

Research Report

Specific activation of the V5 brain area by auditory motion processing: An fMRI study

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Abstract

Previous neuroimaging studies devoted to auditory motion processing have shown the involvement of a cerebral network encompassing the temporoparietal and premotor areas. Most of these studies were based on a comparison between moving stimuli and static stimuli placed at a single location. However, moving stimuli vary in spatial location, and therefore motion detection can include both spatial localisation and motion processing. In this study, we used fMRI to compare neural processing of moving sounds and static sounds in various spatial locations in blindfolded sighted 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 movement was present, subjects had to identify its direction. This comparison of how moving and static stimuli are processed showed the involvement of the parietal lobules, the dorsal and ventral premotor cortex and the planum temporale during auditory motion processing. It also showed the specific recruitment of V5, the visual motion area. These results suggest that the previously proposed network of auditory motion processing is distinct from the network of auditory localisation. In addition, they suggest that the occipital cortex can process non-visual stimuli and that V5 is not restricted to visual processing.

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1. Introduction

Compared to research on visual motion perception, few imaging studies have been devoted to auditory motion perception. Using different stimuli, these studies have shown the involvement of a large cerebral network that includes the parietal lobules, the dorsal and ventral premotor cortex [11,23,25,26,40,63], and in some cases the additional involvement of the planum temporale [6,11,31,40,52,64]. In most of these studies [6,11,23,25,26,40], moving stimuli

were contrasted to static stimuli virtually placed at a single spatial location. However, moving stimuli vary in spatial location and could therefore induce spatial localisation processes. In a recent study, Smith et al. [58] found that the same brain areas could be activated by both auditory motion detection and spatial localisation of sounds, leading these authors to argue against the existence of specialised auditory motion areas. To further disentangle between motion perception and spatial localisation, our study contrasted moving stimuli with static stimuli placed at different virtual spatial locations.

V5 is usually known as a visual motion area [1,8,10,12,16,19,20,22,28,30,35,40,45,46,48–50,59,62,65]. However, Hagen et al. [28] and Blake et al. [9] showed that V5 could be activated by a moving tactile stimulus. In

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their extensive study using PET and fMRI, Warren et al. [64] reported a tiny activation near V5 during auditory motion processing. Berman and Colby [8] also showed that auditory attention to speech stimuli could modulate the V5 activation observed during visual motion processing. These striking results point to the existence of cross-modal interactions between V5 and the other senses and raise the question of possible V5 activation by an auditory stimulus.

The aim of the present study was thus to determine whether some brain areas are selective to auditory motion processing and whether this auditory process can recruit the visual motion area V5.

2. Materials and methods

2.1. Subjects

Six sighted volunteers (4 males, mean age: 32.3, SD: 14.9) participated in the experiment. All but one (male) subject were right-handed. All subjects were healthy, without auditory deficit and without recorded history of neurological problems. They 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).

2.2. Stimulation device

Sounds were delivered by an auditory stimulation system (E.A.R.TONE 3A Insert Earphone, Aero Company Auditory Systems, Indianapolis) normally used for clinical auditory measurements. The system was comprised of transducers and dedicated calibrated plastic conducts. The plastic conducts were inserted into the subjects' ears. Headphones were added for further isolation purposes. The system was assessed in the fMRI environment and found to be functional; response curves in the magnet were found to be similar to nominal curves.

2.3. Stimuli

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 (pulse duration 1 s; inter-pulse interval 0.5 s; duration of each train 4 s; inter-train interval 1 s). We used eight different frequencies for the pure tones without frequency modulation: 872, 891, 910, 931, 952, 973, 994 and 1016 Hz. Eight different combinations of frequencies were used to create eight complex sounds (Table 1). Each complex sound was comprised of six different super-

Table 1
Spectral composition of the eight complex sounds

Stimuli	Spectral composition (in Hz)
CS ₁	344, 508, 910, 1261, 1821
CS ₂	322, 329, 446, 658, 931, 1016
CS ₃	315, 457, 952, 1317, 1405
CS ₄	455, 466, 687, 891, 1744, 1946
CS ₅	436, 476, 486, 872, 1288, 1435
CS ₆	359, 617, 702, 979, 1234, 1987
CS ₇	315, 673, 718, 994, 1345, 1862
CS ₈	308, 336, 630, 644, 1374, 1782

Note. CS = complex sound.

imposed frequencies between 308 and 2032 Hz, all at the same amplitude, and without frequency modulation. The frequencies were chosen to achieve both optimal transmissibility through the transducers and 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). Auditory stimuli were linearly ramped such that the waveform for each ear received opposite slopes (e.g., left ear level was ramped down while right ear level was ramped up, simulating motion from left to right). 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). These stimuli produce a strong percept of intracranial motion along the interaural axis. The velocity of 16 dB/s was chosen in order to allow a subject recognition level of at least 80% of the moving stimuli in the MRI environment and to avoid a ceiling effect. For the static condition, a fixed ILD was randomly selected on each stimulus presentation from the set $-8, -6, -4, -2, 2, 4, 6$ and 8 dB (negative and positive signs denote higher intensity at left and right ears, respectively). This manipulation allowed to induce the sensation that sounds came from eight different spatial locations. Finally, the global intensity of stimuli was adapted to the audition of each subject and was about 70 dB SPL.

2.4. Experimental design

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:

Static sound condition: ~10% pure tones and ~90% complex sounds, both static, in 8 different virtual spatial locations.

Moving sound condition: ~10% pure tones and ~90% complex sounds, both animated with a transverse movement from left to right or from right to left.

We used two types of sounds (pure tones and complex sounds) in order to maintain constant subjects' attention

within a block. To this end, answers needed to vary during the block while the active task kept constant. Using two types of sounds allowed to add a sound nature discrimination task in both conditions and thus to make vary subjects' answers within each block. As the auditory cortex (with the exception of the primary area) responds more strongly to complex sounds rather than to pure tones [66], we mainly used complex sounds.

After hearing 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 ear or the reverse). Subjects' answers were provided 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. Stimuli were trains of three pure-tone or complex-sound pulses. Subjects were requested to freely answer as soon as they recognised the stimulus. When subjects answered before the end of the stimulus, the following stimulus was presented. This was designed to promote constant and similar attention load within and across the different conditions. All subjects underwent a sustained training period (2×30 min) to learn this answering code before taking part in the study.

Each ON block was preceded by the recall of the instructions during the OFF blocks in order to minimise the memory load of the task. The order of the different conditions was pseudo-randomised across subjects.

Behavioural data were computed to determine on the one hand the number of moving stimuli and the number of static stimuli heard by each subject and on the other hand the number of moving stimuli and the number of static stimuli that were correctly identified by each subject. A static stimulus was considered as recognised when its nature and the absence of movement were recognised. A moving stimulus was considered as recognised when its nature and the presence of movement as well as the direction of the movement were recognised.

2.5. Image acquisition and analysis

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 $4 \times 4 \times 4$ mm. Anatomical images required for the localisation of functional responses were obtained using a RARE T_2 -weighted sequence using the

following parameters: 128×128 (80 slices, TE = 73.8 ms, TR = 1.5 s).

Pre-processing and statistical analysis 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 normalised in the Talairach stereotaxic system of coordinates [60]. Images were then spatially smoothed with a 6-mm width Gaussian kernel. The voxel size of the normalised volumes was set to $2 \times 2 \times 2$ mm.

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.

Fixed effect analyses were performed at the group and individual level. V5 and V3/V3A brain areas were identified according functional criteria from literature group analyses [1,8,10,12,16,19,20,22,28,30,35,40,45,46,48–50,59,62,65]. V5 location varies importantly between subjects. In addition to functional criteria coming from literature individual analyses [1,20,28,65], we thus used the anatomical criteria described by Dumoulin et al. [19] to identify V5 in each subject. Accordingly, individual activations inside the V5 region had to be located in the posterior part of the inferior temporal sulcus (ITS), the ascending limb of the ITS or the posterior continuation of the ITS in order to be identified as V5.

Voxels with a statistical significance of $P < 0.05$ corrected for multiple comparison using the false discovery rate method [21] were considered significantly activated. Only clusters with an extent superior to 30 voxels were considered.

2.6. Eye movement monitoring

During the entire fMRI experiment, subjects were transiently blindfolded with an opaque blindfold resting on their closed eyelids. The size of the 2-T MRI system coil (Bruker, Karlsruhe, Germany) did not allow the use of a system for monitoring eye movement. During the fMRI experiment, subjects were instructed to refrain moving their eyes. The experiment was further replicated with the same conditions in five additional subjects outside the magnet (subjects were blindfolded, in the supine position, and gradient noise recording was emitted). Three of these subjects were instructed to refrain from moving their eyes while the other two received no instruction on eye movement. Horizontal and vertical electro-oculograms (EOG) of these five subjects were recorded using silver disk electrodes (\varnothing 10 mm) and the Activtwo system (Biosemi, The Netherlands). To determine if some eye movements were correlated to stimuli, the EOG signal average was computed for each type of stimulus (eight static stimuli, each one in a different

spatial location; two moving stimuli, each one moving in a different direction) in a time window including one stimulus and the gap between this stimulus and the following stimulus.

3. Results

3.1. Behavioural performance

Behavioural results obtained during the fMRI acquisition revealed a highly satisfactory level of performance. Subjects recognised 98.3% (SD: 0.02) of static stimuli and 97.9% (SD: 0.02) of moving stimuli. There was no significant difference in the percentage of correct responses between moving and static stimulus recognition (*t* test for paired samples: $t = -0.4$, $P = 0.71$).

3.2. Eye movements

In the replication of the experiment outside the scanner, we observed no difference in eye movement patterns during rest, static and moving stimuli. The signal average for each type of stimulus revealed no correlation between eye movement and the onset of each type of stimulus in any subject. Moving and static stimuli induced

neither fixation nor pursuit eye movements. Only some fast involuntary eye movements were found during periods of rest, static and moving stimuli. These fast movements appeared randomly during the three types of periods.

3.3. Differential activation between moving and static sounds

The contrast [moving sounds – static sounds] showed significant activation in a large brain network involving the bilateral ventral (BA 6/9) and right dorsal premotor cortices (BA 6) and other frontal areas (BA 10, 45, 46, 47), the right postcentral gyrus (BA 7, 40), the bilateral superior and inferior parietal lobules (BA 7, 40), the insula as well as the right parietal operculum (BA 40) and the right planum temporale (BA 42) (Table 2). The right V5 and the bilateral V3/V3A areas were also found to be activated (Figs. 1 and 2).

3.4. Individual analysis of V5 coordinates in [moving sounds – static sounds] contrast

The individual analysis showed that V5 was recruited by all subjects but one. Results showed some inter-individual and inter-hemispheric variability (Table 3). V5 was bilat-

Table 2
Group analysis: activation differences between motion and static auditory processing

Location		Coordinates			Z score	P corrected	Volume (voxels)
		x	y	z			
Precentral gyrus	LBA6	-28	-10	68	>8	<0.001	8599
Inferior parietal lobule	LBA40	-34	-42	38	>8	<0.001	a
Superior parietal lobule	LBA40	-34	-52	50	>8	<0.001	a
Inferior frontal gyrus (PMv)	LBA9	-56	8	26	7.38	<0.001	a
Cuneus (V3/V3A)	LBA19	-26	-84	24	3.73	0.002	a
Middle frontal gyrus	RBA6	28	-6	48	>8	<0.001	1549
Middle frontal gyrus (PMd)	RBA6	34	0	50	7.77	<0.001	a
Inferior parietal lobule	RBA40	40	-42	38	7.40	<0.001	1868
Superior parietal lobule	RBA7	38	-50	64	4.82	<0.001	a
Middle frontal gyrus	LBA46	-48	28	26	6.97	<0.001	233
Middle temporal gyrus (V5)	RBA39	48	-56	6	5.87	<0.001	75
Inferior frontal gyrus	RBA45	58	10	20	5.68	<0.001	97
Insula	LBA13	-40	-14	14	5.15	<0.001	57
Middle frontal gyrus	RBA10	30	50	20	4.84	<0.001	98
Postcentral gyrus	RBA7	12	-54	72	4.83	<0.001	145
Inferior frontal gyrus	RBA47	34	28	-2	4.75	<0.001	111
Middle occipital gyrus (V3/V3A)	RBA19	28	-80	18	4.40	<0.001	110
Inferior frontal gyrus (PMv)	RBA9	40	6	28	4.39	<0.001	54
Postcentral gyrus	RBA40	60	-28	20	4.37	<0.001	85
Superior temporal gyrus (PT)	RBA42	64	-24	12	3.69	0.003	a
Cerebellum	R	20	-48	-44	4.32	<0.001	42
Cerebellum	R	12	-60	-26	4.32	<0.001	93
Middle frontal gyrus	LBA10	-38	52	10	4.28	<0.001	84
Thalamus	L	-12	-18	4	4.16	0.001	31
Middle frontal gyrus	RBA9	48	34	28	4.01	0.001	190
Insula	LBA13	-34	20	0	3.90	0.001	57
Middle frontal gyrus	LBA46	-44	44	6	3.50	0.005	35

Note. BA = Brodmann area, L = left; R = right; PMv = ventral premotor cortex; PMd = dorsal premotor cortex; PT = planum temporale; a = belonging to the same voxels cluster. *P* values are at the voxel level.

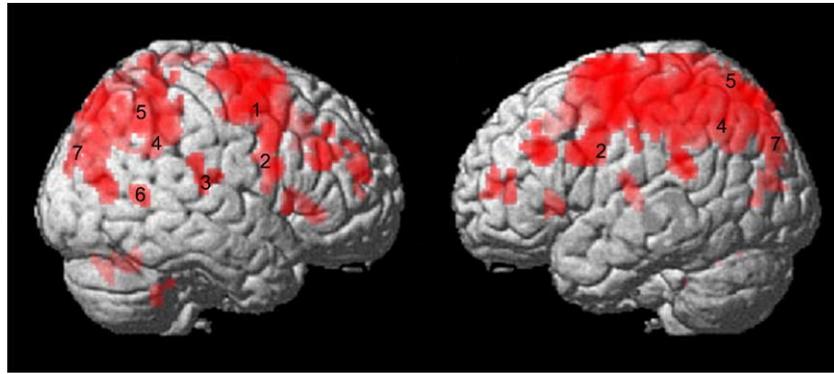


Fig. 1. Surface view of the activated brain network in the contrast [moving sounds – static sounds] in group analysis, at a threshold of $P < 0.05$ corrected for multiple comparisons. 1: dorsal premotor cortex; 2: ventral premotor cortex; 3: planum temporale; 4: inferior parietal lobule; 5: superior parietal lobule; 6: V5; 7: V3/V3A.

erally activated in three subjects. It was activated only on the right side in one subject, and only on the left side in another subject.

4. Discussion

The present study showed the recruitment of a neural network specific to auditory motion processing that mainly involved the planum temporale, the inferior and superior parietal cortex and the dorsal and ventral premotor cortex in healthy humans. In addition, a specific involvement of V5 and V3/V3A, the visual motion areas, was demonstrated during auditory motion processing.

4.1. Influence of eye movements

In the present fMRI experiment, subjects were blindfolded and instructed to refrain from moving their eyes. However, there is no evidence that the subjects followed this instruction. As eye position has recently been shown to have a crucial influence on the processing of auditory spatial information in the occipital cortex [68], potential eye

movements were recorded in a replication of the experiment outside the scanner. We observed neither fixation movement or pursuit movements when subjects were instructed to refrain eye movement as well as when no specific instruction was provided. We only observed some involuntary fast movements appearing randomly during static and moving stimuli periods as well as during rest periods. It is reasonable to postulate that the pattern of eye movements during the fMRI experiment was similar to the one observed in the replication of the experiment outside the magnet. The cerebral activity linked to the potential random movements would thus be subtracted in the contrast [moving sounds – static sounds] and our results not influenced by these eye movements.

4.2. Specific activation of non-visual areas during auditory motion processing

In the present study, auditory motion perception specifically recruited the right planum temporale (BA 42) in accordance with previous studies of Baumgart et al. [6] and Warren et al. [64]. This brain area was recruited during static stimuli processing and further activated during

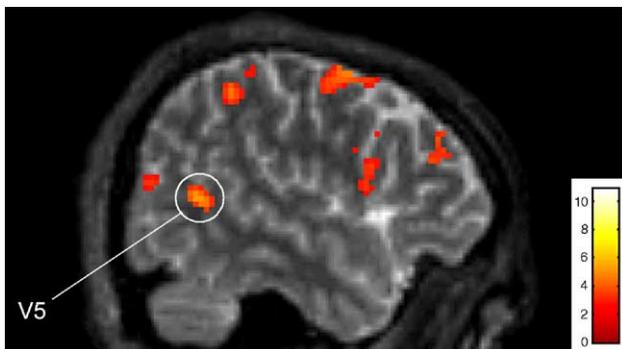


Fig. 2. Brain activation foci observed in moving sound processing, as contrasted to static sound processing. The statistical parametric map for this comparison (group analysis) is superimposed on the sagittal section of an individual normalised brain MRI, allowing the visualisation of the right V5 focus in the parietooccipital junction. Only voxels exceeding a threshold of $P < 0.05$ corrected for multiple comparisons are displayed.

Table 3

Individual analysis: V5 coordinates in the contrast [moving sounds – static sounds]

Subjects	Coordinates			Z score	P corrected	Volume (voxels)	
	x	y	z				
Subject 1	R	48	-54	6	6.79	<0.001	231
	L	-48	-58	14	>8	<0.001	799
Subject 2	R	44	-74	14	5.11	<0.001	185
	L	-54	-70	-2	4.63	<0.001	131
Subject 3	R	46	-58	8	5.64	<0.001	35
	L	-	-	-	-	-	-
Subject 4	R	-	-	-	-	-	-
	L	-46	-76	2	4.48	<0.001	85
Subject 5	R	-	-	-	-	-	-
	L	-	-	-	-	-	-
Subject 6	R	46	-70	12	4.43	0.001	1382
	L	-30	-78	2	4.96	<0.001	273

Note. L = left; R = right. P values are at the voxel level.

auditory motion processing. We also observed the involvement of the parietotemporal operculum, which, similarly to the results of Warren et al. [64], formed a contiguous cluster with the planum temporale. These results are in accordance with previous reports of planum temporale involvement in the analysis of spatial properties of auditory stimuli, in addition to its classical role in the processing of complex sounds (e.g., speech processing; see ref. [24] for a critical review).

Auditory motion perception involved dorsal and ventral premotor cortices. These activation foci included brain areas close to the frontal eye field. The same activation foci were previously observed during auditory motion processing [23,25,26,40,64], polymodal (visual, auditory and tactile) motion processing [11] and unimodal auditory spatial localisation tasks [14]. This activation of premotor areas is thought to be related to preparation for eye tracking movement in response to moving auditory stimuli [11,25].

Auditory motion perception also involved the posterior parietal cortex. Activation peaks were very close to those observed during auditory motion processing [23,26,40], polymodal motion processing [11] as well as unimodal localisation tasks in audition and in vision [14]. The role of the parietal cortex in auditory localisation was also demonstrated using rTMS [38]. Our result supports the idea that this region would be implied in unimodal and polymodal representation of space as well as in spatial attention [4,44].

In the present study, activation peaks during auditory motion processing were very close to those previously observed during auditory localisation tasks. In a recent study, Smith et al. [58] showed that the processing of static auditory stimuli presented at various virtual locations (and thus susceptible to activate brain regions dealing with auditory localisation) activated the same regions as the processing of moving sounds. In the present study, static stimuli perceived at different locations were also contrasted to moving stimuli. However, the contrast [moving sounds – static sounds] resulted in significant activation patterns interpreted as specific activation brain areas related to auditory motion processing. Methodological differences (high spatial resolution and/or enhanced statistical power in the present study) could at least partly explain this discrepancy. Our results sustain the hypothesis that auditory motion perception and auditory sound localisation share close but not identical networks [18].

Our results also suggest that a posterior temporo-parieto-frontal pathway is involved in sound movement processing. A dichotomy between a similar dorsolateral pathway dealing with sound localisation and a ventrolateral pathway involved in sound recognition was previously proposed, based on results from studies in monkeys [27,34,55,61] and in humans [2,15,42,63]. The auditory dorsolateral pathway could thus be implicated in spatial auditory processing, including auditory motion and auditory localisation processing.

4.3. V5 and V3/V3A activations

In the group analysis, we observed activations consistent with V5 [22,35,46,49,50,59] and V3/V3A [45,46,50] locations. These brain areas are known to be components of the visual motion network. The individual analysis further showed that V5 brain activation was present in at least five of the six subjects. Consistently with literature results, we observed inter-individual and inter-hemispheric variability: Watson et al.' [65] reported only 17 of 24 hemispheres presenting V5 activation with a Z score above 3.86, and Kleinschmidt et al. [35] and Tootell et al. [62] only observed V5 activation on the right side. The origin of this variability remains unknown.

In a previous study [22], visual imagery was shown to activate V5 and V3/V3A when subjects were requested to imagine, as intensively as possible, a moving stimulus they had seen a few seconds before. However, in another experiment in which visualisation of stimuli preceded the imagery condition for several minutes, V5 was not found to be activated [9]. In our present study, mental imagery was not requested. To induce any detectable activation with fMRI, subjects should have imagined the stimuli in most of the trials. However, the subjects themselves reported that they did not visually represent the stimuli. Finally, previous studies have shown that, when subjects are asked to imagine a visual rotation either with their eyes opened [17] or closed [54], horizontal pursuit and/or fixation eye movements are usually induced, and as stated before such types of movements do not seem to have occurred in our study.

The alternative hypothesis is that V5 and V3/V3A activations are related to auditory motion processing. On the one hand, from the behavioural point of view, several illusions link visual and auditory motion perception. For instance, a static auditory stimulus is perceived to be moving when it is associated with a moving visual stimulus, a perceptual effect called “visual capture” [43]. The perception of directionality of auditory moving stimuli is enhanced when visual cues are provided, even without motion information [37]. On the other hand, neuroimaging studies in deaf people have demonstrated that visual motion processing is affected by auditory deprivation [5,7,57]. In sighted and hearing subjects, visual motion stimuli activated association auditory cortex [10,32]. Auditory attention also modulated the brain activation related to visual motion processing in V5 [8]. In addition, Hagen et al. [28] and Blake et al. [9] showed that V5 could be recruited by a tactile stimulus. These results indicate that V5 and V3/V3A activations by auditory motion processing is not so striking.

Using the interaural level difference (ILD) as the only auditory spatial cue induces intracranial perception of moving sounds. The stimuli differ from the natural situation in a free sound field, where intensity varies in combination with time and spectral cues. We cannot exclude the possibility that subjects have projected stimuli into external

space even though the sounds were actually heard inside the head. However, static stimuli were also created by manipulating ILD. Thus, the potential cognitive process of coordinate transformation should have been subtracted in the contrast [moving sounds – static sounds]. Moreover, except for the Warren et al.'s study [64] in which a weak activation very close to our V5 activation was mentioned ($x = 46, y = -58, z = 4$), all previous studies about auditory motion processing [6,11,23,25,26,40] have tested intracranially perceived stimuli and occipital activations were never reported. The discrepancy between our study and previous ones more likely comes from the subjects' attention level. Our protocol was designed to control and strengthen the attention of the subjects in several ways. In particular, an additional task involving sound nature was included in both the static and moving conditions; moreover, subjects were requested to provide their answer by depressing a switch, which allowed the experimenter to control whether subjects performed the task correctly. In the previous studies, subjects were instructed to pay attention to the moving stimuli but no answer was requested. Increased attention load is known to induce enhancement of brain activations [29,33,67], especially in the V5 area [12,47]. Activation in occipital regions could thus have been present in previous experiments but too weak to be detectable. However, the addition of the sound nature task associated with a complex decision paradigm could have induced additional cognitive processes. According to the cognitive subtraction hypothesis, these processes, identical in both conditions, should have been excluded in the contrast [moving sounds – static sounds]. However, we cannot completely exclude the possibility that the complex aspect of the paradigm has influenced our results.

Several neuroimaging studies reported the implication of extra-striate areas in tactile [3,41,53] and auditory tasks [31,42,68]. In some of these studies, the authors concluded that the activation of the occipital areas they observed could hardly be attributed to visual imagery, due to the nature of the stimuli, and rather indicated that extra-striate areas could process stimuli of various modalities [3]. Moreover, a recent study in which influence of visual imagery can be largely excluded has evidenced some perturbation of sound lateralisation applying rTMS on extra-striate areas [39]. The results of the present study thus support the hypothesis of multimodal processing abilities in occipital areas.

5. Conclusion

The present study shows that the processing of non-visual stimuli in sighted subjects can activate extra-striate areas. Auditory motion processing seems to induce the recruitment of “visual” motion areas. The fact that occipital brain areas activated by auditory motion processing belong to the traditional visual motion network suggests the

functionality of occipital recruitment by auditory stimuli processing. The occipital cortex might not be strictly unimodal. In early blind people, auditory and tactile discrimination tasks are known to recruit occipital cortices (e.g., [13,36,56]). The results of the present study support a model in which reorganisation processes observed in blind people would be based on pre-existing neuronal connections between the auditory (or tactile) cortex and the occipital cortex [39,51].

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