# Auditory Motion Direction Encoding in Auditory Cortex and High-Level Visual Cortex

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**Abstract:** The aim of this functional magnetic resonance imaging (fMRI) study was to identify human brain areas that are sensitive to the direction of auditory motion. Such directional sensitivity was assessed in a hypothesis-free manner by analyzing fMRI response patterns across the entire brain volume using a spherical-searchlight approach. In addition, we assessed directional sensitivity in three predefined brain areas that have been associated with auditory motion perception in previous neuroimaging studies. These were the primary auditory cortex, the planum temporale and the visual motion complex (hMT/V5+). Our whole-brain analysis revealed that the direction of sound-source movement could be decoded from fMRI response patterns in the right auditory cortex and in a high-level visual area located in the right lateral occipital cortex. Our region-of-interest-based analysis showed that the decoding of the direction of auditory motion was most reliable with activation patterns of the left and right planum temporale. Auditory motion direction could not be decoded from activation patterns in hMT/V5+. These findings provide further evidence for the planum temporale playing a central role in supporting auditory motion perception. In addition, our findings suggest a cross-modal transfer of directional information to high-level visual cortex in healthy humans. *Hum Brain Mapp 33:969–978, 2012.*     © 2011 Wiley Periodicals, Inc.

**Key words:** auditory motion; planum temporale; motion direction; fMRI; multivoxel pattern analysis; audiovisual; SVM

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## INTRODUCTION

When a sound source is moving, our auditory system is able to detect the direction of such a movement by registering relative changes in amplitude and time of arrival of auditory signals across ears [Grantham, 1989; Harris et al., 1971; Perrott and Musicant, 1977; Recanzone and Sutter, 2008]. The neural mechanisms that support this capability have been investigated by numerous human neuroimaging studies by measuring neural responses to moving and static sounds by means of functional magnetic resonance imaging (fMRI), electroencephalography (EEG) and magnetoencephalography (MEG) [Baumgart et al., 1999; Ducommun et al., 2002; Griffiths et al., 1994, 1998, 1999,

2000; Lewis et al., 2000; Pavani et al., 2002; Smith et al., 2007; Warren et al., 2002; Xiang et al., 2002; Zimmer and Macaluso, 2009; Zvyagintsev et al., 2009]. The majority of these studies indicate that the planum temporale as well as frontal and parietal cortices respond more strongly to moving than to static sounds [Baumgart et al., 1999; Ducommun et al., 2002; Griffiths et al., 1994, 1998, 1999, 2000; Lewis et al., 2000; Pavani et al., 2002; Warren et al., 2002; Xiang et al., 2002; Zimmer and Macaluso, 2009], which has led to the conclusion that activation in the planum temporale is critical to auditory motion perception. This conclusion, however, has been challenged by Smith et al. [2007] who did not observe auditory motion sensitivity in the planum temporale. Moreover, the findings of Zvyagintsev et al. [2009] suggest that auditory motion might already be detected at the level of primary auditory cortex.

To clarify which areas in the human brain are important for auditory motion perception we looked for brain regions sensitive to the *direction* of auditory motion. This approach differs fundamentally from that of previous neuroimaging studies [Baumgart et al., 1999; Ducommun et al., 2002; Griffiths et al., 1994, 1998, 1999, 2000; Lewis et al., 2000; Pavani et al., 2002; Smith et al., 2007; Warren et al., 2002; Xiang et al., 2002; Zimmer and Macaluso, 2009; Zvyagintsev et al., 2009], which identified brain areas sensitive to the *presence* of auditory motion compared to static controls. Directional sensitivity was assessed by performing a multivoxel pattern analysis [Haxby et al., 2001; Haynes and Rees, 2005; Kamitani and Tong, 2005; Norman et al. 2006] with which we identified brain areas that contained distributed response patterns that differentiated between left- and rightwards moving sounds. This type of analysis has been shown to allow for the classification of the direction of visual motion based on fine-grained neural response patterns in visual cortices [Kamitani and Tong, 2006].

In this study, we applied multivoxel pattern analysis in a hypothesis-free manner by scanning the entire brain for auditory-motion-direction-sensitive brain areas using a spherical-searchlight approach [Kriegeskorte et al., 2006, 2007]. In addition, we assessed the sensitivity to auditory motion direction in three predefined regions of interest (ROIs). As it is still under debate whether the planum temporale is a specialized human cortical area for the processing of auditory motion [Smith et al., 2007; Zvyagintsev et al., 2009], we measured auditory-motion-direction sensitivity of the planum temporale and compared the directional sensitivity of this area to that of the primary auditory cortex. Because several human neuroimaging studies suggest that activation in the human visual motion area hMT/V5+ is affected by moving sounds [Alink et al., 2008; Poirier et al., 2005, 2006; Saenz et al., 2008; Wolbers et al., 2011], we also tested if response patterns in this visual area differentiate left- from rightwards-moving sounds.

Previous human neuroimaging studies investigated neural responses to moving and static sounds [Baumgart et al., 1999; Ducommun et al., 2002; Griffiths et al., 1994, 1998, 1999, 2000; Lewis et al., 2000; Pavani et al., 2002;

Warren et al., 2002; Xiang et al., 2002; Zimmer and Macaluso, 2009] without controlling for attention. Therefore, it is possible that the enhanced responses for auditory motion observed in these studies resulted from moving sounds capturing the attention of subjects more readily than static sounds. This would be in line with the findings of Franconeri and Simons [2003] and could explain why several of these studies [Griffiths et al., 1998, 2000; Lewis et al., 2000; Pavani et al., 2002; Warren et al., 2002; Zimmer and Macaluso, 2009] found enhanced responses for moving sounds in frontal and parietal cortex [Corbetta et al., 1998]. In this study we have made an effort to reduce the effects of attention by presenting moving sounds while subjects performed a visual detection task. In addition, this task reduced possible confounding effects of visual mental imagery [Goebel et al., 1998; Reddy et al., 2010]. Moreover, we verified outside the scanner that auditory motion did not affect eye movements.

## MATERIALS AND METHODS

### Participants

Nineteen healthy volunteers participated in the fMRI study (age range, 20–31 years; 13 females) and 6 healthy volunteers participated in the eye-tracking study (age range, 22–32 years; 4 females). All subjects had normal hearing and normal or corrected-to-normal vision. All subjects gave their informed consent after being introduced to the experimental procedure in accordance with the Declaration of Helsinki.

### Stimuli and Task—fMRI Experiment

Visual stimuli were presented using an MR-compatible goggle system with two organic light-emitting diode displays (MR Vision 2000, Resonance Technology, Northridge, CA), and auditory stimulation was realized using an MR-compatible headphone system (Commander XG, Resonance Technology, Northridge, CA). The screen had a width of 30° and a height of 22.5°, and the luminance of the gray background was 24 cd/m$^2$.

Auditory stimulation consisted of seven types of 100-ms-long pink-noise bursts. Subjects perceived these pink-noise bursts as originating 15°, 10°, and 5° to the left or to the right or in front of the head in the horizontal plane with a distance of 1.4 m. This spatial perception was induced by convolving the pink-noise bursts with a generic head-related transfer function [Wightman and Kistler, 1989] derived from the KEMAR head model [Gardner and Martin, 1994] as previously implemented by Altmann et al. [2007] and in our lab [Alink et al., 2008]. Leftwards auditory motion sweeps contained each noise burst once going from the outer right to the outer left position and vice versa for rightwards motion sweeps. This resulted in motion sweeps covering an arc of 30° traversed in 700 ms (speed = 43°/s) containing exactly the same
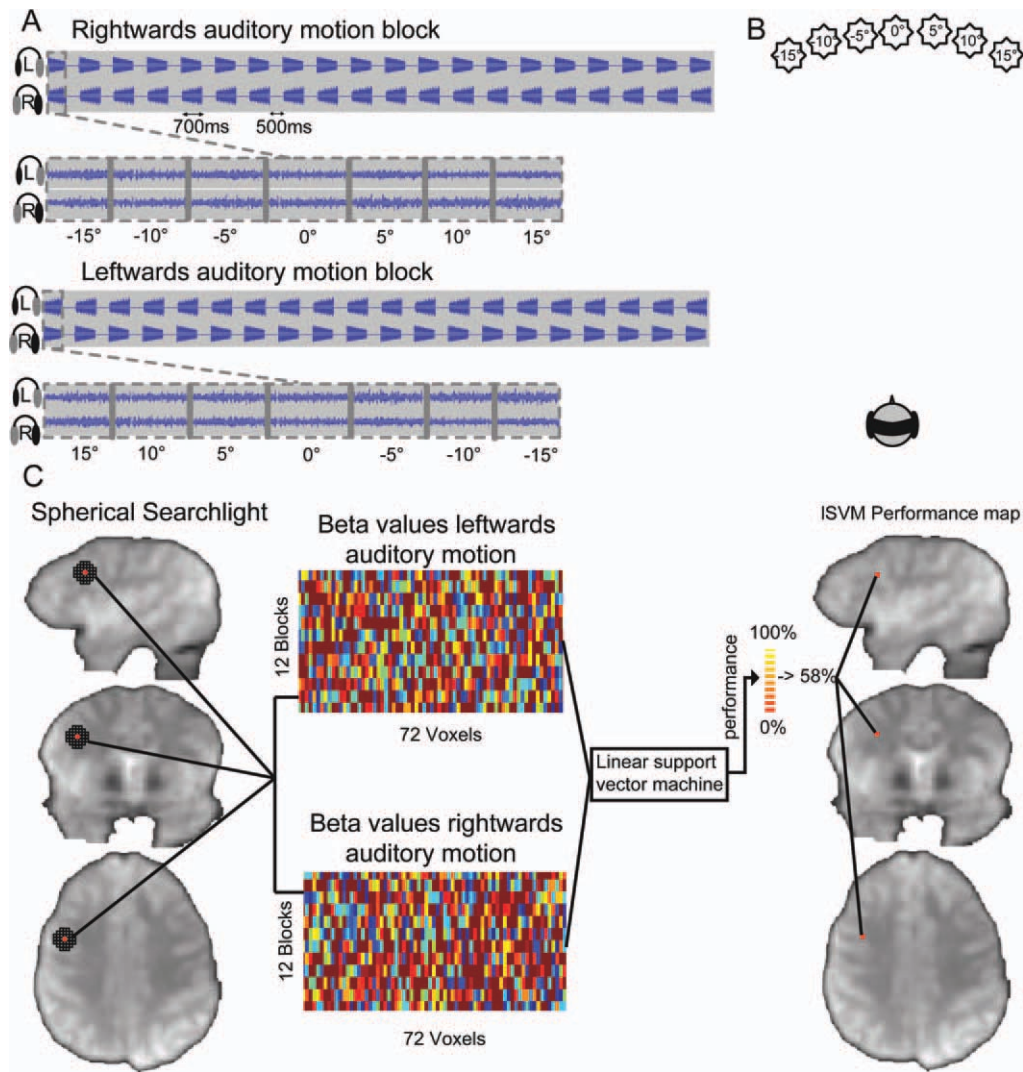
**Figure 1.**

Experimental design and analysis. (**A**) Sound stimuli used in the experiment that induced the percept of left- or rightwards auditory motion in blocks containing 20 motion sweeps covering an arc of 30°. (**B**) Schematic display of the sound locations covered during auditory motion sweeps. (**C**) Overview of the searchlight-based multivoxel pattern analysis employed in this study.

sounds for left- and rightwards motion sweeps. Hence, only the order in which the sounds were presented differed across conditions (see Fig. 1A,B).

Motion sweeps of one directionality were presented in blocks containing twenty sweeps, which were presented with an interstimulus interval of 500 ms. This interval was introduced to avoid that subjects would perceive vivid apparent motion in the direction opposite to the motion-sweep direction in between stimulus presentations. This resulted in blocks containing left- or rightwards motion sweeps lasting 24 s. During each of the four functional runs, we presented each type of auditory-motion block three times. Furthermore, each run contained three blocks

of left- and three blocks of rightwards visual motion with an identical duration. Visual motion consisted of a white vertical bar (height: 7.5°, width: 1.9°, luminance: 24 cd/m$^2$) that moved between the far left and the far right position of the screen (30°) along the horizontal midline within 700 ms. Our original intention was to determine whether brain areas exist that encode both auditory motion direction and visual motion direction. Because brain responses were found to be much higher in the hemisphere representing the visual motion onset, the multivariate analysis of visual motion direction would be dominated by univariate effects. Therefore, we chose to focus fully on auditory-motion-direction encoding and only used the visual

motion blocks to determine the approximate location of the visual motion area hMT/V5+ [Dumoulin et al., 2000]. The order of all types of stimulation blocks was randomized for each run. Between stimulation blocks, there were 24-s periods during which no auditory stimuli were presented, which served to assess a baseline signal.

During stimulation blocks as well as during the baseline periods, subjects continuously performed a visual-attention control task. This involved fixating 5.6° below the center of the screen, where a stream of letters and numbers appeared at a rate of two symbols per second. The task of the subjects was to press a button with their right index finger as soon as possible when a number appeared. During each stimulation or baseline period, nine numbers appeared with at least one letter being presented between two consecutive numbers. We registered button presses as hits if they occurred within 100 ms and 1,000 ms after the number onset.

### Stimuli and Task—Eye-Tracking Experiment

Subjects were seated in a fully darkened room and placed their heads on a chin rest with forehead support to ensure a constant eye-to-screen distance of 70 cm. Visual and auditory stimulation and the task of the subjects during the eye-tracking experiment was the same as during the fMRI experiment. During the eye-tracking experiment we, however, did not present visual motion blocks. Stimuli were presented on a CRT screen (Hewlet Packard P1230) with a width of 32° and a height of 24°. The luminance of the gray background was 21 cd/m$^2$.

### Eye Tracking—Data Acquisition

Pupil position, pupil diameter, and corneal-reflection (CR) position were recorded for both eyes at a rate of 1,000 Hz using the EyeLink 1000 Desktop Mount system. Calibration was performed for each subject just before the start of each of the four runs.

### Eye Tracking—Data Analysis and Results

Eye blinks were defined as the time points at which the pupil-diameter change, as compared with the last time point, was five times larger than the standard deviation of pupil diameter changes over the entire run. These time points, as well as the 200-ms time window before and 200-ms time window after these time points, were discarded from the analysis to exclude eye-blink artifacts. We determined the mean and standard deviation of the horizontal and vertical position of fixation for all conditions separately for each subject and separately for the left and the right eye. We tested whether there were differences in mean and variance across conditions using a repeated-measures test over subjects. Furthermore, we created a density plot of eye position for all conditions, separately for the left and right eye, using eye-tracking data across all subjects.

Eye-tracking data obtained outside the scanner showed that the mean horizontal and vertical position of fixation differed less than 0.3 visual degrees from the instructed fixation position for all conditions without a significant effect of stimulus condition (mean horizontal position: $F(2,4) = 0.98$, $P = 0.45$; mean vertical position: $F(2,4) = 0.12$, $P = 0.89$). The mean standard deviation for the horizontal and vertical position of fixation was found to be less than 1.0 visual degrees for all conditions and was not found to be affected by stimulus condition (horizontal standard deviation: $F(2,4) = 0.94$, $P = 0.46$; vertical standard deviation: $F(2,4) = 1.66$, $P = 0.30$). Eye-position density plots also did not indicate any gross differences in the distribution of fixation position across conditions.

### fMRI—Data Acquisition

Functional and anatomical MRI data were acquired with a 3T-MRI system (Siemens Allegra; Siemens, Erlangen, Germany) using a four-channel head coil. For each subject, we obtained 300 volumes containing 40 slices covering the entire brain during each of the four functional scans using a gradient-echo echo-planar-imaging (EPI) sequence [repetition time (TR), 2,000 ms; echo time (TE), 25 ms; flip angle (FA), 70°; voxel size, 3.28 × 3.28 × 3.0 mm$^3$; field of view (FOV), 210 mm; gap thickness, 0.3 mm]. We corrected for spatial distortions in the EPI images using a point-spread-function (PSF) sequence [Zaitsev et al., 2004]. We also obtained a T1-weighted anatomical scan for each of the subjects using a Siemens magnetization-prepared rapid-acquisition gradient echo (MPRAGE) sequence (1 × 1 × 1 mm$^3$).

### fMRI—Data Analysis

Functional as well as anatomical MRI data were analyzed using the Brainvoyager QX software package (Brain Innovation, Maastricht, The Netherlands). The first four volumes of the functional runs were discarded to preclude T1 saturation effects. After preprocessing (motion correction, linear trend removal, temporal high pass filtering at 0.01 Hz and slice-scan-time correction), functional data for all subjects were aligned with the individual high-resolution anatomical MPRAGE image and transformed into Talairach space [Talairach and Tournoux, 1988] interpolating the data to a four-dimensional matrix (three for space, one for time) containing 3.0 mm isotropic voxels using trilinear interpolation.

A multivoxel pattern analysis, using a spherical-searchlight approach [Kriegeskorte et al., 2006, 2007], was performed over these data separately for each subject using custom-made code programmed in Matlab (The Mathworks, Inc, Natick, US). The first step of this analysis consisted of defining spherical searchlights centered on each single voxel in Talairach space. These searchlights contained the 72 voxels that were inside a radius of 1.05 cm around the center voxel. As a first step, we subtracted the

average time course across voxels (searchlight mean) from each single voxel time course to ensure that homogeneous univariate effects would not influence classification. Within each searchlight, we then determined the response patterns that were evoked by each single auditory-motion stimulus block using a general linear model (GLM). This we realized by using a design matrix that contained twelve columns for each condition with each column corresponding to a single stimulation block. This resulted in 12 β-value vectors (corresponding to the number of blocks) with a length of 72 units (corresponding to the number of searchlight voxels) for each auditory motion direction. Note that the twelve beta values for leftwards and rightwards auditory-motion stimulation blocks originate from all four runs with each run containing three stimulation blocks per condition. We assessed whether a linear support-vector machine (lSVM) could classify motion direction based on pattern differences between auditory motion directions. To this end, we used an lSVM defined in LIBSVM [Chang et al., 2001]. The lSVM was trained on β-value patterns for 11 left- and 11 rightwards blocks, after which the lSVM attempted to classify the direction of the remaining two blocks. This procedure was performed 12 times using each pair of blocks once for testing. The output of this analysis was the average performance over these twelve classifications. Performance of the lSVM for each searchlight was stored in Talairach space with each searchlight projecting its performance to the position of its center voxel (see Fig. 1C). The outcome of this analysis were nineteen individual performance maps aligned in Talairach space.

To assess whether a region in Talairach space contained directional information we performed a subject-level *t*-test to test whether performance for this region was consistently higher than chance level (50%) across subjects after spatially smoothing the individual performance maps using a Gaussian kernel (6 mm FWHM). A *t*-threshold of 4.0 was used in conjunction with a cluster threshold which required *t*-values of at least four adjacent voxels to exceed the *t*-threshold. This cluster threshold was computed using the method introduced by Forman et al. [1995] and implemented in BrainVoyager QX by Fabrizio Esposito and Rainer Goebel (University of Maastricht, Maastricht, The Netherlands) and corresponds to a *P*-value lower than 0.001 corrected for multiple comparisons. The cluster threshold was selected from a range of cluster thresholds after determining the false-positive rate for these thresholds over a thousand randomly generated statistical maps with the same spatial smoothness as the map acquired in our group analysis. We also performed a typical per-voxel GLM analysis. This GLM was computed using a design matrix with one column for all leftwards auditory blocks and one column for all rightwards auditory blocks. Based on this GLM we determined whether brain areas exist in which one auditory motion direction induces higher signal levels than the other auditory motion direction. This we determined for the entire brain volume, for predefined

ROIs and for ROIs that were defined by the spherical-searchlight analysis. In addition, we generated event-related averages for all ROIs.

In addition to the hypothesis-free searchlight analysis, we also analyzed directional information in predefined cortical ROIs for the Heschl's gyrus, the planum temporale and the visual motion complex hMT/V5+. ROIs covering the Heschl's gyrus and the planum temporale were defined anatomically according to the tracing guidelines by Kim et al. [2003]. The Heschl's gyrus was defined as the most anterior transverse gyrus on the supratemporal plane that arises from the retro-insular region. This structure is known to be covered by the koniocortical type of cortex and serves as the primary auditory cortex in humans [Galaburda and Sanidess, 1980; Rademacher et al., 1993]. The planum temporale was defined as the triangular region lying caudal to the Heschl's gyrus on the supratemporal plane. The ROI for hMT/V5+ was defined functionally as the area nearby the posterior part of the inferior temporal sulcus that was significantly activated by the visual motion stimuli (*P* < 0.0005, uncorrected) as compared with baseline stimulation. ROIs were defined on an individual level on an inflated cortex reconstruction for both hemispheres. ROIs for two exemplary subjects are visualized in Figure 4A.

Within these three ROIs auditory-motion-direction sensitivity was assessed in the exact same way as for the searchlight analysis with the only difference being that training and classification was performed based on data from all voxels inside a ROI instead of inside a spherical searchlight. In addition, to control for differences in the amount of voxels per ROI, we performed an analysis in which we reduced the number of voxels for all ROIs to that of the smallest ROI for each subject. This was realized by random subsampling of voxels. The latter analysis we performed 20 times with 20 different voxel subsamples for each of these analyses. The outcome of this procedure was the mean lSVM performance for each subject for each ROI over these twenty analyses.

## fMRI—Results

### Spherical-Searchlight analysis

Our spherical-searchlight analysis identified two cortical regions whose activation patterns contained directional information (*P* < 0.001, corrected, Fig. 2). One of these regions was located on the right supratemporal plane near the right Heschl's sulcus (mean lSVM performance 56.9%, SEM 1.4%, Talairach coordinates: $x = 54$, $y = -13$, $z = 7$). The second region was located in the right lateral occipital cortex (mean lSVM performance 56.2%, SEM 1.1, Talairach coordinates: $x = 35$, $y = -67$, $z = -8$). A comparison of the Talairach coordinates of this lateral occipital area with the previously reported Talairach coordinates for hMT/V5+ [Dumoulin et al., 2000] indicate that this area is
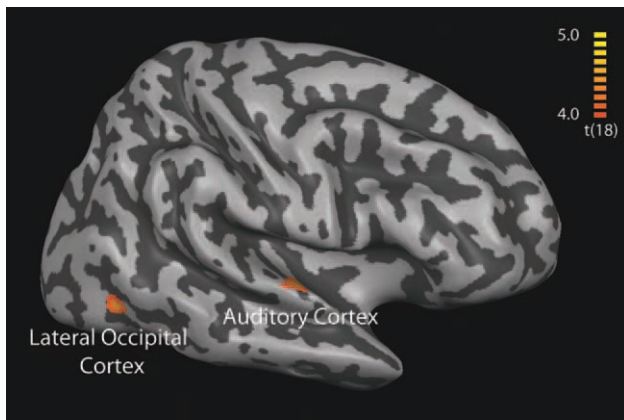
**Figure 2.**

Results of searchlight-based multivoxel pattern analysis. Group statistics projected on a cortical reconstruction of the right hemisphere of one of the subjects. *T*-values indicate the extent to which performance for a location in Talairach space was higher than chance level (50%) across our nineteen subjects. Significant areas displayed on this map are a region in the right auditory cortex (mean lSVM performance = 56.9%, SEM 1.4%) and a region in the lateral occipital cortex (mean lSVM performance 56.2%, SEM 1.1%).

located more ventral and more lateral as compared to the average location of hMT/V5+. We could not determine whether this area corresponds to the object-selective lateral occipital complex as our experiment did not contain a functional localizer for this area. Comparing the location of the area identified in the lateral occipital cortex with the location typically reported for object-selective lateral occipital complex (LOC; Larsson and Heeger, 2006; Malach et al., 1995], however, does not indicate a spatial overlap between this area and LOC.

We also performed a conventional univariate analysis where we looked for single voxels in which BOLD responses differed between left- and rightwards motion blocks. No such voxels were found ($P > 0.05$ corrected). A ROI-based analysis over the two regions identified by the multivariate analysis also showed no univariate effect of motion direction ($P > 0.05$ corrected).

The region within the right auditory cortex responded robustly to the auditory motion stimuli ($P < 0.001$, corrected), but no BOLD response was detectable in the lateral occipital cortex ($P > 0.05$, uncorrected; Fig. 3B). Thus, activation patterns in this area contained directional information about sound-source motion in the absence of a significant average BOLD response. Figure 3A shows a comparison between univariate auditory activation and multivariate classification maps. Similar results of significant decoding performance for non-activated regions have been described previously [Harrison and Tong, 2007; Serences and Boynton, 2007; Smith and Muckli, 2010].

## Region-of-Interest-Based Analysis

The coordinates of the right auditory region found in our whole-brain analysis fall within the area previously reported for primary auditory cortex [$x = 32$–57, $y = -28$–3, $z = 0$–16; Rademacher et al., 2001]. But consideration of individual anatomy might allow for a more specific identification of directionally sensitive subregions. In addition, ROI-based analyses provide more statistical sensitivity to address the issue of lateralization. ROIs were defined for all 19 subjects based on anatomical landmarks for the primary auditory cortex and planum temporale and were based on activation induced by moving visual stimuli for
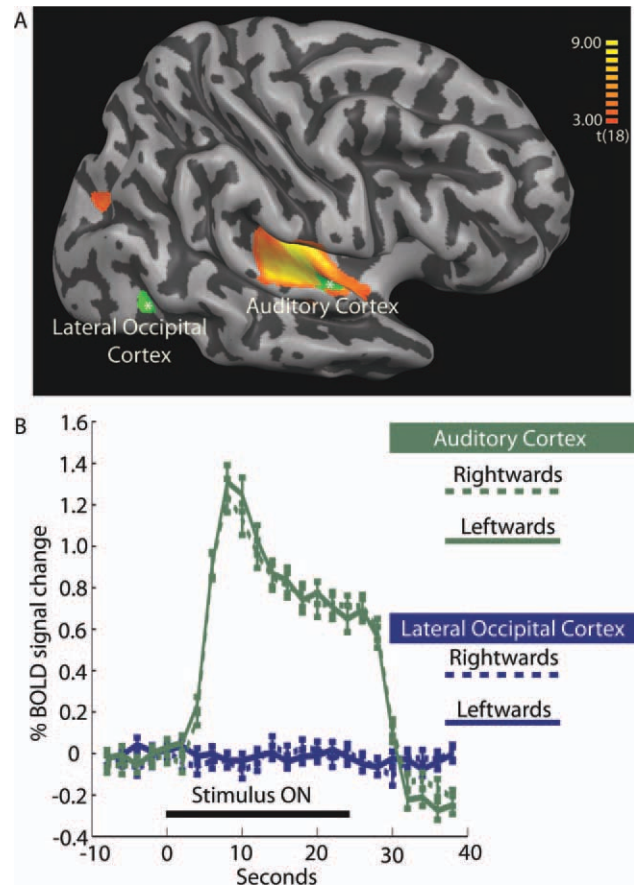


**Figure 3.**

Comparison of multivariate and univariate results. (**A**) Overlay of areas with significant multivoxel pattern classification from Figure 1 (green, marked with asterisk) on a random-effects map of univariate responses to auditory stimulation (average of rightwards and leftwards auditory motion). (**B**) Event-related average responses to rightwards and leftwards auditory motion for the two areas identified by the spherical searchlight analysis: right auditory cortex (dark green) and right lateral occipital cortex (blue). Error bars represent the standard error of the mean across subjects.

**TABLE I. Predefined regions of interest**

| Region of interest | Average number of voxels | Average Talairach coordinates | | | Average % lSVM Performance (SEM) | |
|---|---|---|---|---|---|---|
| | | $x$ | $y$ | $z$ | Unbalanced number of voxels | Balanced number of voxels |
| Primary Auditory Cortex | | | | | | |
| Left | 78 | −43 | −19 | 10 | 53.9 (2.6) | 53.4 (2.1) |
| Right | 67 | 45 | −18 | 11 | 54.2 (2.9) | 54.5 (3.0) |
| Planum Temporale | | | | | | |
| Left | 167 | −50 | −31 | 14 | 60.5 (3.0) | 59.5 (3.0) |
| Right | 161 | 52 | −28 | 16 | 61.2 (2.0) | 59.7 (1.9) |
| hMT/V5+ | | | | | | |
| Left | 58 | −41 | −72 | 5 | 47.1 (3.0) | 47.0 (3.2) |
| Right | 58 | 42 | −67 | 6 | 50.9 (3.5) | 50.7 (3.7) |

hMT/V5+. See Table I for a detailed description of the mean number of voxels, Talairach coordinates, and lSVM performance levels for all ROIs.

The main outcome of our ROI-based analysis was that lSVM performance was significantly above chance level for the planum temporale in both hemispheres (Left: $P < 0.05$ Bonferroni-corrected for the number of ROIs; Right $P < 0.0005$ Bonferroni-corrected for the number of ROIs). No such an effect was observed in the ROIs for the primary auditory cortex and hMT/V5+ although a marginally significant effect was observed for the primary auditory cortex (Left and Right: $P < 0.10$, unc.). Balancing the number of voxels per ROI made no difference for the outcome of this analysis (see Table I and Fig. 4A,B). A within-subject $t$-test indicated that the mean lSVM performance for the left and right planum temporale was greater than the mean lSVM performance for the left and right primary auditory cortex ($P > 0.05$ for both balanced and unbalanced number-of-voxel analyses). This indicates that auditory-motion-direction sensitivity in the planum temporale is higher than that in the primary auditory cortex. A within-subject t-test comparing lSVM performance levels between the left and right planum temporale did not indicate an effect of hemisphere on directional sensitivity ($P > 0.47$, unc.). lSVM performance for the right planum temporale, however, was above chance level for 17 of the 19 subjects while lSVM performance for the left planum temporale exceeded chance level only for 13 out of 19 subjects. This might explain why the searchlight-based analysis identified directional sensitivity in the right but not in the left auditory cortex.

Univariate analyses for these ROIs showed that both the primary auditory cortex and the planum temporale exhibited a robust response to moving sounds (Left and Right: $P < 0.001$ corrected) while such a response is lacking in hMT/V5+. The direction of auditory motion was not found to affect univariate responses within the primary auditory cortex nor the planum temporale ($P > 0.05$ corrected). Event-related averages for the primary auditory cortex, the planum temporale and hMT/V5+ are included in the Supporting Information Figure.

## DISCUSSION

Our hypothesis-free searchlight-based analysis indicated that activation patterns located in the right auditory cortex encode the direction of moving sounds. Although this area lies within close vicinity of the typical coordinates for the primary auditory cortex, our ROI-based analysis showed that auditory-motion-direction sensitivity was most pronounced in the planum temporale. Moreover, the latter analysis revealed that both the left and the right planum temporale encoded the direction of auditory motion. Directional encoding, however, was more consistent across subjects for the right planum temporale, which might explain why our searchlight-based analysis only detected directional encoding within the right auditory cortex. This finding is consistent with previous human neuroimaging studies whose findings indicate that neural responses of the planum temporale can be related to auditory motion perception [Baumgart et al., 1999; Griffiths et al., 1994, 1998, 1999, 2000; Lewis et al., 2000; Pavani et al., 2002; Warren et al., 2002; Zimmer and Macaluso, 2009]. Our results extend the knowledge about the planum temporale by showing that neural responses in this area carry information about the direction of moving sounds in both hemispheres.

We would like to mention, however, that we also observed a trend for a significant effect of the direction of moving sounds on activation patterns in left and right primary auditory cortex. Therefore, we would not rule out that some directional sensitivity also exists within the primary auditory cortex. This would be consistent with electrophysiological studies in cats and monkeys [Ahissar et al., 1992; Sovijärvi and Hyvärinen, 1974; Stumpf et al., 1992] and a recent study showing that motion-specific magnetic potentials are generated in the human primary auditory cortex [Zvyagintsev et al., 2009].
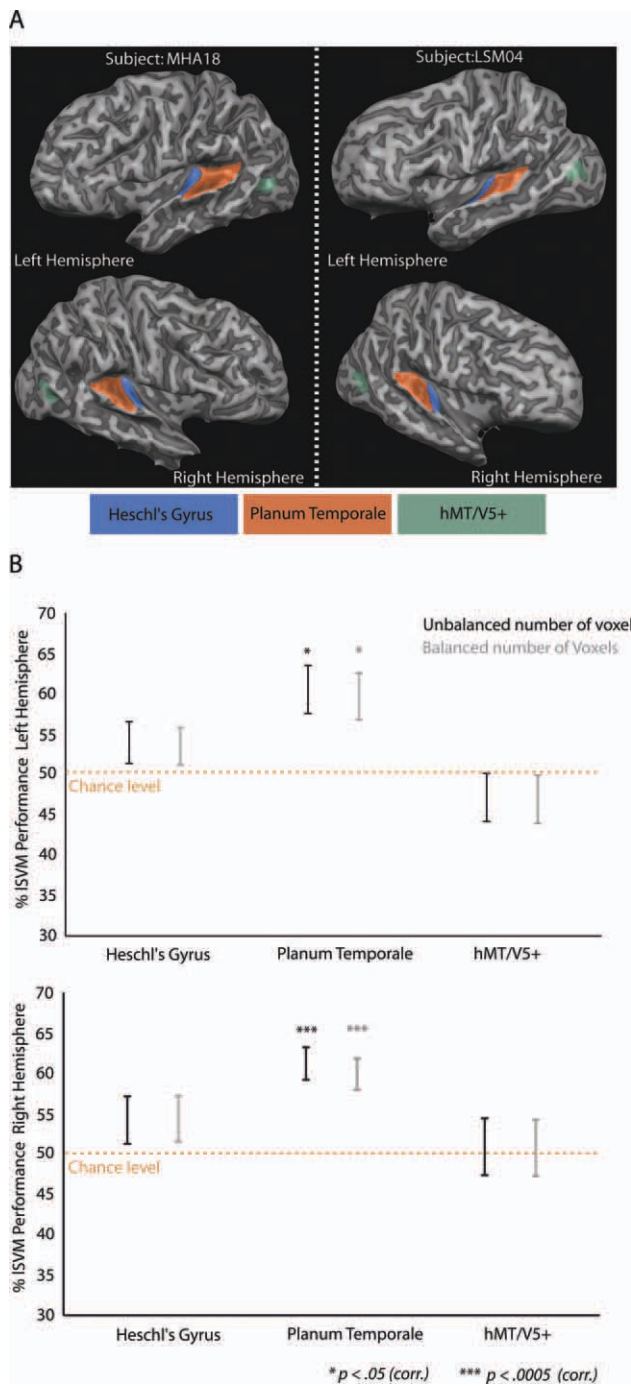
**Figure 4.**

Region-of-interest-based analysis; (**A**) Regions of interest for the Heschl's gyrus, the planum temporale and hMT/V5+ as defined for the two exemplary subjects MHA18 and LSM04. (**B**) Group mean linear support vector machine classification performance for all regions of interest. Error bars represent the standard error of the mean across subjects.

Our searchlight-based analysis, and to some extent also our ROI-based analysis, indicates that auditory-motion-direction sensitivity is more pronounced in the right hemisphere. This appears to be in line with the findings of Baumgart et al. [1999] and with neurophysiological evidence for a specific impairment of auditory motion perception after right-hemisphere lesions [Griffiths et al., 1996]. Furthermore, this finding is in agreement with the suggestion that spatial processing tends to occur more dominantly in the right hemisphere [Corballis, 1991].

In contrast to several previous neuroimaging studies [Ducommun et al., 2002; Griffiths et al., 1998, 2000; Lewis et al., 2000; Pavani et al., 2002; Warren et al., 2002; Xiang et al., 2002; Zimmer and Macaluso, 2009], our study does not provide an indication for the parietal cortex nor frontal cortex being involved in auditory motion processing. This discrepancy is most likely due to fundamental differences in experimental paradigm and data analysis between our study and previous studies. First of all, during our study we compared brain responses to leftwards and rightwards moving sounds while previous studies compared brain responses to moving and static sounds. Second, we investigated brain responses to moving sounds while the attention of our subjects was focused on a visual detection task. Previous studies did not implement such a vigorous control for attention. Third, we investigated effects of auditory motion direction on brain responses by looking for areas in which distributed response patterns differed between left- and rightwards moving sounds. Previous studies, on the other hand, searched for brain areas in which overall responses were higher for moving than for static sounds. How exactly these differences across experiments explain the differences in findings goes beyond the scope of this study. However, we would like to stress that the fact that we did not observe auditory motion direction sensitivity in the frontal and parietal cortex does not necessarily imply that these areas are not important for auditory motion processing as suggested by previous studies.

The second brain area that was found to encode the direction of auditory motion was located in the lateral occipital cortex. This area was located ventrally and more lateral from the location of hMT/V5+ while not spatially overlapping with the location typically reported for the object-selective lateral occipital complex [Larsson and Heeger, 2006; Malach et al., 1995]. Our ROI-based analysis also confirmed that this occipital area is not part of the visual motion complex hMT/V5+. As our data does not allow for a more precise classification of this area we refer to it as high-level visual cortex.

The encoding of sound features in high-level visual cortex suggests that representations of sounds might interact with representations of visual stimuli within the occipital cortex. This would be in line with the finding of the study of Meienbrock et al. [2007] that activation in a lateral occipital area in the right hemisphere is affected by spatial incongruity of audiovisual stimulation as well as with the finding that audiovisual motion direction congruity

facilitates responses in the directly adjacent area hMT/ V5+ [Alink et al., 2008]. This finding also provides support for the idea that the reorganization that allows early-blind subjects to utilize visual cortex to support auditory motion perception [Bedney et al., 2010; Poirier et al., 2006; Renier et al., 2010; Saenz et al., 2008; Wolbers et al., 2011] is based on pre-existing neuronal connections between the auditory and occipital cortex in sighted subjects [Poirier et al., 2005]. Finally, the effect of auditory motion direction on activation within high-level visual cortex might be related to the psychophysical observation that the perceived direction of visual motion can be affected by the direction of moving sounds [Hidaka et al., 2009; Maeda et al. 2004; Meyer and Wuerger, 2001; Meyer et al., 2005; Sadaghiani et al., 2009; Wuerger et al., 2003].

Multivoxel pattern analysis allowed us to detect auditory-motion-direction sensitivity in the human cerebral cortex that would not have been captured by a conventional univariate analysis because none of the motion-sensitive areas reported here responded more strongly to one of the two motion directions. Information being present in areas that do not show an overall BOLD-response amplitude difference between stimulus conditions is in line with previous studies [Harrison and Tong, 2007; Serences and Boynton, 2007; Smith and Muckli, 2010]. This finding raises the question what kind of neural organization allowed us to decode auditory motion direction from multivoxel activation patterns. Kamitani and Tong [2005] suggested that patterns informative about visual grating orientation result from randomly biased sampling of orientation columns in low-level visual cortex by fMRI voxels. Accordingly, each voxel shows a slight preference for a specific orientation and these small preferences are summed up by multivariate analysis techniques. Results from an electrophysiological study by Stumpf et al. [1992] indicate that neurons preferring a specific auditory motion direction in the cat auditory cortex tend to be clustered together. Such a clustering could be the basis of decoding performance in our study.

In conclusion, by analyzing the information content of multivoxel patterns, we showed that auditory motion direction is encoded by activation patterns of the planum temporale. We further showed that responses in high-level visual cortex also contain information about the direction of sound-source motion, suggesting a convergence of motion signals from both modalities in visual cortex.

# REFERENCES

Ahissar M, Ahissar E, Bergman H, Vaadia E (1992): Encoding of sound-source location and movement: Activity of single neurons and interactions between adjacent neurons in the monkey auditory cortex. J Neurophysiol 67:203–215.

Alink A, Singer W, Muckli L (2008): Capture of auditory motion by vision is represented by an activation shift from auditory to visual motion cortex. J Neurosci 28:2690–2697.

Altmann CF, Bledowski C, Wibral M, Kaiser J (2007): Processing of location and pattern changes of natural sounds in the human auditory cortex. Neuroimage 35:1192–1200.

Baumgart F, Gaschler-Markefski B, Woldorff MG, Heinze HJ, Scheich H (1999): A movement-sensitive area in auditory cortex. Nature 400:724–726.

Bedny M, Konkle T, Pelphrey K, Saxe R, Pascual-Leone A (2010): Sensitive period for a multimodal response in human visual motion area MT/MST. Curr Biol 20:1900–1906.

Chang C-C, Lin C-J. 2001. LIBSVM: A library for support vector machines. Software available at http://www.csie.ntu.edu.tw/ ~cjlin/libsvm.

Corbetta M, Akbudak E, Conturo TE, Snyder AZ, Ollinger JM, Drury HA, Linenweber MR, Petersen SE, Raichle ME, Van Essen DC, Shulman GL (1998): A common network of functional areas for attention and eye movements. Neuron 21:761–773.

Corballis MC. 1991. The Lopsided Ape: The Evolution of the Generative Mind. New York, NY: Oxford University Press.

Ducommun CY, Murray MM, Thut G, Bellmann A, Viaud-Delmon I, Clarke S, Michel CM (2002): Segregated processing of auditory motion and auditory location: An ERP mapping study. Neuroimage 16:76–88.

Dumoulin SO, Bittar RG, Kabani NJ, Baker CL Jr, Le Goualher G, Pike GB, Evans AC (2000): A new anatomical landmark for reliable identification of human area V5/MT: A quantitative analysis of sulcal patterning. Cereb Cortex 10:454–463.

Forman SD, Cohen JD, Fitzgerald M, Eddy WF, Mintun MA, Noll DC (1995): Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): Use of a cluster-size threshold. Magn Reson Med 33:636–647.

Franconeri SL, Simons DJ (2003): Moving and looming stimuli capture attention. Percept Psychophys 65:999–1010.

Galaburda A, Sanidess F (1980): Cytoarchitectonic organization of the human auditory cortex. J Comp Neurol 190:597–610.

Gardner WG, Martin KD. 1994. HRTF measurements of a KEMAR dummy-head microphone. MIT Media Lab Perceptual Computing Technical Report #280.

Grantham DW (1989): Motion aftereffects with horizontally moving sound sources in the free field. Percept Psychophys 45:129–136.

Goebel R, Khorram-Sefat D, Muckli L, Hacker H, Singer W (1998): The constructive nature of vision: Direct evidence from functional magnetic resonance imaging studies of apparent motion and motion imagery. Eur J Neurosci 10:1563–1573.

Griffiths TD, Green GGR (1999): Cortical activation during perception of a rotating wide-field acoustic stimulus. Neuroimage 10:84–90.

Griffiths TD, Green GGR, Rees A, Rees G (2000): Human brain areas involved in the analysis of auditory movement. Hum Brain Mapp 9:72–80.

Griffiths TD, Bench CJ, Frackowiak RSJ (1994): Human cortical areas selectively activated by apparent sound movement. Curr Biol 4:892–895.

Griffiths TD, Rees A, Witton C, Shakir RA, Henning GB, Green GGR (1996): Evidence for a sound movement area in the human cerebral cortex. Nature 383:425–427.

Griffiths TD, Rees G, Rees A, Green GGR, Witton C, Rowe D, Büchel C, Turner R, Frackowiak RSJ (1998): Right parietal cortex is involved in the perception of sound movement in humans. Nat Neurosci 1:74–79.

Harris JD, Sergeant RL (1971): Monaural/binaural minimum audible angles for a moving sound source. J Speech Lang Hear Res 14:618–629.

Harrison SA, Tong F (2009): Decoding reveals the contents of visual working memory in early visual areas. Nature 458:632–635.

Haxby JV, Gobbini MI, Furey ML, Ishai A, Schouten JL, Pietrini P (2001): Distributed and overlapping representations of faces and objects in ventral temporal cortex. Science 293:2425–2430.

Haynes JD, Rees GP (2005): Predicting the orientation of invisible stimuli from activity in human primary visual cortex Nat Neurosci 8:686–691.

Hidaka S, Manaka Y, Teramoto W, Sugita Y, Miyauchi R, Gyoba J, Suzuki Y, Iwaya Y (2009): Alternation of sound location induces visual motion perception of a static object. PLoS One 4:e8188.

Kamitani Y, Tong F (2005): Decoding the visual and subjective contents of the human brain. Nat Neurosci 8:679–685.

Kamitani Y, Tong F (2006): Decoding seen and attended motion directions from activity in the human visual cortex. Curr Biol 16:1096–1102.

Kim JJ, Crespo-Facorro B, Andreasen NC, O'Leary DS, Zhang B, Harris G, Magnotta VA (2000): An MRI-based parcellation method for the temporal lobe. Neuroimage 11:271–288.

Kriegeskorte N, Formisano E, Sorger B, Goebel R (2007): Individual faces elicit distinct response patterns in human anterior temporal cortex. Proc Natl Acad Sci USA 104:20600–20605.

Kriegeskorte N, Goebel R, Bandettini P (2006): Information-based functional brain mapping. Proc Natl Acad Sci USA 103:3863–3868.

Larsson J, Heeger DJ (2006): Two retinotopic visual areas in human lateral occipital cortex. J Neurosci 26:13128–13142.

Lewis JW, Beauchamp MS, DeYoe EA (2000): A comparison of visual and auditory motion processing in human cerebral cortex. Cereb Cortex 10:873–888.

Maeda F, Kanai R, Shimojo S (2004): Changing pitch induced visual motion illusion. Curr Biol 14:R990–R991.

Malach R, Reppas JB, Benson RR, Kwong KK, Jiang H, Kennedy WA, Ledden PJ, Brady TJ, Rosen BR, Tootell RB (1995): Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc Natl Acad Sci USA 92:8135–8139.

Meienbrock A, Naumer MJ, Doehrmann O, Singer W, Muckli L (2007): Retinotopic effects during spatial audio-visual integration. Neuropsychologia 45:531–539.

Meyer GF, Wuerger SM (2001): Cross-modal integration of auditory and visual motion signals. Neuroreport 12:2557–2560.

Meyer GF, Wuerger SM, Röhrbein F, Zetzsche C (2005): Low-level integration of auditory and visual motion signals requires spatial co-localisation. Exp Brain Res 166:538–547.

Norman KA, Polyn SM, Detre GJ, Haxby JV (2006): Beyond mind-reading: Multi-voxel pattern analysis of fMRI data. Trends Cogn Sci 10:424–430.

Pavani F, Macaluso E, Warren JD, Driver J, Griffiths TD (2002): A common cortical substrate activated by horizontal and vertical sound movement in the human brain. Curr Biol 12:1584–1590.

Perrott DR, Musicant AD (1977): Minimum auditory movement angle: Binaural localization of moving sound sources. J Acoust Soc Am 62:1463–1466.

Poirier C, Collignon O, DeVolder AG, Renier L, Vanlierde A, Tranduy D, Scheiber C (2005): Specific activation of the V5 brain area by auditory motion processing: An fMRI study. Brain Res Cogn Brain Res 25:650–658.

Poirier C, Collignon O, Scheiber C, Renier L, Vanlierde A, Tranduy D, Veraart C, De Volder AG (2006): Auditory motion perception activates visual motion areas in early blind subjects. Neuroimage 31:279–285.

Rademacher J, Caviness VS Jr, Steinmetz H, Galaburda AM (1993): Topographical variation of the human primary cortices: Implications for neuroimaging, brain mapping, and neurobiology. Cereb Cortex 3:313–329.

Rademacher J, Morosan P, Schormann T, Schleicher A, Werner C, Freund H-J, Zilles K (2001): Probabilistic mapping and volume measurement of human primary auditory cortex. Neuroimage 13:669–683.

Recanzone GH, Sutter ML (2008): The biological basis of audition. Annu Rev Psychol 59:119–142.

Reddy L, Tsuchiya N, Serre T (2010): Reading the mind's eye: Decoding category information during mental imagery. Neuroimage 50:818–825.

Renier LA, Anurova I, De Volder AG, Carlson S, VanMeter J, Rauschecker JP (2010): Preserved functional specialization for spatial processing in the middle occipital gyrus of the early blind. Neuron 68:138–148.

Sadaghiani S, Maier JX, Noppeney U (2009): Natural, metaphoric, and linguistic auditory direction signals have distinct influences on visual motion processing. J Neurosci 29:6490–6499.

Saenz M, Lewis LB, Huth AG, Fine I, Koch C (2008): Visual motion area MT/V5 responds to auditory motion in human sight-recovery subjects. J Neurosci 28:5141–5148.

Serences JT, Boynton GM (2007): Feature-based attentional modulations in the absence of direct visual stimulation. Neuron 55:301–312.

Smith KR, Saberi K, Hickok G (2007): An event-related fMRI study of auditory motion perception: No evidence for a specialized cortical system. Brain Res 1150:94–99.

Smith FW, Muckli L (2010): Nonstimulated early visual areas carry information about surrounding context. Proc Natl Acad Sci USA 107:20099–20103.

Sovijärvi ARA, Hyvärinen J (1974): Auditory cortical neurons in the cat sensitive to the direction of sound source movement. Brain Res 73:455–471.

Stumpf E, Toronchuk JM, Cynader MS (1992): Neurons in cat primary auditory cortex sensitive to correlates of auditory motion in three-dimensional space. Exp Brain Res 88:158–168.

Talairach J, Tournoux P. 1988. Co-Planar Stereotaxic Atlas of the Human Brain: 3-Dimensional Proportional System—An Approach to Cerebral Imaging. New York, NY: Thieme Medical Publishers.

Warren JD, Zielinski BA, Green GGR, Rauschecker JP, Griffiths TD (2002): Perception of sound-source motion by the human brain. Neuron 34:139–148.

Wightman FL, Kistler DJ (1989): Headphone simulation of free-field listening. I. Stimulus synthesis. J Acoust Soc Am 85:858–867.

Wolbers T, Zahorik P, Giudice NA (2011): Decoding the direction of auditory motion in blind humans. Neuroimage (in press).

Wuerger SM, Hofbauer M, Meyer GF (2003): The integration of auditory and visual motion signals at threshold. Percept Psychophys 65:1188–1196.

Xiang J, Chuang S, Wilson D, Otsubo H, Pang E, Holowka S, Sharma R, Ochi A, Chitoku S (2002): Sound motion evoked magnetic fields. Clin Neurophysiol 113:1–9.

Zimmer U, Macaluso E (2009): Interaural temporal and coherence cues jointly contribute to successful sound movement perception and activation of parietal cortex. Neuroimage 46:1200–1208.

Zaitsev M, Hennig J, Speck O (2004): Point spread function mapping with parallel imaging techniques and high acceleration factors: Fast, robust, and flexible method for echo-planar imaging distortion correction. Magn Reson Med 52:1156–1166.

Zvyagintsev M, Nikolaev AR, Thönnessen H, Sachs O, Dammers J, Mathiak K (2009): Spatially congruent visual motion modulates activity of the primary auditory cortex. Exp Brain Res 198:391–402.