Auditory motion perception activates visual motion areas in early blind subjects

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We have previously shown that some visual motion areas can be specifically recruited by auditory motion processing in blindfolded sighted subjects [Poirier, C., Collignon, O., De Volder, A.G., Renier, L., Vanlierde, A., Tranduy, D., Scheiber, C., 2005. Specific activation of V5 brain area by auditory motion processing: an fMRI study. Brain Res. Cogn. Brain Res. 25, 650–658]. The present fMRI study investigated whether auditory motion processing may recruit the same brain areas in early blind subjects. The task consisted of simultaneously determining both the nature of a sound stimulus (pure tone or complex sound) and the presence or absence of its movement. When a movement was present, blind subjects had to identify its direction. Auditory motion processing, as compared to static sound processing, activated the brain network of auditory and visual motion processing classically observed in sighted subjects. Accordingly, brain areas previously considered as specific to visual motion processing could be specifically recruited in blind people by motion stimuli presented through the auditory modality. This indicates that the occipital cortex of blind people could be organized in a modular way, as in sighted people. The similarity of these results with those we previously observed in sighted subjects suggests that occipital recruitment in blind people could be mediated by the same anatomical connections as in sighted subjects.
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Introduction

Cross-modal plasticity due to sensory deprivation has been the focus of major attention from the neuroimaging community, especially over the past 10 years. Studies in blind people have shown the involvement of extrastriate and/or striate areas in various tasks using tactile stimuli (Sadato et al., 1996, 1998, 2002; Röder et al., 1996; Büchel et al., 1998b; Burton et al., 2002a, 2004; Amedi et al., 2003;), or auditory stimuli (Alho et al., 1993; Kujala et al., 1995; Röder et al., 1996; Liotti et al., 1998; Leclerc et al., 2000; Weeks et al., 2000; Gougoux et al., 2005), as well as in language tasks (Röder et al., 2000, 2002; Burton et al., 2002b, 2003; Amedi et al., 2003), memory tasks (Röder et al., 2001; Röder and Rösler, 2003; Amedi et al., 2003; Raz et al., 2005) and mental imagery (De Volder et al., 2001; Vanlierde et al., 2003; Lambert et al., 2004). Virtual lesions of the occipital cortex with rTMS (Cohen et al., 1997; Amedi et al., 2004) as well as the study of a neuropsychological case of occipital stroke (Hamilton et al., 2000) have demonstrated further the functional nature of the occipital activations observed in early blind people.

Questions remain about the potential organization of the visual cortex in blind people. Does the occipital cortex process different stimuli in a global way or does it present some functional modularity? Is this potential organization similar to that in sighted subjects? As an attempt to gain further insight into that question, the present study aimed to investigate the neural substrates of motion processing. Motion processing was chosen because motion perception may be mediated through different sensory modalities and because its neural substrates in vision modality are well known (e.g., Watson et al., 1993; Büchel et al., 1998a; Sunaert et al., 2000; Kleinschmidt et al., 2002). The specific aim in the present study was to test whether non-visual processing of motion stimuli in blind people can recruit the visual motion areas described in sighted subjects. Auditory motion processing is a relevant candidate to answer this question since this process provides crucial information for mobility and is used in everyday life by blind people.

In a previous study, we investigated the neural bases of auditory motion processing in sighted subjects (Poirier et al., 2005) and showed the recruitment of the classical auditory motion areas and of some visual motion areas, i.e., V5 and V3/V3A. In the present study, we hypothesized that the same auditory and visual motion brain areas should be activated in blind subjects but, due to cross-modal plasticity, to a larger extent than in sighted subjects.

Material and methods

Subjects

Six early blind volunteers (4 males, mean age: 34.8, SD: 17.4) participated in the experiment (Table 1). They were affected by complete blindness (absence of light perception) as the result of bilateral ocular or optic nerve lesions from birth or before the first 2 years after birth. All subjects were right-handed, healthy, without auditory deficit, without recorded history of neurological problems and well integrated socially. Age-matched sighted volunteers, involved in the previous study (Poirier et al., 2005), were considered as controls. All subjects gave their written consent to participate to the experiment. This experiment was approved by the Ethics Committee of the School of Medicine and the University Hospital of the Université catholique de Louvain (Belgium) as well as by the Ethical Committee for the Protection of People taking part in Biomedical Research of Alsace (France).

Image acquisition

The fMRI data were obtained in a 2 T MRI system (Bruker, Karlsruhe, Germany) with BOLD contrast echo planar imaging (flip angle 90°, TE = 50.3 ms, TR = 4.8 s). Thirty-two continuous slices covering the whole brain were acquired. Voxel size was 4 × 4 × 4 mm. Anatomical images required for the localization of functional responses were obtained using a RARE T_2-weighted sequence (128 × 128, 80 slices, TE = 73.8 ms, TR = 1.5 s) and a spoiled grass technique (T1-weighted images, TR = 25 ms, TE = 6 ms, flip angle 25°, slice thickness 1.5 mm) in the bicommissural (AC–PC) orientation.

Stimuli and experimental design

The methodology has been described previously (Poirier et al., 2005). Briefly, sounds were delivered by an auditory stimulation system (E.A.R.TONE 3A Insert Earphone, Aero Company Auditory Systems, Indianapolis) normally used for clinical audition measurements. The system was comprised of transducers and dedicated calibrated plastic conducts, which were inserted in the subjects' ears. Headphones were added for further isolation.

Stimuli were created using *Labview* software (National Instruments). They consisted of trains of three identical pure-tone pulses and trains of three identical complex-sound pulses (duration of each pulse 1 s; inter-pulse interval 0.5 s; duration of each train 4 s; inter-train interval 1 s). We used eight different frequencies comprised between 872 and 1016 Hz for pure tones. Eight different combinations of frequencies were used to create eight complex sounds. Each complex sound was comprised of six different

Table 1
Characteristics of blind volunteers

Gender	Age	Onset of blindness	Diagnosis	Handedness
M	18	Congenitally	Premature birth	R
M	26	Congenitally	Premature birth	R
F	30	6–18 months	Retinoblastoma	R
M	30	Congenitally	Premature birth	R
F	37	Congenitally	Premature birth	R
M	68	18 months	Accident (*)	R

Note. M, male, F, female, (*) no additional details available.

superimposed frequencies between 308 and 2030 Hz, all at the same amplitude. These artificial sounds did not evoke any memories in the subjects and were not susceptible to inducing mental imagery. In addition, according to pre-tests, these frequencies allowed for optimal transmission through the transducers and for optimal separation between sound stimuli and the disturbing scanner noise.

Half of the stimuli were static and half were virtually animated with a transverse movement. Motion was simulated by dynamically changing the interaural level difference (ILD). The total level change was 16 dB in 1 s (starting 8 dB higher in one ear and ending 8 dB higher in the other ear). For the static condition, a fixed ILD was randomly selected on each stimulus presentation from the set −8, −6, −4, −2, 2, 4 and 8 dB (negative and positive signs denote higher intensity at left and right ears, respectively). This manipulation induced the sensation that static sounds were emitted at eight different spatial locations. Finally, the global intensity of stimuli was adapted to the audition of each subject and was about 70 dB.

The experimental protocol was divided into 40 blocks (each lasting 24 s.), which were distributed over two sessions. Two active conditions (100 brain volumes per condition) were recorded with a rest period in between. The static sound condition contained ∼10% pure tones and ∼90% complex sounds, both static, in 8 different virtual spatial locations. The moving sound condition contained ∼10% pure tones and ∼90% complex sounds, both animated with a transverse movement from left to right or from right to left. Using two types of sounds allowed the addition of a sound nature discrimination task in both conditions. This forced variety in the subjects' answers within a block, thus helping sustain their attention. As the auditory cortex, (with the exception of the primary area) responds more strongly to complex sounds rather than to pure tones (Wessinger et al., 2001), we mainly used complex sounds.

After having heard a stimulus, subjects were requested to determine its nature (i.e., "is it a pure tone or a complex sound?") and to detect whether any movement was present. If a movement was detected, subjects were also asked to determine its direction (i.e., from right to left or vice versa). Subjects gave their answers by pressing switches held in each hand. When the stimulus was identified as a static pure tone or as a pure tone moving towards the right, subjects had to press the right switch. When the stimulus was identified as a static complex sound or as a complex sound moving towards the left, subjects had to press the left switch. In all other cases (i.e., pure tone moving towards the left or complex sound moving towards the right), subjects had to press both switches simultaneously. All subjects underwent a sustained training period (2 × 30 min) to learn this answering code before participating in the study.

In order to minimize the memory load of the task, each ON block was preceded by repeating the instructions during the OFF blocks. The order of the different conditions was pseudo-randomized across subjects and for each early blind subject, the conditions were presented in an order identical to that of the matched control subject.

Image analysis

Pre-processing and statistical analyses of fMRI data were carried out using SPM99 (http://www.fil.ion.ucl.ac.uk/spm). For each subject, all functional volumes were motion-corrected using SINC interpolation and spatially normalized in the referential space defined by the atlas of Talairach and Tournoux (1988) and the MRI

template supplied by the Montreal Neurological Institute (MNI) to allow group analysis (voxel size: 2 × 2 × 2 mm). Images were further spatially smoothed with a 6-mm wide Gaussian kernel.

Both active conditions, as well as periods of verbal instructions, were fitted with a box-car function convolved with the hemodynamic response function. A temporal derivative was added for active conditions. Verbal instructions and the six parameters of head movements were declared as regressors of no interest. Low-frequency temporal drifts were removed by applying a 115-s high-pass filter.

A fixed-effect ROI analysis of the contrast [Motion vs. Static] was performed. The ROI were defined on the basis of independent functional data provided by the auditory and the visual motion literature in sighted subjects. We delimited each ROI using the most extreme coordinates from the literature: this resulted in the smallest ROI that still included all described coordinates from the reviewed literature. The ROI names must be considered with caution. For instance, the V1/V2 ROI does not correspond to the whole V1/V2 region but only to the part that was previously demonstrated to be specifically activated by visual motion in sighted subjects (e.g., Watson et al., 1993; Paradis et al., 2000). ROI centre coordinates, ROI sizes and references used to define the ROI are listed in Table 2. To test the hypothesis of a functional modularity in the occipital cortex of blind subjects, we also performed an analysis of the [Motion vs. Static] contrast restricted to the whole occipital cortex. To this end, we used a box shaped ROI defined on anatomical criteria (see Table 2), including Brodmann areas 17, 18 and 19 in a complete way as well as some parts of surrounding brain areas.

Comparison between early blind (EB) subjects and sighted controls (SC) was assessed in each ROI by the two following contrasts: [Motion vs. Static]$_{EB}$ − [Motion vs. Static]$_{SC}$ inclusively masked by [Motion vs. Static]$_{EB}$ and the reverse contrast [Motion vs. Static]$_{SC}$ − [Motion vs. Static]$_{EB}$ inclusively masked by [Motion vs. Static]$_{SC}$.

A threshold of $P < 0.01$ corrected for multiple comparisons inside each ROI at the voxel level and at the cluster level was applied. Only clusters with an extent greater than 20 voxels were considered.

A last analysis was carried out to disentangle brain areas activated only by motion processing from those activated in both conditions but more so by motion processing than by static sound processing. For this purpose, the contrasts [Static vs. Rest] and [Motion vs. Rest] were computed in the regions found to be specifically recruited by auditory motion processing, i.e., the activated brain regions in the previous ROI analysis of the [Motion vs. Static] contrast. This analysis was performed using the Marsbar toolbox (Brett et al., 2002).

Results

Behavioral performances

Behavioral results obtained during the fMRI acquisition revealed a highly satisfying level of performance for all blind subjects but one. This one subject recognized only 70% of the

Table 2
Description of the ROI in the group analysis

Regions of interest (ROI)	Coordinates of the ROI centre	ROI size (in mm)	Literature references
From auditory motion literature			
1. Dorsal premotor cortex	+/−46, 4, 50	24 × 8 × 16	(Griffiths et al., 1998, 2000)
2. Ventral premotor cortex	+/−50, 4, 30	36 × 16 × 16	(Griffiths et al., 1998, 2000; Bremmer et al., 2001; Griffiths and Green, 1999; Lewis, 2000; Warren et al., 2002)
3. Inferior parietal lobule	+/−52, −36, 38	20 × 16 × 16	(Griffiths et al., 1998, 2000; Bremmer et al., 2001; Lewis, 2000)
4. Planum temporale	+/−52, −28, 10	24 × 16 × 12	(Warren et al., 2002; Hart et al., 2004; Pavani et al., 2002)
From visual motion literature			
5. V5	+44, −64, 0	20 × 24 × 12	(Berman and Colby, 2002; Braddick et al., 2001; Büchel et al., 1998a; Culham et al., 1998; Dumoulin et al., 2000; Ffytche et al., 1995; Goebel et al., 1998; Hagen et al., 2002; Hampson et al., 2004; Kleinschmidt et al., 2002; Lewis et al., 2000; McKeefry et al., 1997; Muckli et al., 2002; Orban et al., 2003; Oreja-Guevara et al., 2004; Paradis et al., 2000; Sunaert et al., 2000; Tootell et al., 1995; Watson et al., 1993)
	−44, −68, 2	16 × 18 × 8	
6. V3/V3A	+/−26, −84, 20	32 × 16 × 36	(Braddick et al., 2001; Büchel et al., 1998a; Goebel et al., 1998; McKeefry et al., 1997; Muckli et al., 2002; Orban et al., 2003; Sunaert et al., 2000)
7. V1/V2	+/−14, −90, −2	28 × 20 × 16	(Goebel et al., 1998; McKeefry et al., 1997; Muckli et al., 2002; Orban et al., 2003; Paradis et al., 2000; Watson et al., 1993)
From anatomical criteria			
Whole occipital cortex	0, −74, 10	124 × 64 × 68	(Talairach and Tournoux, 1988)

Table 3
Activation patterns related to Motion auditory processing, as compared to Static sound processing in early blind subjects and blindfolded sighted controls (group analysis of 2 × 5 subjects)

ROI		Early blind subjects						Sighted controls				
		Coordinates			Z score	P value		Coordinates			Z score	P value
		x	y	z				x	y	z		
1. Dorsal premotor cortex	R	36	0	58	4.64	0.001	~	34	0	50	6.88	<0.001
	L	−50	2	42	4.99	<0.001	~	–	–	–	–	–
2. Ventral premotor cortex	R	52	10	28	5.04	<0.001	~	60	10	34	5.23	<0.001
	L	−50	4	30	6.31	<0.001	>	−56	8	26	6.70	<0.001
3. Inferior parietal lobule	R	–	–	–			~	42	−42	38	6.67	<0.001
	L	−44	−30	44	5.51	<0.001	~	−50	−30	44	5.97	<0.001
4. Planum temporale	R	–	–	–	–	–		–	–	–	–	–
	L	–	–	–	–	–		–	–	–	–	–
5. V5	R	44	−72	−2	4.51	0.003	~	48	−56	6	5.41	<0.001
	L	–	–	–	–	–		–	–	–	–	–
6. V3/V3A	R	24	−88	10	5.27	<0.001	>	–	–	–	–	–
	L	−14	−84	38	6.44	<0.001	>	−26	−80	34	4.50	0.007
7. V1/V2	R	2	−82	−8	5.05	<0.001	>	–	–	–	–	–
	L	−24	−88	−8	6.47	<0.001	>	–	–	–	–	–

Note. L: left; R: right. >: statistically more activated in blind subjects than in sighted controls; ~: no statistical difference between both groups.

stimuli whereas the five remaining subjects recognized 96.5% (SD: 2.9) of them. This subject was thus excluded from the subsequent analyses. The group of five blind subjects recognized 98.4% (SD: 1.8) of static stimuli and 93.9% (SD: 6.5) of moving stimuli. There was no significant difference in the percentage of correct responses between moving and static stimuli recognition (t test for paired samples: $Z = −1.5$, $P = 0.21$). Performances of blind subjects were not significantly different from those of the five matched sighted controls (t tests for unpaired samples: static stimuli: $t = 0.21$, $P = 0.84$; moving stimuli: $t = −1.38$, $P = 0.21$).

ROI analysis of [Motion vs. Static] contrast

The ROI analysis of the [Motion vs. Static] contrast in the five early blind subjects showed significant activation of the bilateral dorsal and ventral premotor cortex, the left inferior parietal lobule, the right V5 area, the bilateral V3/V3A area and the bilateral V1/V2 area (Table 3, Fig. 1). This activation pattern was close to the one observed in sighted controls. In left ventral premotor cortex, bilateral V3/V3A and bilateral V1/V2, the activation was significantly stronger in early blind subjects than in sighted

controls. In all other ROI, we found no significant difference between both groups.

The analysis of the [Motion vs. Static] contrast restricted to the whole occipital cortex showed that bilateral V1/V2 and left V3/V3A foci were the foci with the highest Z scores.

ROI analysis of [Static vs. Rest] and [Motion vs. Rest] contrasts

The ROI analysis of [Static vs. Rest] and [Motion vs. Rest] contrasts showed that the two visual motion areas (V5, V3/V3A) as well as the V1/V2 brain area were significantly activated by moving sound processing but also, to a lesser extent, by static sound processing (Table 4).

Discussion

Using an ROI analysis based on independent functional criteria, we observed that the brain areas that are known as auditory or visually motion-sensitive in sighted subjects were recruited by auditory motion processing in early blind subjects. More precisely, auditory motion processing recruited three of the four predefined
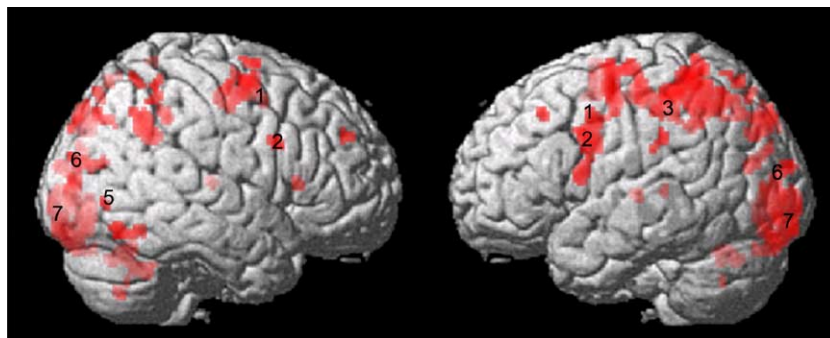

Fig. 1. Surface view of the activated brain network in the [Motion vs. Static] contrast in blind subjects group. The activation pattern is at a threshold of $P < 0.0001$ not corrected for multiple comparisons for display purposes. Numbers indicate the ROI in which significantly activated clusters were found at the threshold used in statistical analyses ($P < 0.01$ corrected for multiple comparisons). 1: dorsal premotor cortex; 2: ventral premotor cortex; 3: inferior parietal lobule; 4: planum temporale (not significantly activated, thus not indicated); 5: area V5; 6: area V3/V3A; 7: area V1/V2.

Table 4

Statistic values of [Static vs. Rest] and [Motion vs. Rest] contrasts in blind subjects, in an analysis restricted to the visual motion areas found recruited in the [Motion vs. Static] contrast

	Static vs. Rest		Motion vs. Rest	
	t score	P value	t score	P value
R V5	4.2	<0.001	>8	<0.001
R V3/V3A	>8	<0.001	>8	<0.001
L V3/V3A	>8	<0.001	>8	<0.001
R V1/V2	6.5	<0.001	>8	<0.001
L V1/V2	6.5	<0.001	>8	<0.001

Note. L: left; R: right.

auditory motion areas, the two predefined visual motion areas as well as the V1/V2 brain area in early blind subjects. This brain activated network is globally similar to the one previously observed in sighted subjects (Poirier et al., 2005), with the exception of a V1/V2 activation, which was additionally observed in blind subjects only.

The present study brings additional evidence of cross-modal plasticity in blind subjects. This kind of compensatory plasticity, in which occipital areas are recruited by non-visual stimuli, has been described in blind humans (e.g., Röder et al., 1996; Sadato et al., 1996; Büchel et al., 1998b; Weeks et al., 2000) as well as in animals visually deprived from birth, in whom visual brain areas are taken over by auditory or somatosensory inputs (e.g., Rauschecker and Korte, 1993; Rauschecker, 1995).

An activation focus in the V5 ROI was found in both groups of subjects. Despite the absence of significant differences in intensity and/or location of this focus between both groups, the voxel with the highest Z score was found to be more posterior in blind subjects (44, −72, −2) than in sighted (48, −56, 6). Due to the limited number of subjects involved in the present study, this difference could be a consequence of the high inter-individual variability in V5 location frequently observed in visual motion literature (e.g., Watson et al., 1993; Ffytche et al., 1995; Hagen et al., 2002). However, interestingly, tactile motion processing was recently found to induce the recruitment of the V5 area in sighted and blind subjects, but, as in our study, the voxel with the highest Z score in blind subjects was found to be more posterior than this in sighted controls (Ricciardi et al., 2005). The variability in V5 location between both groups could thus not be due to subject sample alone. Additional experiments are required to elucidate this point.

In the present study, visual motion areas were recruited by auditory motion processing in blind subjects. Since the ROI approach is based on a priori hypotheses, this method does not allow activation foci to be shown outside of the predetermined brain areas. For this reason, we performed an additional ROI analysis restricted to the whole occipital cortex to determine if the activation of the visual motion areas corresponded to the main occipital foci. This analysis showed that V1/V2 and V3/V3A were the foci with the highest Z scores in the occipital lobe. Weeks et al. (2000) also showed that an auditory localization task performed by blind people mainly induced the recruitment of a visual area normally devoted to visual localization. This convergence of results suggests that blind subjects' occipital areas could have a functional role similar to those of sighted subjects. This role would
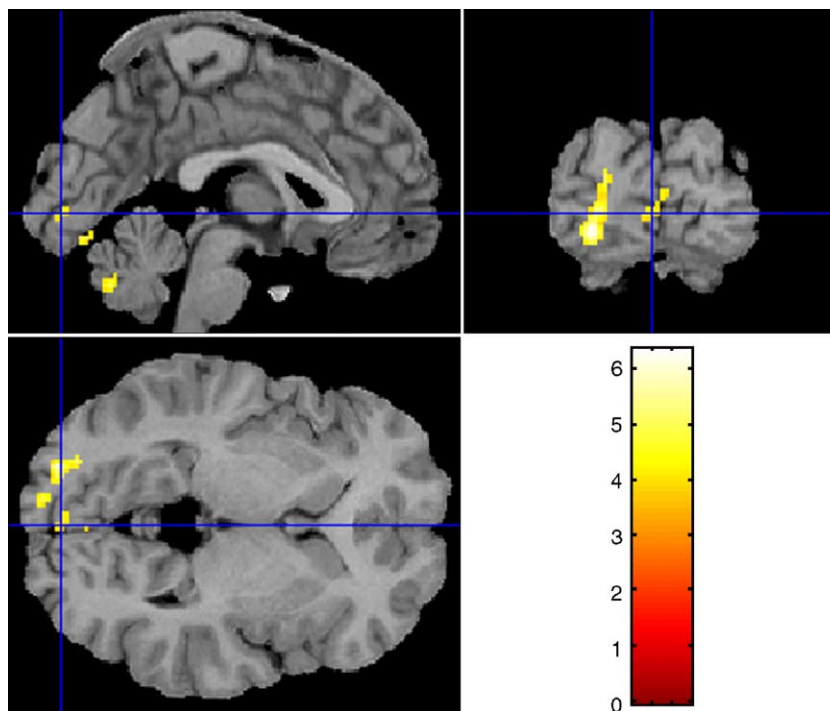

Fig. 2. Brain activation foci that were significantly more activated in early blind subjects than in sighted controls in the [Motion vs. Static] contrast. The statistical parametric map for this comparison (group analysis) is superimposed on the sagittal, coronal, and transverse sections of an individual normalized brain MRI (subject #1). Only positive differences exceeding a threshold of $P < 0.0001$ (uncorrected) are shown according to the color scale that codes the T values. The lines intersect at coordinates ($x, y, z = 0, -90, 0$) on a voxel in the V1 brain area with a Z value of 4.40 ($P = 0.006$, corrected for multiple comparisons in the V1/V2 ROI). The V1/V2 brain area was more activated in early blind subjects than in sighted controls during motion perception. Coordinates refer to the referential space defined by the atlas of Talairach and Tournoux (1988) and the MNI template (see Materials and methods).

be independent of the modality used to transmit the information. The recruitment of visual motion areas also suggests that the occipital cortex of blind people presents a modular functional organization, as in sighted subjects.

Auditory motion processing induced the recruitment of a similar network in early blind and blindfolded sighted subjects. Although we cannot completely exclude the possibility that a similar set of brain areas may be recruited by different anatomical connections, it is worth noting that V5 and V3/V3A were already activated in sighted subjects to an equal or a lesser extent as compared to blind subjects. This suggests that activations of visual brain areas in blind subjects are mediated by anatomical connections that are still present in sighted subjects but more developed or more recruited in blind subjects through brain plasticity.

V1/V2 was recruited in blind subjects but not in blindfolded sighted subjects. This activated region included some parts of V1 and some parts of V2 (Table 3, Fig. 2). This brain region was already activated by static stimuli but more strongly activated by auditory motion processing. Previous studies have shown that V1 may be recruited by tactile perceptual tasks (Burton et al., 2004), Braille reading tasks, (Amedi et al., 2003; Burton et al., 2002a, 2004; Sadato et al., 1996, 2002), auditory perceptual tasks (Gougoux et al., 2005), language tasks (Amedi et al., 2003; Burton et al., 2002b, 2003), memory tasks (Amedi et al., 2003; Raz et al., 2005) and mental imagery tasks (Lambert et al., 2004). The present results extend the role of V1 to other perceptual auditory tasks: the identification of sound nature (Static condition) and the discrimination of moving sounds (Motion condition). The higher recruitment of V1/V2 during the Motion condition as compared to the Static condition indicates that early visual activation, in addition to extrastriate visual cortex, can, in blind people, be modulated by the task. This brings additional evidence supporting the functionality of the occipital activation recurrently observed in blind subjects during non-visual tasks.

To conclude, it has been shown that brain areas devoted to a specific visual process (i.e., visual motion processing) can be recruited by the corresponding process in the auditory modality in blind people. This indicates that the occipital cortex of blind people could be organized in a modular fashion, as in sighted people. We suggest that the underlying neural mechanism could consist of the recruitment of direct or indirect anatomical connections between the auditory and visual cortices. These connections would be present but rarely recruited in sighted subjects, and could be more developed in the case of visual deprivation. TMS experiments could be useful in order to further define the precise functional role of visual brain areas in auditory motion processing in sighted as well as in blind subjects.

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