

Voice perception in blind persons: A functional magnetic resonance imaging study

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ABSTRACT

Early blind persons have often been shown to be superior to sighted ones across a wide range of non-visual perceptual abilities, which in turn are often explained by the functionally relevant recruitment of occipital areas. While voice stimuli are known to involve voice-selective areas of the superior temporal sulcus (STS) in sighted persons, it remains unknown if the processing of vocal stimuli involves similar brain regions in blind persons, or whether it benefits from cross-modal processing. To address these questions, we used fMRI to measure cerebral responses to voice and non-voice stimuli in blind (congenital and acquired) and sighted subjects. The global comparison of all sounds vs. silence showed a different pattern of activation between blind (pooled congenital and acquired) and sighted groups, with blind subjects showing stronger activation of occipital areas but weaker activation of temporal areas centered around Heschl's gyrus. In contrast, the specific comparison of vocal vs. non-vocal sounds did not isolate activations in the occipital areas in either of the blind groups. In the congenitally blind group, however, it led to a stronger activation in the left STS, and to a lesser extent in the fusiform cortex, compared to both sighted participants and those with acquired blindness. Moreover, STS activity in congenital blind participants significantly correlated with performance in a voice discrimination task. This increased recruitment of STS areas in the blind for voice processing is in marked contrast with the usual cross-modal recruitment of occipital cortex.

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1. Introduction

It is a common belief that blind people perform better than sighted ones at a variety of non-visual tasks, probably because they compensate for their lack of vision with increased processing within other sensory modalities. Indeed, many studies have confirmed that blind persons have superior abilities for non-visual perceptual tasks, such as pitch-change direction discrimination (Gougoux et al., 2004), verbal memory (Amedi, Raz, Pianka, Malach, & Zohary, 2003; Hull & Mason, 1995; Röder, Rosler, & Neville, 2001), speech discrimination (Muchnick, Efrati, Nemeth, Malin, & Hildesheimer, 1991; Niemeyer & Starlinger, 1981), sound localization (Ashmead et al., 1998; Gougoux, Zatorre, Lassonde, Voss, & Lepore, 2005; Lessard, Paré, Lassonde, & Lepore, 1998; Rice, 1970; Röder et al., 1999; Voss, Lassonde, Gougoux, Guillemot,

& Lepore, 2004) or tactile discrimination (Goldreich & Kanics, 2003; Van Boven, Hamilton, Kauffman, Keenan, & Pascual-Leone, 2000).

What are the neural mechanisms involved in these superior behavioral abilities? One influential hypothesis is that the recruitment of visual areas is involved in this compensation. Some insight into the neural substrates of these enhanced capacities is provided by animal studies (for a review, see Rauschecker, 1995). For instance, in cats deprived of visual input for several years by eyelid suture shortly after birth, the auditory cortical representation occupied larger portions of the multi-modal Anterior Ectosylvian area (Rauschecker & Korte, 1993), and auditory spatial tuning of the neurons was sharper (Korte & Rauschecker, 1993). Similarly, in neonatally enucleated rats, electrophysiological recordings have shown somatosensory (Toldi, Farkas, & Volgyi, 1994) and auditory (Piche et al., 2007) responses in visual cortex, and an enlargement of receptive fields or an increased deflection angular sensitivity for cells in different whisker barrels (Toldi, Rojik, & Feher, 1994). Thus, cortical representations of non-visual modalities indeed seem to invade the visual cortex in blind animals while some sensory-

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specific cortical cells seem to show improved characteristics such as, for example, sharper tuning or better angular sensitivity.

In humans, several studies using neuroimaging techniques have shown that occipital areas in blind persons are recruited to carry out non-visual tasks such as Braille reading (Burton, Snyder, Conturo, et al., 2002; Sadato et al., 1996), memory retrieval (Amedi et al., 2003) sound localization (Gougoux et al., 2005; Leclerc, Saint-Amour, Lavoie, Lassonde, & Lepore, 2000; Weeks et al., 2000) or other auditory functions (Arno et al., 2001; Burton, Snyder, Diamond, & Raichle, 2002; Kujala et al., 1995; Liotti, Ryder, & Woldroff, 1998; Röder, Stock, Bien, Neville, & Rosler, 2002). A few studies have also suggested increased cortical representation in the expected areas for auditory (Elbert et al., 2002), somatosensory (Sterr et al., 1998) or motor functions (Pascual-Leone & Torres, 1993) in blind persons. Little is known, however, about the brain mechanisms involved in voice perception in blind persons.

Voice perception is a crucial aspect of human social communication, allowing us to extract from a voice not only the linguistic message contained in speech, but also a wealth of information about the speaker's identity (gender, age, region of origin) and affective state (Belin, Fecteau, & Bédard, 2004). Voice perception is especially important for blind individuals in allowing them to recognize other people. Interestingly, the philosopher Diderot reported over two centuries ago, in his *Lettre pour les aveugles* (1749), the case of a blind man able to recognize voices with a very high accuracy. Although a wealth of anecdotal observations indeed suggests better voice processing in the blind, empirical evidence for such a superiority of blind persons is quite scarce. The few available behavioral studies have yielded only conflicting results, with only one study showing superiority in the blind (Bull, Rathborn, & Clifford, 1983) while two others did not find any difference between sighted and blind individuals (Gunzburger, Bresser, & Ter Keurs, 1987; Winograd, Kerr, & Spence, 1984).

In sighted persons, it has been shown that auditory cortex along anterior superior temporal sulcus (STS) contains voice-selective regions more active specifically in response to vocal sounds compared to non-vocal sounds (Belin, Zatorre, & Ahad, 2002; Belin, Zatorre, Lafaille, Ahad, & Pike, 2000; Fecteau, Armony, Joannette, & Belin, 2004; von Kriegstein, Eger, Kleinschmidt, & Giraud, 2003; Warren, Scott, Price, & Griffiths, 2006). It is as yet unknown whether the processing of vocal stimuli involves similar brain regions in blind persons, or recruits additional visual areas as is the case for many other non-visual tasks. We used functional magnetic resonance imaging (fMRI) to measure brain responses to vocal and non-vocal sounds in blind and sighted subjects in order to test the hypothesis that vocal processing would engage not only voice-sensitive regions, but also occipital cortices.

2. Material and methods

2.1. Participants

The participants were 14 healthy sighted volunteers and 15 blind subjects who either lost their vision at birth (congenital blindness; $n = 5$) or later in life (acquired blindness; $n = 10$), from one year to 45 years after birth (see Table 1). In each case, the visual deficit was of peripheral origin and led to total blindness except for some residual light perception in four subjects (categories 4 and 5, according to the World Health Organization [WHO] classification, 1996). All participants underwent audiometric testing to ensure good hearing, with no difference between ears superior to 25 dB for frequencies between 500 Hz and 8 kHz. They gave their written informed consent in accordance with guidelines approved by the Ethics and Research Committees of the Montreal Neurological Institute and the Nazareth and Louis-Braille Institute for the Blind.

2.2. Scanner experiment

2.2.1. Procedure and stimuli

Following the procedure developed by Belin et al. (2000, 2002) in sighted individuals, subjects were asked to listen passively to vocal or to overall energy (RMS) matched non-vocal sounds while they were lying within the scanner. Auditory stim-

Table 1
Characteristics of blind and sighted participants.

Subject	Gender	Age (years)	Age at blindness onset	Etiology (years)	Residual light perception
Congenitally blind group ($n = 5$; mean age 30.4 years)					
1	F	36	0	Bilateral retinal dysplasia	Y
2	F	23	0	Retinopathy of prematurity	N
3	F	21	0	Retinal detachment	N
4	M	40	0	Congenital, non-specified	N
5	M	32	0	Leber's disease	Y
Acquired blind group ($n = 10$; mean age 34.2 years)					
1	F	25	1	Retinoblastoma	N
2	M	23	2	Retinoblastoma	N
3	F	41	5	Retinoblastoma	Y
4	F	24	8	Retinal detachment	N
5	M	34	14	Leber's disease	N
6	M	36	14	Juvenile inflammatory rheumatism	N
7	F	33	22	Glaucoma	N
8	F	46	45	Retinitis pigmentosa	Y
9	M	40	37	Glaucoma	N
10	M	40	37	Glaucoma cataract	N
Sighted group ($n = 14$; mean age 26.3 years)					
1	M		27		
2	M		25		
3	M		22		
4	F		25		
5	F		22		
6	M		26		
7	F		37		
8	F		27		
9	F		37		
10	M		25		
11	F		21		
12	F		25		
13	M		27		
14	M		22		

uli were presented binaurally over electrostatic MR-compatible headphones (KOSS) and additional plastic muffs were added to attenuate the sounds of the scanner. Stimuli were presented at 75 dB SPL. The participants were asked to close their eyes while they listened to the sounds. The paradigm was identical to the one used in a previous study (see Belin et al., 2000). Sounds were presented in blocks of 20 s duration: 21 blocks of vocal sounds and 21 blocks of environmental sounds; the inter-block interval was 10 s. Each block included 12 different speakers (for vocal sounds) or sources (for non-vocal sounds) of similar overall energy (RMS). Vocal stimuli within the same block could be either speech (33%: words, non-words, foreign language) or non-speech (67%: laughs, sighs, various onomatopoeia). Sounds that did not involve vocal-fold vibration were excluded (for example, whistling, whispered speech). Non-vocal stimuli consisted of sounds from nature (14%: for example, wind, streams), animals (29%: cries, gallops), the modern human environment (37%: cars, telephones, aeroplanes) or musical instruments (20%: bells, harp, instrumental orchestra).

2.2.2. MRI acquisition and fMRI scanning

Scans were obtained on a 1.5-T Siemens Magnetom scanner. A T1-weighted MR image was first acquired to provide anatomical detail (TE = 10 ms; TR = 22 ms, sagittal acquisition plane, head coil, flip angle 30°). Then a series of 128 gradient-echo BOLD images was acquired for the experiment (TE = 50 ms, head coil, matrix size: 64 × 64; voxel size: 5 mm × 5 mm × 5 mm; 10 slices acquired in the orientation of the Sylvian fissure covering the auditory cortex and centered on Heschl's gyrus). To avoid artifacts caused by scanning noise, we used a sparse-sampling (TR = 10 s) echo-planar imaging fMRI (Belin, Zatorre, Hoge, Evans, & Pike, 1999; Hall et al., 1999). The 20 s blocks were presented in a pseudo-random order with 10 s silence intervals using Media Control Function software (Digivox, Montreal) and block onset was synchronized with acquisition of the first brain image.

2.2.3. Data analysis

Blood oxygenation-level dependent (BOLD) images were smoothed (6-mm gaussian), corrected for motion artefacts and transformed into standardized stereotaxic space (Talairach & Tournoux, 1988) using in-house software (Collins, Neelin, Peters, & Evans, 1994) and the MNI 305 average as the target. Statistical maps were obtained for each individual using a voxel-based analysis based on a linear model with correlated errors, with direct specification of the design matrix (Worsley et al., 2001). Group-average statistical images were obtained by computing an omnibus-test on individual *t*-maps using a pooled estimate of standard deviation (Worsley, Evans, Marrett, & Neelin, 1992). Depending on the analysis, criteria of $t = 4.8$ – 5.0 were calculated for the whole brain (Worsley et al., 1996). However, a less strict threshold ($t > 2.5$) was considered for regions of interest defined a priori, such as occipital and temporal areas.

In the group contrast analyses that follow in Section 3, we use the blindness categories congenital vs. acquired; however, four individuals in the acquired group lost their vision early in life but not at birth (between the ages of 1 and 8), and could also be grouped along with the congenitally blind to form an *early blind* that would then be compared to a *late-blind* group. We therefore also tested for group differences using this classification. The pattern of results reported below did not change with this re-classification, with the exception of the vocal vs. non-vocal contrast, as identified within the results.

2.3. Behavioral task

2.3.1. Procedure

After the scanning session, participants performed a voice discrimination task in the laboratory. On each trial, subjects heard two different syllables and had to decide whether the two syllables were spoken by the same or a different speaker. Participants were seated in front of a computer and the stimuli were delivered through headphones at a comfortable intensity level for each individual. Compliance to all instructions was ascertained by an experimenter remaining seated beside the subject. The response was obtained via two buttons of a computer mouse and thus the procedure was the same for sighted and blind subjects. One late-blind subject was excluded from analysis because the task was not well understood.

2.3.2. Stimuli

Stimuli consisted of 81 spoken syllables: 9 syllables (head, had, hawed, haid, heid, heard, hid, heed, hoard) each spoken by 9 speakers: 3 men, 3 women and 3 male children. They were part of a database of American English vowels recorded in similar controlled conditions across a large number of speakers, described in detail elsewhere (Hillenbrand, Getty, Clark, & Wheeler, 1995) and kindly made available to the present authors. All stimuli (16-bits, mono, 16 kHz sampling rate) were equated for RMS amplitude using Mitsyn software (WLH, MA, USA). On each trial, one of the 81 syllables was paired randomly with another of the 80 remaining syllables, such that on about half of the trials the two syllables were pronounced by a same speaker (50% "same" and 50% "different" trials). Two stimuli with a mean duration of 451 ms were presented one after the other without pause except for the silence included in the wave files (mean "inter-stimuli-interval" of 156 ms).

3. Results

3.1. General auditory activation

Both conditions of auditory stimulation (vocal and non-vocal) were first pooled together and compared to the silent baseline (ALL vs. SIL) in order to delineate the functionally active auditory cortex. Mean BOLD signal (% change) values were extracted at different regions of interest (see histograms in Fig. 1). A group comparison was also carried out on these data to evaluate the presence of any differences between blind and sighted individuals in their global response to these sounds.

A first finding was the expected bilateral activation of auditory areas in all groups of subjects. Group comparison showed that activations in auditory cortical areas, specifically in the lateral portion of Heschl's gyrus, were of lesser magnitude in both groups of blind subjects when compared to the sighted group (Fig. 1 and Table 2). The bilateral temporal "deactivation" (seen in blue on the inter-group contrast of Fig. 1) thus corresponds to this relative difference in activations between the blind and the sighted groups (not to a BOLD signal decrease as such).

Another striking group difference was observed at the level of the occipital areas. While the sighted group showed the usual pattern of deactivation – less BOLD signal during auditory stimulation than during baseline – both blind groups showed in contrast an increase of activation relative to baseline in striate and extra-striate areas.

The opposite pattern was observed in prefrontal regions: while the sighted group showed activation of these regions, both blind groups presented deactivations. Importantly, no difference was found between the two groups of blind subjects in any of our regions of interest located in the temporal and occipital cortices.

As mentioned in Section 2, the aforementioned contrasts were also performed with a different group arrangement: early blind (the five congenitally along with the four acquired blind subjects with the earliest onsets; see Table 1) vs. late-blind (the remaining acquired blind subjects). We found no difference in the pattern of results in this analysis compared to the congenital vs. acquired contrasts.

3.2. Voice-selective areas

In order to identify the neural basis of voice perception in these three groups, a contrast between the vocal and non-vocal (VOC vs. NVO) conditions was carried out and revealed greater activation of bilateral temporal areas, most notably the superior temporal sulcus, for vocal than non-vocal stimuli in each group of participants, but without any differential activation of occipital areas (Fig. 2 and Table 2).

Congenital and acquired blind persons were subsequently separated in two groups for more specific inter-group comparisons. Each of these groups was then compared to the sighted group. These contrasts did not reveal the expected differences in occipital areas, but revealed stronger activation in left STS (and a trend for the right STS, see Table 2) for the congenitally blind group when compared to the other two groups (Fig. 3 and Table 2). Furthermore, a trend for an increased activation was also seen in favour of the congenitally blind group in the fusiform regions bilaterally – slightly anterior to the fusiform face area (FFA) in normal subjects – when compared to the two other groups (see Table 2).

The re-grouping of the blind subjects to produce early and late-blind groups did not alter the pattern of results obtained from the group contrast analysis for the first peak seen in Fig. 3 (top panel). However the pattern did change for the second peak (Fig. 3, bottom panel), where the early and late-blind groups were significantly different from the sighted one, but were indistinguishable from each other.

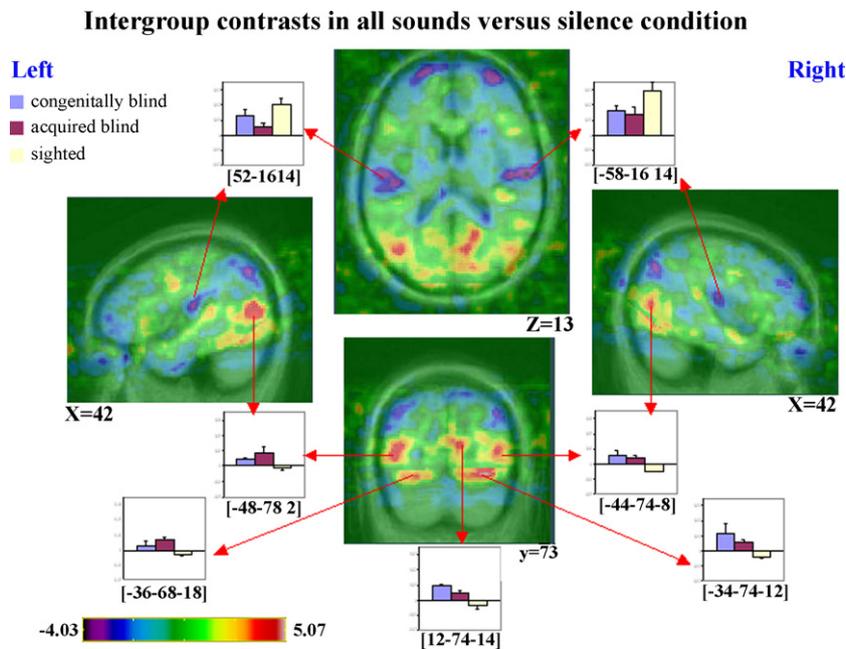


Fig. 1. Intergroup contrasts in all sounds versus silence condition. Brain images represent the contrast between the blind (congenital and acquired pooled together) and the sighted group in sagittal (left and right), horizontal (middle upper image) and coronal (middle lower image) planes. Regions of greater signal change in favour of the blind groups are shown as “relative activation” in color scale (*t* statistics) overlaid on the subject’s average anatomical MR image in standard stereotaxic space. Conversely, regions of relative greater activation in favour of the sighted group are also shown as “relative deactivation”. Bar diagrams indicate mean signal change from silence for the three groups of participants (blue bars: congenitally blind, red bars: acquired blind group, yellow bars: sighted group). For the two blind groups, activations were seen in both occipital and temporal areas. In the case of the sighted group, a relatively more important temporal activation was seen and deactivation of occipital areas was observed. Some differences were also seen for frontal and parietal areas. Y and Z coordinates refer to standardized stereotaxic space. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

3.3. Correlation analysis

Performance at the speaker discrimination task performed offline was compared between the three groups. No difference was found between them ($F(2, 23) = 0.066, p = 0.937$). The lack of dif-

ference is essentially attributable to a ceiling effect – on average all groups performed above 85%. In order to investigate the possible functional role of the observed activations, correlation analyses were performed. These analyses examined voxelwise covariation between behavioral performance at the speaker discrimination task

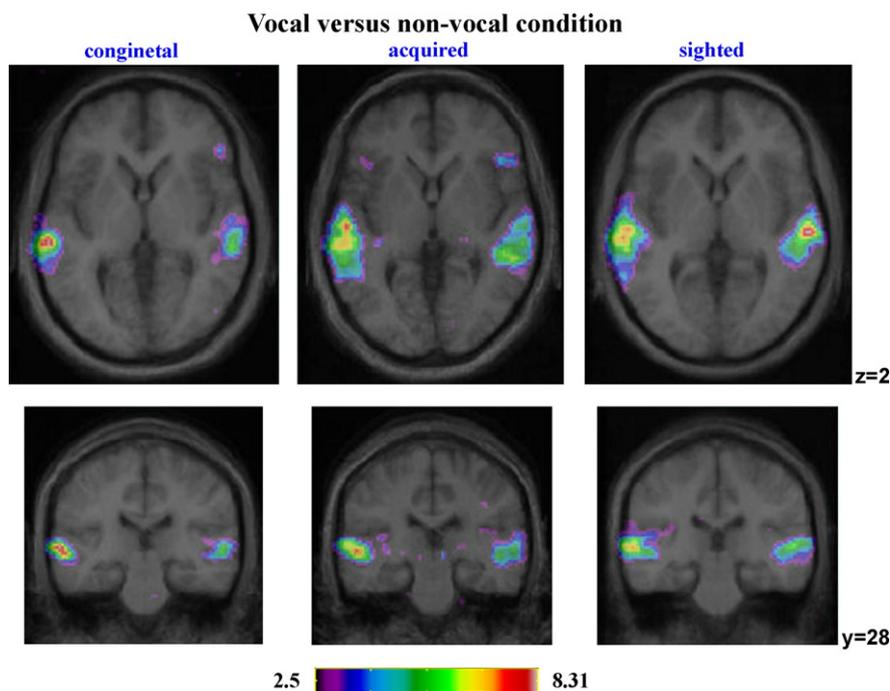


Fig. 2. Vocal versus non-vocal condition: voice-sensitive activations in fMRI experiments for the three groups of participants. Regions of significantly greater signal change to vocal than to non-vocal sounds are shown in color scale (*t* statistics) overlaid on the subjects’ average anatomical MR image in standard stereotaxic space. All groups show bilateral activations in regions along the STS in horizontal (upper panel) and coronal (lower panel) slices. Y and Z coordinates refer to standardized stereotaxic space.

Table 2
Stereotaxic coordinates and *t*-values of activation and deactivation foci in occipital and temporal areas.

Groups/contrasts	Areas	x	y	z	<i>t</i> -values	
ALL vs. SIL comparison ALL blind vs SIG	Right Heschl gyrus, lateral portion	58	–16	14	–4.033	
	Left Heschl gyrus, lateral portion	–52	–16	14	–3.319	
	Right lingual/inf occipital (BA 19)	34	–74	–12	5.026	
	Right V1 (BA 17)	12	–74	14	4.041	
	Right med occipital gyrus (BA 19)	44	–74	8	4.026	
	Left med occipital gyrus (BA 19)	–48	–78	2	5.070	
	Left lingual/inf occipital (BA 19)	–36	–68	–18	4.168	
VOC vs. NVO comparison	SIG	Right STS (BA 22)	62	–22	2	8.351
		Right STS (BA 22)	56	–38	8	6.130
		Left STS (BA 22)	–58	–20	0	7.427
		Left STS (BA 22)	–62	–34	4	6.771
	ACQ	Right STS (BA 21)	64	–12	–2	7.877
		Right STS (BA 21)	54	–20	–6	6.914
		Left STS (BA 22)	–58	–20	2	7.624
		Left STS (BA 21)	–56	–32	0	7.548
	CONG	Right STS (BA 21)	60	–32	4	6.104
		Left STS (BA 21)	–64	–28	2	8.313
		Left fusiform (BA 37)	–46	–46	–16	4.843
	CONG–SIG	Right STS (BA 21)	60	–27	–2	3.286
		Left STS (BA 21)	–62	–30	–2	5.259
		Right fusiform (BA 37)	34	–52	–16	3.795
		Right lingual/inf occipital (BA 19)	36	–70	–16	3.498
		Left fusiform (BA 37)	–46	–48	–16	4.069
	CON–ACQ	Right ITG (BA 37)	50	–69	–2	3.562
		Right STS (BA 21)	58	–33	4	2.777
		Left STS (BA 21)	–70	–34	–2	5.526
		Left STS (BA 21)	–64	–28	2	5.523
		Right fusiform (BA 37)	34	–52	–16	3.444
		Right lingual/inf occipital (BA 19)	35	–68	–20	2.777
		Left fusiform (BA 37)	–46	–48	–16	3.405
	Covariation with behavioral measure (% correct) all blinds only: VOC vs. NVO comparison	Right STS (BA 21)	60	–44	2	4.812
		Right STS (BA 21)	60	–12	–2	4.183
		Left STS (BA 21)	–55	–50	–2	2.787

Coordinates *x*, *y* and *z* refer to standardized stereotaxic space (Talairach and Tournoux, 1988).

and BOLD signal in the VOC vs. NVO condition. Correlation results for the blind subjects (the two groups pooled together) yielded two foci in the right temporal areas, one in the central portion and one in the posterior portion of the right STS (Fig. 4 and Table 2). Correlations between BOLD values (extracted from 5-mm radius spheres) at the two locations and individual behavioral scores yielded high values: the highest correlation peak was found in the right posterior portion of STS ($r=0.86$, $p<0.01$) while the second one was in the central portion of STS ($r=0.48$, $p=0.08$). No significant peak was found in left temporal areas but, once again, a trend was observed (see Table 2). No significant correlation between activation and behavior, though, was observed in the sighted group. Furthermore, there were no significant correlations between brain activation and either the age of onset of blindness or the duration of blindness.

4. Discussion

Several important findings emerged from the comparison of brain activity in blind and sighted subjects during auditory stimulation with natural vocal and non-vocal sounds of the environment. First, when compared to silence, BOLD responses elicited by the mix of natural sounds were notably found in occipital areas in the blind, but not in sighted subjects, who instead showed BOLD signal decreases in visual cortices. In marked contrast, activation of auditory areas was significantly less strong in the blind when compared to sighted subjects. Second, when activations elicited by vocal and

non-vocal stimuli were compared, all groups showed the expected recruitment of STS voice-sensitive regions, but the congenitally blind subjects showed enhanced responses along left posterior STS, whereas they did not show recruitment of occipital-lobe visual cortex. Finally, it was found that the voice stimuli activated the fusiform cortex bilaterally in the congenitally blind group (though slightly under the threshold for statistical significance). Quite interestingly, positive significant correlations between performance on a voice discrimination task (performed offline) and activations in voice-selective areas along the left posterior STS were observed for the blind group; but not such correlation was observed in the sighted group.

4.1. Recruitment of visual areas in blind persons

When a large variety of voices and non-vocal sounds of different sources were compared to silence, blind persons showed activations in many occipital areas, both striate and extra-striate. This finding was not unexpected since several previous studies have shown that occipital areas are recruited for various non-visual tasks or conditions (for a review: Kujala, Alho, & Naatanen, 2000; Pascual-Leone, Amedi, Fregni, & Merabet, 2005; Rauschecker, 1995). In contrast, the sighted group showed a deactivation in these occipital areas. In line with this, many previous studies have shown that following stimulation in one modality, cross-modal inhibition might occur in the unattended modalities in sighted participants (Drzezga et al., 2005; Gougoux et al., 2005; Haxby et al., 1994; Johnson &

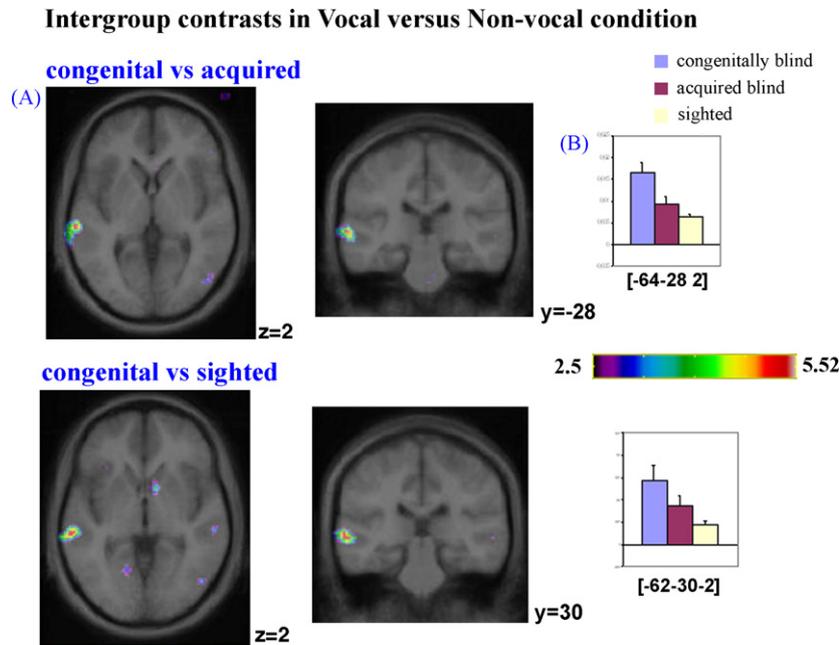


Fig. 3. Intergroup contrasts in vocal versus non-vocal condition. (A) Imaging results. Horizontal (left) and coronal (middle) images showing the congenitally blind group compared to acquired blind group (upper panel) and sighted group (lower panel), respectively. These contrasts yielded the differences in region along the STS between the congenitally blind group and the two other groups, especially on the left side. Y and Z coordinates refer to standardized stereotaxic space. (B) Histograms. In the right section of the figure, intergroup maxima are seen for the vocal versus non-vocal contrast between congenitally blind and acquired group (upper panel) and sighted group (lower group), respectively. Bars represent signal changes in percent (mean \pm s.e.). Significant differences are seen between the congenitally blind groups and the two other groups. Blue bars indicate the congenitally blind group, red bars indicate the acquired blind group while the yellow bars represent the sighted group. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Zatorre, 2005; Kawashima, O'Sullivan, & Roland, 1995; Laurienti et al., 2002; Shulman et al., 1997). In addition, deactivation of the primary visual areas in sighted persons coupled with activation of these same areas in blind persons has been previously observed

(Gougoux et al., 2005; Sadato et al., 1996; Weeks et al., 2000). The contrasting results between blind and sighted groups at the occipital level might suggest a possible difference in cross-modal inhibitory processes.

Correlation analysis for Vocal versus Non-vocal condition

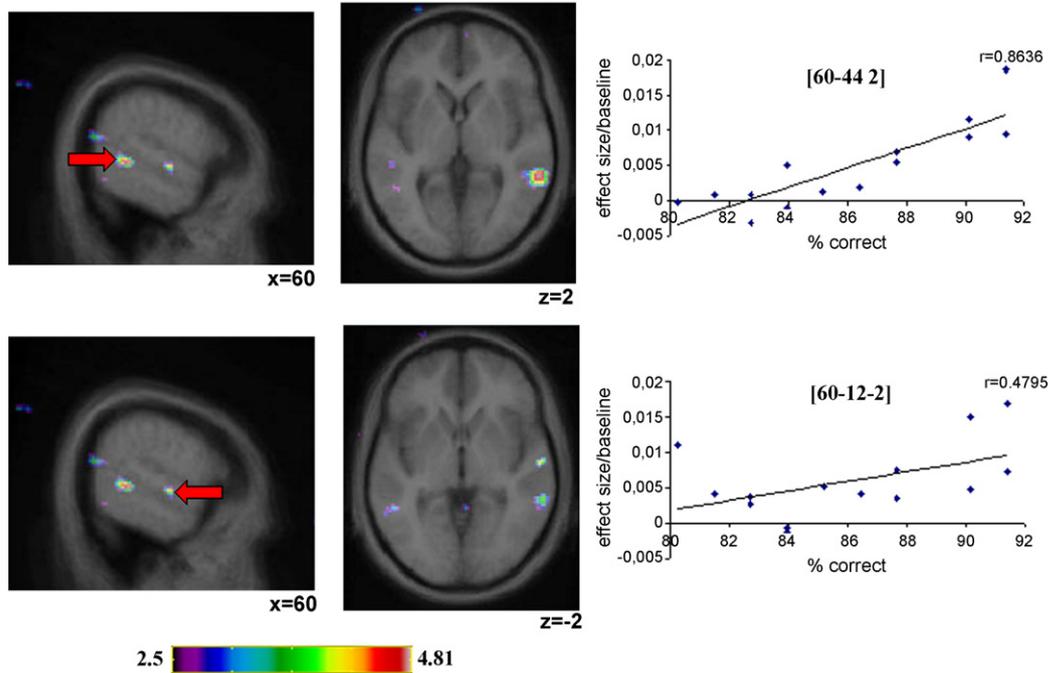


Fig. 4. Correlation analysis for vocal versus non-vocal condition. These panels show the correlation analysis between performances in speaker discrimination task (% correct) and BOLD signal in a group of congenitally and acquired blind subjects. The two columns of brain images (left images, sagittal sections; middle images, horizontal sections) illustrate the statistical map of the correlation which is significant for two regions along the STS. The red arrows in the sagittal slices indicate the focus selected for the respective horizontal slices. The scatter grams show the individual values (effect size/individual baseline) extracted from these two regions. X and Z coordinates refer to standardized stereotaxic space. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Another important finding is that blind persons also showed significantly less activation in the lateral portion of Heschl's gyri bilaterally when compared to the sighted group. For the blind group, we hypothesize that the recruited visual areas might take over part of the auditory processing at the expense of normal auditory areas. An "extended network" would thus be responsible for general auditory stimulation in the blind persons, which would lead to a less concentrated and intense activation pattern in areas normally dedicated for general auditory processing. Such a pattern has not been observed before with other tasks, such as spatial localization or verbal memory (Amedi et al., 2003; Gougoux et al., 2005), which instead show recruitment of occipital cortices in the congenitally blind.

4.2. Extended voice-selective activation in the blind person

When vocal stimuli were compared to non-vocal ones, all three groups showed significant activations along the STS regions, suggesting their implication in voice processing in the blind person as well. Activations of regions along the STS areas have already been reported in many studies with sighted persons. In auditory brain imaging studies, such activations were seen in the context of not only voice perception (Belin et al., 2000, 2002; Fecteau et al., 2004) but also speech processing (Liebenthal, Binder, Spitzer, Possing, & Medler, 2005; Narain et al., 2003). In the present study, STS maxima of each group were close to the voice-sensitivity maxima reported in previous experiments on voice perception, especially in the middle and posterior parts of STS (see Table 2). Blind and sighted persons thus seem to share the same known and dedicated structures for voice processing. This is an important finding considering that cross-modal processes are in general functionally implicated in auditory-driven tasks and could have potentially been important for voice processing.

However, the groups did not seem to rely on STS regions to the same extent. Indeed, the inter-group comparison showed a relative increase in activation in the left STS, but only for the congenitally blind group (see Fig. 3). It would appear that the congenitally blind group uses more of their temporal cortex, especially the STS, for voice processing. The increased STS recruitment in the blind may therefore indicate a more important contribution of intra-modal plasticity vs. cross-modal plasticity in voice processing. However STS is a multi-modal region, so it is possible that the visual STS neurons were simply converted into auditory processing neurons following blindness. This nonetheless contrasts sharply with the massive cross-modal recruitment of occipital cortices often observed in blind individuals.

Furthermore, correlation analyses provided additional evidence that these more posterior STS areas might be more important in voice processing for the blind groups than the sighted one. Indeed, even if the blind persons did not outperform the sighted group in the speaker discrimination task, their individual performances were positively correlated to the activations of voice-sensitive areas, while it was not the case for the sighted individuals. It can be speculated that blind persons rely more on these STS areas even if it did not give them a behavioral advantage, at least in the present task, possibly because of a ceiling effect. In a related study, Hugdahl et al. (2004) did however show that blind individuals could outperform sighted subjects in a syllable identification task, possibly reflecting a more extensive usage of STS areas in the blind.

In addition to STS regions, the congenitally blind group shows a trend for more activation in both fusiform areas when compared to the other two groups. This is remarkable as a wealth of evidence suggests that this part of the cortex is involved in face processing in sighted persons (Haxby et al., 1999; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997), and yet the congenitally blind have never seen a face. This result is in good

line with suggestions that voices are "auditory faces", and that the functional architecture underlying face and voice processing in the sighted could be organized following very similar principles (Belin et al., 2004). This finding is also coherent with recent reports of FFA activation in sighted subjects during familiar voice recognition (von Kriegstein, Kleinschmidt, Sterzer, & Giraud, 2005). It appears that at this level of cortical processing, computations performed are quite similar for voice and face stimuli, or at least that these regions show strong interaction even during processing of unimodal stimuli, and even in the complete absence of relevant visual experience.

5. Conclusion

Cortical reorganization in blindness may mediate a variety of behavioral adaptations relevant to everyday activities. While this often implies increased activations of occipital areas, it might not be the only means to accomplish adaptation in the auditory domain. The present study establishes for the first time in blind persons an overreliance on the STS regions in voice perception, suggesting that intra-modal plasticity, or at least plasticity in already dedicated pathways, might constitute another means of enhancing specialized auditory functions. Voice perception might be a highly specialized function which therefore recruits a hard-wired substrate, similar to the visual face area.

Conflicts of interest

The authors have declared that no conflicts of interest exist with any aspect of this study.

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