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Decoding the direction of auditory motion in blind humans

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ABSTRACT

Accurate processing of nonvisual stimuli is fundamental to humans with visual impairments. In this population, moving sounds activate an occipito-temporal region thought to encompass the equivalent of monkey area MT+, but it remains unclear whether the signal carries information beyond the mere presence of motion. To address this important question, we tested whether the processing in this region retains functional properties that are critical for accurate motion processing and that are well established in the visual modality. Specifically, we focussed on the property of 'directional selectivity', because MT+ neurons in non-human primates fire preferentially to specific directions of visual motion. Recent neuroimaging studies have revealed similar properties in sighted humans by successfully decoding different directions of visual motion from fMRI activation patterns.

Here we used fMRI and multivariate pattern classification to demonstrate that the direction in which a sound is moving can be reliably decoded from dorsal occipito-temporal activation in the blind. We also show that classification performance is at chance (i) in a control region in posterior parietal cortex and (ii) when motion information is removed and subjects only hear a sequence of static sounds presented at the same start and end positions. These findings reveal that information about the direction of auditory motion is present in dorsal occipito-temporal responses of blind humans. As such, this area, which appears consistent with the hMT+ complex in the sighted, provides crucial information for the generation of a veridical percept of moving non-visual stimuli.

Introduction

For humans with visual impairments, independence and efficient interaction with the environment critically depends on accurate processing of nonvisual stimuli. For example, moving sounds produced by vehicles can provide essential and reliable information about street layout, approaching vehicles, and traffic cycles. To compensate for the lack of visual information, blind observers often show exceptional performance in other modalities, i.e. when localizing a sound source (Lessard et al., 1998; Röder et al., 1999). This enhanced performance has been linked to cross-modal plasticity, because many nonvisual tasks reliably activate occipital areas that are recruited for processing visual stimuli in the sighted but are deprived of this visual input in the blind (Theoret et al., 2004).

Given that non-visual motion processing is crucial to visually impaired travellers, it is important to understand how their brains process such cues. Two studies have directly addressed this issue: Poirier et al. (2006) compared moving and static auditory stimuli and found that the presence of motion induced stronger activation in a large network of regions, including an occipito-temporal region assumed to encompass the motion-sensitive hMT+ complex. Similar results have been reported for tactile motion (Ricciardi et al., 2007), suggesting that regions implicated in visual motion processing in the sighted are recruited for non-visual motion processing in the blind.

One important unresolved question is whether the motion related activation observed in blind humans plays a functional role in nonvisual motion processing or whether the activation merely reflects unspecific coactivation (Collignon et al., 2009). Specifically, in order to generate a veridical percept of a moving stimulus, the brain needs to extract crucial properties such as speed and direction. In the visual modality, MT+ neurons in non-human primates respond preferentially to specific directions and speeds of visual motion, thus conveying information about the characteristics of the stimulus (Born and Bradley, 2005). Neuroimaging studies have revealed similar functional properties in the human homologue (hMT+), as evidenced by different directions of linear and rotational optic flow being decoded from multivariate fMRI activation patterns in this area (Kamitani and Tong, 2006; Seymour et al., 2009). These findings indicate that neuronal populations in hMT+ have similar properties as their monkey counterparts.

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Here we used fMRI to determine the functional significance of auditory motion processing in dorsal occipito-temporal cortex of blind humans. Four blind participants underwent fMRI scanning while listening to blocks of leftward or rightward moving broadband noise sources that were realistically simulated using binaural recording techniques. Using multivariate pattern classification, we then tested whether the direction of motion could be decoded from ensemble responses in dorsal occipito-temporal cortex and in a posterior parietal control region.

Materials and methods

Subjects

The study involved four blind, male volunteers, aged 35–62 (mean duration of blindness: 44.3 years). The experiment was approved by the local ethics committee, and informed consent was obtained for all participants. The etiology of blindness was Retinopathy of Prematurity for two congenitally totally blind participants, Leber's Congenital Amaurosis and Retinitis Pigmentosa (onset age: 24 years, duration of blindness: 25 years) for the other two who had only minimal light perception. All subjects were free of auditory deficits and did not have any known neurological or psychiatric disorders. They understood the instructions without difficulties, and were not aware of the hypotheses at the time of testing.

Experimental stimuli and paradigm

In order to accurately simulate a naturalistic moving sound source under headphone playback, we employed binaural recording techniques (Møller, 1992) in which a real sound source was moved along a 0.9 m right-to-left straight-line path in front of a dummy head (KEMAR® Manikin Type 45BA with Type 40AP pressure-field microphones positioned at the entrance to the ear canal, G.R.A.S. Sound & Vibration A/S) within a double-walled audiometric test booth (Acoustic Systems). The path was parallel to the interaural axis and symmetric about the midline. The point of closest approach (at midline) was approximately 20 cm from the interaural axis. The sound source was a small full-range loudspeaker (Fostex model FF85K 3-inch driver mounted in a 0.7-l sealed enclosure) emitting a broadband noise signal (0.1–20 kHz, 3 s duration). The recordings were stored on a high-quality flash memory recorder (Model 702, Sound Devices, LLC) with 24-bit resolution at a sampling frequency of 48 kHz. Two different motion velocities were recorded: 0.9 m/s and 0.45 m/s. All recordings were 3 s in duration, with a beginning stationary period, a period of motion, and then a final stationary period. For the 0.9 m/s velocity, stationary, motion, and stationary periods were all 1 s in duration. For the 0.45 m/s velocity, the motion period was 2 s in duration, with the initial and final stationary periods being each 0.5 s in duration. Motion in the opposite direction (left-to-right) was simulated by reversing the recording channels. Overall, these recording methods allowed for accurate reproduction of the acoustic cues to auditory direction and motion that are present in natural environments, including: changes in overall sound level, changes in interaural level (ILD) and time delay (ITD), and changes in the directionally-dependent filtering of the external ears and head (Middlebrooks and Green, 1991). Note that relatively small changes to sound frequency were also present due to Doppler shift, although informal testing confirmed that these changes were inaudible for the inharmonic noise signals used in this study.

To verify that any results of the pattern classification analyses were not driven by the specific sequence of spatial positions (left followed by right for rightward moving sounds vs. right followed by left for leftward moving sounds), we also created static control stimuli by replacing the middle motion portions of the recordings with silence and thus preserving the beginning and ending static portions of the recordings. All recordings were equalized in level such that the root-mean squared (RMS) amplitude of the audio waveform in each ear was the same over the entire stimulus time interval from 0 to 3 s. The recordings were downsampled to 44.1 kHz, and presented using Vizard 3.0 (WorldViz, Santa Barbara, CA). Examples of motion and static stimuli can be found in the supplementary material.

A 2 × 2 factorial design with factors condition (moving vs. static) and direction (leftward vs. rightward) served to identify neural ensembles coding for the direction of auditory motion. Subjects listened to blocks of moving and static stimuli (Fig. 1, block duration: 19s), and within each block, five stimuli were presented in rapid succession (stimulus duration: 3 s, ISI: 1 s). For the motion stimuli, four stimuli moved at 0.45 m/s and one deviant stimulus moved at 0.9 m/s. For the static stimuli, four stimuli were presented with the initial and final stationary periods lasting 1 s each, and one deviant stimulus with durations of 0.5 s.

Within each block, stimuli were presented in a pseudo-randomised order: to ensure that the subject was aware of the standard speed or duration of the sounds, the first two stimuli in each block were always presented at baseline speed/duration, and the deviant sound was randomly presented at positions three, four or five. Subjects were instructed to press a button on a keypad with the right index finger as quickly as possible upon detecting the deviant stimulus. Subjects were not informed about the number of deviant sounds per block and were not given any feedback about their performance. Importantly, following previously established procedures for the decoding of visual motion (Kamitani and Tong, 2006), our paradigm ensured that subjects were attending to the speed/duration of the stimuli while the direction was irrelevant.

Procedure

All participants first completed one training session outside the MR environment to eliminate any learning and habituation effects. Detailed instructions about the task were followed by a sequence of training trials. Each of the four block types was presented once, and subjects were asked to indicate the deviant stimuli as quickly as possible. This procedure proved successful since all participants were subsequently able to perform the task with very low error rates (see Results). After being positioned within the bore of the magnet, subjects completed eight experimental runs with concurrent fMRI recording. In each run, we presented eight blocks (two blocks of each of the four conditions) in a fully randomised order. Blocks were separated by silent rest periods (duration: 5 s).

MRI acquisition

MR scanning was performed on a 3 T MRI Scanner (Siemens Trio) with a standard headcoil. Subjects lay on their backs within the bore of the magnet and listened to the stimuli presented via MR-compatible headphones (Optime 1, Peltor). To minimize head movement, all subjects were stabilized with tightly packed foam padding surrounding the head.

Functional data were acquired using a gradient echo echo-planar T2*-sensitive sequence (TR = 1.92 s, TE = 30 ms, flip angle 90°, matrix 64 × 64, field of view 192 × 192 mm) with thirty-six axial slices (slice thickness: 3 mm, gap: 0.5 mm). High-resolution anatomical scans were acquired using a T1-sensitive FLASH sequence (TR = 15 ms, TE = 4.2 ms, flip angle 20°, voxel size: 0.9 × 0.9 × 0.9 mm).

fMRI data preprocessing and univariate statistical analysis

In order to preserve as much information as possible in the functional dataset, we did not normalise the data but carried out all analyses in the space of individual subjects. For the univariate analyses, we first realigned all volumes to the first volume in the time series to correct for spatial displacements within and across runs, using SPM8

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(Wellcome Department of Imaging Neuroscience, London, UK). Next, we performed a standard univariate statistical analysis with a general linear model as implemented in SPM8. For each subject, we smoothed the preprocessed images with a 6-mm full-width at half-maximum isotropic Gaussian kernel before specifying design matrices that contained separate regressors for each of the four trial types (motion/static * leftward/rightward). Blocks were modelled as boxcar functions convolved with a hemodynamic response function. Differences between leftward and rightward motion were tested with *F*-contrasts on the parameter estimates, using a threshold of $p<0.05$ corrected for multiple comparisons.

ROI definition

For each subject we sought to define a region of interest (ROI) that was presumed to encompass the hMT+ complex. Identifying this region by anatomical landmarks and/or stereotaxic coordinates alone is problematic because of significant anatomical variability across individuals (Dumoulin et al., 2000; Watson et al., 1993), and standard hMT+ localiser paradigms are based on visual stimuli (Tootell et al., 1995). Given that activation supposed to encompass hMT+ has been observed in blind and sight recovery subjects when comparing moving vs. stationary sounds (Poirier et al., 2006; Saenz et al., 2008), we applied a similar criterion here. Specifically, we performed a standard *t*-test, using a liberal threshold of $p<0.01$ uncorrected, to identify voxels that showed stronger BOLD responses for moving vs. static sounds, collapsed across both directions. Note that this contrast was orthogonal to the main question of the experiment (differences between directions). We then defined an occipito-temporal region in each participant as the cluster of contiguous voxels near the intersection of the lateral occipital sulcus and the inferior temporal sulcus. Responses from the left and the right hemisphere were combined into one ROI.

To test whether or not any potential classification results were specific to the occipito-temporal ROI, we defined a control ROI that also showed sensitivity to auditory motion but where we did not expect directional tuning. Several groups have reported responses to auditory motion in the posterior parietal cortex of sighted and blind subjects (Bremmer et al., 2001; Griffiths et al., 1998; Lewis et al., 2000; Poirier et al., 2006). Therefore, we applied the same statistical test to identify clusters of contiguous voxels in posterior parietal cortex that showed stronger BOLD responses for moving vs. static sounds, collapsed across both directions. Voxels from the left and the right hemisphere were combined into one ROI. Importantly, note that the number of voxels entering pattern classification analyses was identical in the parietal and the occipito-temporal ROIs since we subsequently applied feature selection (see below).

Multivariate pattern classification

We employed the Princeton Multi-Voxel Pattern Analysis Toolbox (MVPA, www.pni.princeton.edu/mvpa) to test whether BOLD responses contained information about the direction of the stimuli. Data samples used for decoding were created by minimally smoothing the realigned images with a 3 mm full-width at half-maximum isotropic Gaussian kernel. Next, we detrended the images to remove linear trends and applied low and high-pass filtering to increase signal-to-noise ratio. Finally, response amplitudes of individual voxels were normalised relative to the average of the entire time course within each run (excluding rest periods) to minimise baseline differences across runs and to reduce the impact of outliers. Note that we did not average the data to preserve the information contained in individual volumes.

In order to test whether leftward and rightward stimuli could be distinguished, we performed separate analyses for moving and static stimuli. To maximise the sensitivity of the classification analyses, we first applied feature selection and restricted our analysis to the most relevant voxels. Specifically, in both ROIs, using a similar criterion as previously established for the decoding of visual motion stimuli (Kamitani and Tong, 2006), we only included the 80 voxels that showed the strongest activation for the contrast moving vs. static sounds (see above). Given that the different conditions were presented in a block design (five stimuli per block), we focussed on the TRs once the hemodynamic response was assumed to have reached its plateau. We therefore shifted all stimulus onset times forward in time by 4 TRs before dividing fMRI patterns into two segments: a training set used to train a logistic regression classifier with L2-regularisation to identify response patterns related to the conditions being discriminated and a test set used to independently test classification performance. We employed a standard *k*-fold crossvalidation regime (Duda et al., 2001), wherein *k* equalled the number of runs ($k=8$), with each run set aside, in turn, as the test data and the remaining runs used to train the classifier. This procedure was repeated until all runs had been assigned once as the test data, allowing for an unbiased estimate of the overall classification performance.

To test whether classification performance is better than chance, one can perform non-parametric tests by permuting condition labels to create empirical null distributions. Due to the temporal autocorrelation of the BOLD signal, this approach was not feasible here because we used consecutive volumes for classification and hence exchangeability was not given. Therefore, we used a wavelet-based signal decomposition procedure as implemented in the MVPA toolbox (for details, see Polyn et al., 2005). In short, for each analysis, we generated 1000 surrogate classifier estimate time courses with the same spectral characteristics as the original time-courses to create a null distribution of performance values. By comparing the actual classifier performance to these distributions, we were able to generate a *p* value: the proportion of surrogate-based performance scores that exceeded the result obtained in the experiment. Finally, to characterize how classification was affected by the number of features, we repeated classification analyses while gradually changing the size of the search volume to the 20 to 85 (in steps of five) most activated voxels (for the contrast motion vs. static).

Results

Deviant stimuli were detected with near-perfect accuracy (>95%) in all four conditions, and a repeated measures ANOVA did not reveal any differences between moving and static stimuli (accuracy: $p=0.49$, reaction times: $p=0.13$). In addition, stimulus direction did not affect behavioural performance (accuracy: $p=0.49$, reaction times: $p=0.38$), and there was no evidence for an interaction between stimulus direction and the presence or absence of motion (accuracy: $p=0.09$, reaction times: $p=0.39$).

We first identified individual regions of interest (ROI) in dorsal occipito-temporal cortex by testing for BOLD responses that were

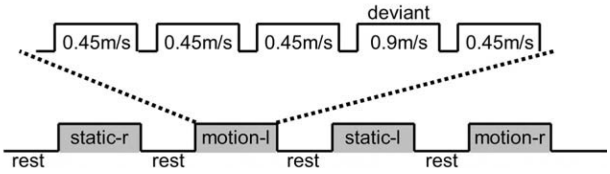

Fig. 1. Experimental paradigm. During fMRI scanning, subjects listened to blocks of moving and static stimuli (block duration: 19 s), presented in a randomised order. Within each block, five stimuli were presented in rapid succession (stimulus duration: 3 s, ISI: 1 s). Moving stimuli moved either in a rightward or leftward direction, and subjects attended to the speed of motion and indicated the deviant stimulus with a button press. To ensure that any results of the pattern classification analyses were not driven by the specific sequence of spatial positions (left followed by right for rightward moving sounds and vice versa), we also presented static control stimuli that preserved the beginning and ending static portions of the motion stimuli but lacked the intervening motion component (see Materials and methods for details).

stronger for moving than for static stimuli, averaged across both directions (Fig. 2). To ease comparison with previous studies, we also performed this analysis with spatially normalised data; the resulting local maxima are reported in Table 1. Next, we applied univariate general linear models and performed voxel-wise *F*-tests to check whether leftward and rightward motion stimuli evoked differential BOLD responses. In three subjects, this analysis did not reveal any significant effects, and in the fourth subject, we only observed one small cluster in the left occipito-temporal region and two small clusters in the occipito-parietal junction. To maximise sensitivity, we performed a separate analyses focussing only on the voxels within the individual dorsal occipito-temporal ROIs. Specifically, we extracted the mean time course across all voxels and estimated statistical models for the averaged time courses. As the left panel of Fig. 3 shows, this analysis also failed to reveal significant differences between leftward and rightward stimuli (motion: $p = 0.76$; static: $p = 0.26$). Taken together, these results suggest either that directional information was not present in this region or that the signal to noise ratio within individual voxels was not sufficient to differentiate between motion directions.

We therefore used a standard pattern classification approach to test whether directional information could be decoded from the multi-voxel responses within both ROIs. Imaging data were divided into independent training and test sets based on the eight experimental runs. We then trained a logistic regression classifier and evaluated its performance by predicting stimulus direction on each fMRI volume in the independent test data, using an eight-fold crossvalidation. In the dorsal occipito-temporal ROI, decoding of the two motion directions exceeded chance performance in each of the four participants (Fig. 3). Importantly, non-parametric testing confirmed that classification accuracy was significantly above chance for the motion stimuli ($p < 0.001$ in all cases). Classification accuracy improved as patterns of activity from larger numbers of voxels were taken into account and reached an asymptotic value at around 80 voxels (Fig. 4).

To test for the anatomical and functional specificity of these decoding results, we performed three control analyses. First, we checked for the effect of the specific sequence of start and end positions. Stimuli that move in a rightward or leftward direction not only differ with respect to the motion direction, but their initial and final locations differ as well. Therefore, we performed a decoding analysis on the static stimuli that were identical to the motion stimuli with respect to the start and end positions but lacked the intermediate motion cues. As the right panel of Fig. 3 shows, classification performance did not differ significantly from chance in any of the four participants ($p > 0.05$ in all cases). Furthermore, varying the number of voxels included in the decoding analysis did not improve classification accuracy, thus demonstrating that the BOLD responses in occipito-temporal cortex did not contain information about sequences of spatial positions.

Secondly, we tested whether the successful decoding of the motion directions was specific to the dorsal occipito-temporal ROI. Applying the same permutation procedure for statistical testing (see Materials and methods), classification performance in the posterior parietal control region did not differ from chance in any of the four participants ($p > 0.05$ in all cases). In addition, classification accuracy did not change with varying numbers of voxels (Fig. 4), demonstrating that the

Table 1
Local maxima in dorsal occipito-temporal cortex, based on spatially normalized data.

Spatial coordinates of the local maxima for the contrast: $(\text{motion}_{\text{leftward}}\ \&\ \text{motion}_{\text{rightward}})-(\text{static}_{\text{leftward}}\ \&\ \text{static}_{\text{rightward}})$			
Subject	Coordinate (*x*, *y*, *z*, in mm)		Voxel level (*t*-score)
	LH	RH	
S01	−39, −61, 7		7.79
	−54, −64, −2		7.52
		39, −55, 10	9.65
		42, −64, 10	9.08
S02	−39, −67, 4		4.89
	−42, −70, 16		4.27
		45, −64, 10	6.11
S03	−33, −76, 19		3.60
	−48, −76, 13		3.54
		39, −55, 10	4.88
		45, −73, 16	3.40
S04	−48, −73, 13		6.07
	−42, −61, 13		4.68
		42, −64, 1	3.96

RH/LH—right/left hemisphere; threshold: $p < 0.01$ uncorrected.

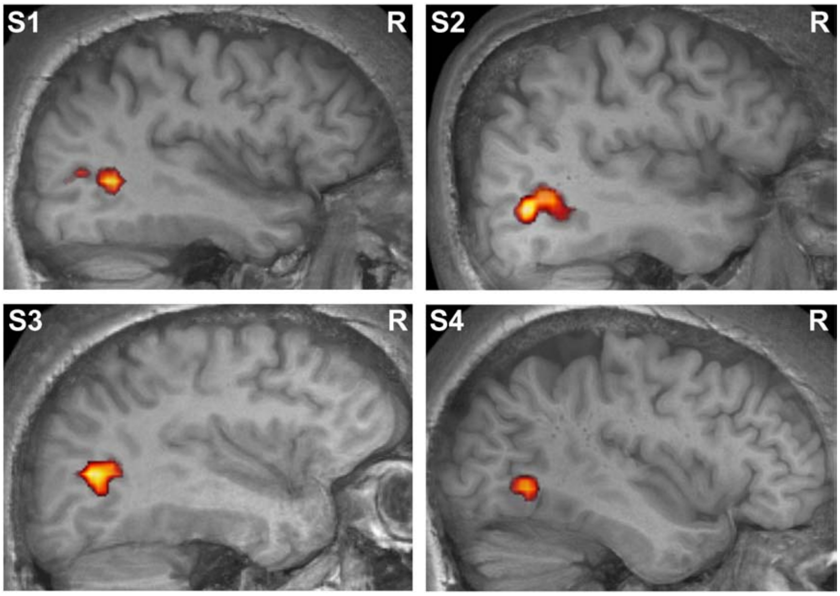

Fig. 2. Main effect of stimulus motion within hMT+. Dorsal occipito-temporal ROIs as identified by the univariate analysis that compared moving vs. static sounds, collapsed across both directions. Dorsal occipito-temporal voxels, shown here for the right hemisphere on the individual T1-weighted anatomical scans, could be identified bilaterally in each of the four participants. Voxels from both hemispheres were combined to obtain the classification results.

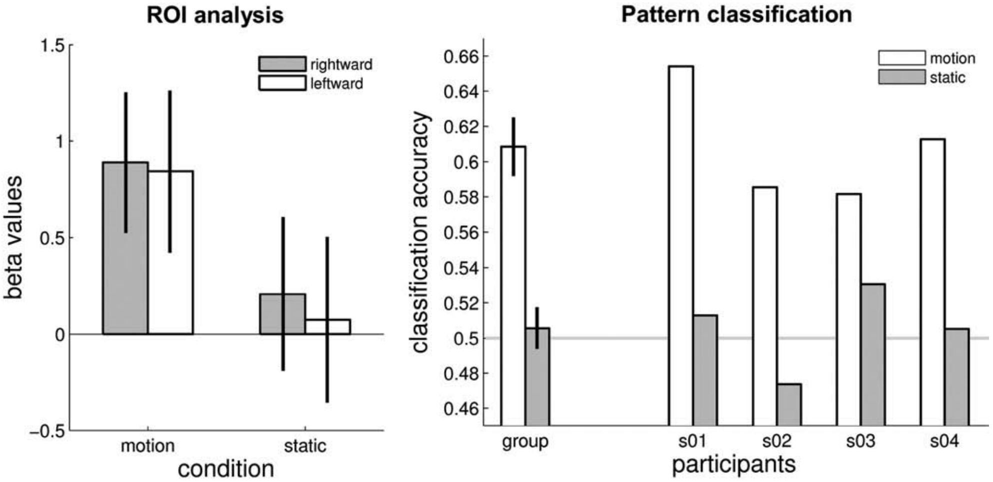

Fig. 3. Coding for motion directions in dorsal occipito-temporal cortex. Left panel: a conventional ROI analysis, based on the mean activation from all dorsal occipito-temporal voxels in both hemispheres, did not reveal significant differences between rightward and leftward stimuli, both for moving and four static sounds. The graph shows the regression coefficients (mean ± sem) averaged across the four participants. Right panel: a logistic regression classifier was trained to decode the direction of the stimuli (right vs. left) from BOLD responses in the dorsal occipito-temporal ROI. The graph shows the classification accuracy for moving and for static sounds separately, the grey line indicates chance performance. In contrast to the conventional ROI analysis, the classifier was able to reliably differentiate between leftward and rightward moving stimuli. This pattern of results was observed in each of the four participants, since nonparametric testing revealed that classification accuracy was significantly above chance for the motion stimuli but did not differ from chance for the static stimuli.

absence of a significant result was not related to the specific size of the ROI.

Finally, listening to different directions of auditory motion could induce different patterns of head motion (i.e. following the stimulus), which could have a systematic effect on the BOLD signals. To exclude this potential confound, we performed a control analysis on the motion parameters obtained from the realignment procedure. Specifically, we computed the scan-to-scan displacement for rotations (yaw, pitch and roll) and translations (movement along x-, y- and z-axes) before testing whether the direction of the auditory motion could be decoded from these six parameters. These analyses did not reveal above chance classification performance in any of the four participants ($p>0.05$ in all cases).

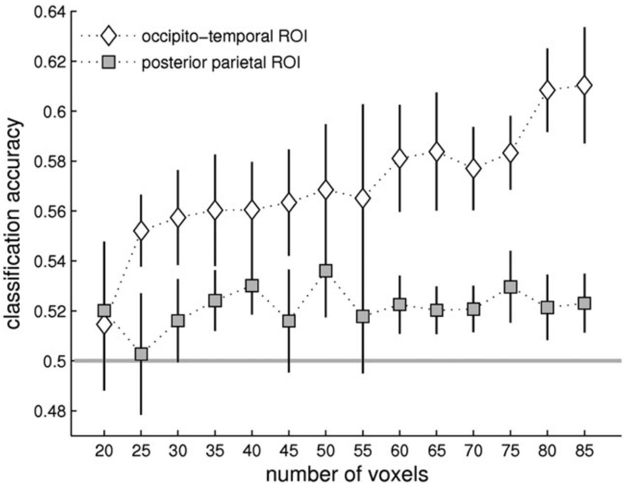

Fig. 4. Classification accuracy for motion directions with varying numbers of voxels. Classification performance for the motion stimuli, averaged across participants (mean ± sem), is shown separately for the dorsal occipito-temporal and the posterior parietal ROI. In the former, performance improved when more voxels were taken into account, suggesting that information about the direction of motion was spread across the population of voxels. In contrast, decoding accuracy was consistently close to chance level in the posterior parietal ROI, demonstrating that the direction of motion did not induce a systematic modulation of the BOLD response.

Discussion

Using multivariate pattern classification, we have shown that the direction in which an auditory stimulus is moving can be decoded from ensemble responses in dorsal occipito-temporal cortex. These results were not driven by the specific sequence of start and end positions since decoding accuracy was at chance for the corresponding static stimuli that lacked the intervening motion component. Furthermore, we did not observe evidence for specific patterns of head motion to accompany the motion stimuli. And finally, decoding accuracy was at chance in a posterior parietal control region, thus demonstrating anatomical specificity of the results. We therefore conclude that information about the direction of auditory motion is present in dorsal occipito-temporal responses of blind humans, which goes beyond previous demonstrations of overall motion-related activation in this region. Specifically, having demonstrated an important functional property of the responses elicited by auditory motion stimuli, our findings provide an important step towards characterising how non-visual motion cues are processed under conditions of sensory deprivation.

Identifying the hMT+ complex in blind humans is problematic. Standard localiser paradigms are based on visual stimuli, and anatomical variability across individuals prevents the use of standardised templates. As a consequence, previous work showing hMT+ activation in blind humans when contrasting moving with stationary auditory or tactile stimuli cannot exclude the recruitment of adjacent multisensory areas (Poirier et al., 2005; Ricciardi et al., 2007). Given that we used a similar criterion to define the dorsal occipito-temporal ROI, it is possible that our ROIs encompassed voxels outside hMT+, which is why we refer to this region as dorsal occipito-temporal cortex.

Although we were able to reliably decode motion directions in each of the four subjects, classification accuracy was below optimal levels. Interestingly, in the two previous studies that have decoded directions of visual motion from fMRI patterns in sighted subjects, classification accuracy in hMT+ was significantly lower than in early visual areas (Kamitani and Tong, 2006; Seymour et al., 2009). Given that decoding performance does not rely solely on the presence of feature information but also on the spatial layout of this information in the brain, the dense arrangement of directionally selective units in hMT+

possibly leads to very similar BOLD responses across directions, which in turn prevents a classification algorithm from reaching higher accuracy levels (Bartels et al., 2008). In addition, if voxels outside hMT+ that were included in our ROIs did not convey directional information, this could have further reduced decoding accuracy for the motion directions.

Two previous studies have demonstrated dorsal occipito-temporal activation in blind subjects elicited by moving auditory and tactile stimuli (Poirier et al., 2006; Ricciardi et al., 2007). However, Collignon et al. (2009) have pointed out that these effects could reflect unspecific coactivation. Specifically, the non-visual recruitment could result from non-functionally related connections with early sensory cortices. Our findings provide an important first step in resolving this controversy as they go beyond demonstrating stronger BOLD responses for moving vs. stationary auditory stimuli. Specifically, we have shown that across the population of the dorsal occipito-temporal voxels, BOLD responses differ consistently between rightward and leftward moving stimuli. In other words, the underlying neural responses appear to be modulated by the direction of motion in a similar manner as has been shown for visual stimuli (Kamitani and Tong, 2006). As a consequence, the non-visual motion responses in dorsal occipito-temporal cortex can provide crucial information for generating a veridical percept of a moving stimulus.

While we have demonstrated an important property of auditory motion processing in blind humans, our findings raise a number of questions. First of all, it is unclear whether our findings are specific to the auditory modality or whether they generalise to other modalities such as tactile motion. Secondly, in the visual modality, hMT+ also conveys information about the speed of motion (Chawla et al., 1999), a critical dimension that remains to be demonstrated for non-visual stimuli. Finally, the direction of visual motion can also be decoded from responses in early visual areas (Kamitani and Tong, 2006). Although standard techniques for localising these areas (i.e. retinotopic mapping) cannot be applied to blind subjects, one way to address this issue could be to study sight recovery subjects (Saenz et al., 2008).

Our results also relate to the growing body of literature supporting sensory substitution in the blind, which can be based on very different mechanisms (Loomis and Klatzky, 2007). For example, the concept of functional equivalence includes the notion that modality-specific perceptual processing could ultimately give rise to supramodal or amodal representations in higher-order cortical regions. In the context of motion processing, hMT+ and neighbouring structures could be supramodal regions–similar to regions in the ventral visual pathway (Mahon et al., 2009)–that are implicated in motion processing independent of the specific sensory modality. In sighted subjects, previous evidence regarding a non-visual hMT+ recruitment is mixed (Baumann and Greenlee, 2007; Griffiths et al., 1998; Lewis et al., 2000; Poirier et al., 2005; Ricciardi et al., 2007; Saenz et al., 2008), but none of these studies have specifically examined functional properties such as speed or directionality. Alternatively, crossmodal reorganization triggered by sensory deprivation could allow for auditory input to reach hMT+ (Bavelier and Neville, 2002). A number of neuroimaging experiments have demonstrated that devices substituting auditory information for vision show similar patterns of recruitment of occipital regions, and TMS applied to occipital cortex can interfere with the perception of Braille in blind readers (Amedi et al., 2007; Arno et al., 2001; Cohen et al., 1997; De Volder et al., 1999). Such results suggest that compensatory non-visual processing is also supported by cross-modal modulation of (extra)striate cortices.

In closing, our results confirm that dorsal occipito-temporal activation evoked by auditory motion in blind humans does not reflect unspecific coactivation. Rather, the directional responses suggest the functional significance of these responses for nonvisual motion processing. Although a precise functional localisation is not possible in blind subjects, it appears likely that the region we have identified encompasses the hMT+ complex. These findings add to the growing body of evidence that non-visual recruitment of extrastriate areas is not unspecific, but that it is related to the specific computational contribution that a given region makes to sensory processing.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2010.04.266.

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