each individual subject’s functional data were aligned with that subject’s high resolution (1 × 1 × 1 mm) anatomical scan. For analyses within the auditory cortex, individual subject datasets were additionally transformed into the standard T&T stereotaxic space for statistical comparison across subjects.

## Size of Visual Areas

As described above (Engel, Glover, et al., 1997; DeYoe et al., 1996; Sereno et al., 1994), we defined visual areas using standard rotating wedge and expanding ring stimuli. These evoke a traveling wave of neuronal activity in retinotopically organized visual brain areas, and the boundaries of early visual areas can be defined based on discontinuities in this traveling wave. Using in-house software, the temporal phase of the fMRI response was projected onto a computationally flattened representation of each individual subjects’ visual cortical surface. Gray matter was identified from a high-resolution

anatomical MRI scan using a Bayesian classification algorithm (Teo, Sapiro, & Wandell, 1997), and a multi-dimensional scaling algorithm was used to flatten the cortical sheet (Engel, Glover, et al., 1997). Retinotopy measurements were then projected onto this flattened representation and blurred spatially (note that this spatial blurring smoothes the pixelated representation and makes boundaries more visible, but does not change the position of the phase reversals). The locations of visual area boundaries were drawn by hand along the reversals in the polar angle component of the retinotopic map and orthogonal to the radial (expanding ring) component of the retinotopic map by one of the authors (IF). Where there was some uncertainty as to the location of a boundary, definitions were cross-checked by a second researcher blind to the purpose of the experiment (given we obtained a null result, we feel that researcher bias was unlikely to be a concern). It has been shown that the locations of the boundaries can be determined reliably using very similar techniques, across repeated measurements, to within an error of 2–4 mm (Engel, Glover, et al., 1997). Finally, the selected areas (V1, V2d, V2v, V3v, V3d, V3a, and V4) were projected back into three-dimensional coordinates within the gray matter of the brain, and their volumes ( $\text{cm}^3$ ) were computed.

Unlike the other visual areas studied, area MT+ does not exhibit clear retinotopy with our fMRI methods. Instead, the size of area MT+ was defined by localizing a contiguous group of voxels with a time series that correlates with the motion phase of the MT+ reference stimulus. One problem with this method, inherent in all fMRI studies that localize brain areas based on correlation with a reference stimulus, is that the determined size depends heavily on the correlation threshold that is chosen. To avoid possible errors in interpretation based on this confound, we calculated the volume of MT+ as a function of the correlation threshold. Our initial definition of MT+ was based on choosing voxels that correlated ( $r > .1$ ) in phase with the motion phase of the MT+ reference stimulus, given a temporal phase lag of 4 sec. MT+ was found to localize in a similar position across subjects, specifically, near the intersection of the anterior occipital sulcus and the lateral occipital sulcus. Besides demonstrating whether or not any differences between two subject groups is sensitive to the choice of correlation threshold, these curves also de-confound the relationship between the amount of correlation with the reference stimulus and the size of a given visual area. Differences in the amount of correlation with the reference stimulus results in a shift along the  $x$ -axis (correlation threshold or significance level), and differences in the size of the area activated results in a shifts along the  $y$ -axis (area volume).

For all visual areas, volumes were determined separately for both the RH and LH. Also, note that because the size of visual areas did not differ between deaf and

hearing subjects (see Results), these measurements were not obtained from CODA subjects.

### *Visual Motion Responses in the Visual Cortex*

Responses to the lateralized motion stimulus (obtained in Session 3) within the visual cortex were measured within the visual areas defined using retinotopic mapping and the MT+ reference stimulus (described above). Using in-house software, we used a “bootstrapping” technique to further restrict the analysis to the particular voxels within each visual area that were found to be responsive to our lateralized motion stimulus (i.e., the portion of each visual area that represented the location in visual space where the motion stimulus had been presented). Specifically, for each of the four visual motion conditions (attend-motion LVF, attend-motion RVF, ignore-motion LVF, and ignore-motion RVF), responses to the first of the two scans were calculated after selecting those voxels that correlated with the second scan with a threshold of 0.2. Responses to the second scan were calculated after selecting those voxels that correlated with the first scan with a threshold of 0.2 (i.e., each of the two scans acted as the reference stimulus for the other). We then averaged the mean responses for the first and second scans within the subset of selected voxels. Consequently, the subset of voxels over which responses were averaged was generally slightly different between the two scans. This bootstrapping approach has the advantage of avoiding circularity issues in which voxels are chosen for analysis on the basis of showing strong correlations during that particular scan, and consequently by definition, necessarily show strong activations. However, these estimates also tend to be more variable than estimates based on averaging responses within a predetermined ROI. Having selected voxels for further analysis, we then calculated the FIT coefficient for the selected voxels across both scans, and the averaged FIT coefficient was taken as the magnitude of activity for that condition for that subject. When fewer than 10 voxels passed the bootstrapping threshold across both scans, we took the response in that area for that condition to be zero. A few individual subjects’ responses within individual visual areas were excluded as obvious outliers (outside 3 standard deviations from the mean).

To measure activation within MT+, we used a fixed correlation threshold of 0.2. Analyses were also carried out using both stricter and laxer definitions of MT+ (and a fixed size of MT+), but the results of these analyses did not differ significantly from those obtained with a 0.2 threshold. Note that this bootstrapping approach could not be used in auditory cortex because ROIs were obtained in the auditory cortex by averaging responses to auditory stimuli across hearing subjects (see below).

Visual responses were obtained separately for the LH and RH, for LVF and RVF stimulus presentation, and for attend-motion and ignore-motion conditions. This allowed us to compare ipsilateral versus contralateral responses, hemispheric asymmetries and attentional effects between our subject groups. The average number of voxels that passed our bootstrapping criterion did not differ between deaf and hearing subjects for any visual area. Because we did not find any significant differences in responsivity within the visual cortex between deaf and hearing subjects (see Results), we did not analyze responsivity within the visual cortex of CODA subjects.

### *Defining Auditory ROIs in Hearing Subjects*

We defined auditory ROIs in hearing subjects based on responses to auditory stimuli (see Data Acquisition, above). Using AFNI software, ROIs were defined by establishing clustering and significance criteria for voxels that were activated significantly to the auditory stimulus across all hearing subjects (voxelwise  $t$  test, minimum cluster volume =  $0.540 \text{ cm}^3$ , minimum  $p$  value =  $.2$ ). Clustering and significance criteria were deliberately generous so that auditory ROIs included primary, secondary, and association auditory areas. The two largest clusters satisfying these criteria localized to the right and left auditory cortices and were used for the right and left auditory ROIs, respectively. We then projected this region that responded in phase with the auditory stimulus (green regions in Figure 5) onto an average structural image resulting from combining reference anatomies across both deaf and hearing subjects. Note that averaging deaf and hearing anatomies is justified based on previous studies demonstrating that the two groups do not differ anatomically in the region of the auditory cortex (Eckert, Gauger, & Leonard, 2000; Cismaru et al., 1999), nor do deaf and hearing subjects differ in their gray matter volumes within the auditory cortex (Emmorey, et al., 2003). The cortical locations (Brodmann's areas) of voxels activated by auditory stimuli were identified within the T&T coordinate system in two ways: (i) the on-line Talairach Daemon (<http://biad73.uthscsa.edu>), and (ii) the anatomical atlas of Talairach and Tournoux (1988). As expected, auditory stimuli activated regions in both the right and left auditory cortex, including Brodmann's areas 41, 42, and 22 (Brodmann, 1909), although, consistent with known hemispheric asymmetries for music processing (Christman, 1997), the total volume of the right auditory ROI ( $13.1 \text{ cm}^3$ ) was larger than that of the left ( $7.24 \text{ cm}^3$ ). Similar results were obtained for ROIs defined from the white-noise stimulus, including the fact that the RH ROI was larger than the left (although both ROIs were about half the size of those obtained with music). Analysis of visually evoked fMRI responses (below) was limited to these music-defined auditory ROIs.

### *Visual Motion Responses in the Auditory Cortex*

Responses to the lateralized motion stimulus (obtained in Session 3) were measured within the left and right auditory ROIs of deaf and hearing subjects using AFNI software. Differences in activation to visual stimuli between groups were assessed by a voxelwise two-factor ANOVA (Subject group  $\times$  Visual field, Bonferroni corrected for multiple comparisons), separately for the "attend-motion" and "ignore-motion" conditions. Areas of significant difference (see Figure 5 and Table 2) were further required to pass clustering and significance criteria to guard against false positives due to multiple comparisons, using clustering and  $p$ -value criteria established with AlphaSim (MCW AFNI; Cox, 1996), after 1000 Monte Carlo simulations. Minimum cluster sizes were 4 voxels ( $0.216 \text{ cm}^3$ ) and 3 voxels ( $0.162 \text{ cm}^3$ ) for right and left ROIs, respectively. All surviving voxels have an adjusted  $p$  value of  $<.05$ .

Because the results of these analyses revealed significant differences between deaf and hearing subjects (see Results), data from CODA subjects were compared with data from both hearing and deaf subjects. The magnitude of activation for CODA subjects was determined within the region of effect within the auditory cortex (i.e., the region for which deaf subjects exhibited significantly greater responses than hearing subjects).

As for analyses within the visual cortex (see above), visual responses in the auditory cortex were obtained separately for the LH and RH, for LVF and RVF stimulus presentation, and for "attend-motion" and "ignore-motion" conditions.

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Reprint requests should be sent to Karen Dobkins, Department of Psychology, University of California, San Diego, La Jolla, CA 92093, or via e-mail: [kdobkins@ucsd.edu](mailto:kdobkins@ucsd.edu).

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