

# A Common Cortical Substrate Activated by Horizontal and Vertical Sound Movement in the Human Brain

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## Summary

Perception of movement in acoustic space depends on comparison of the sound waveforms reaching the two ears (binaural cues) as well as spectrotemporal analysis of the waveform at each ear (monaural cues) [1]. The relative importance of these two cues is different for perception of vertical or horizontal motion, with spectrotemporal analysis likely to be more important for perceiving vertical shifts. In humans, functional imaging studies have shown that sound movement in the *horizontal* plane activates brain areas distinct from the primary auditory cortex, in parietal and frontal lobes [2–7] and in the planum temporale [6, 8]. However, no previous work has examined activations for *vertical* sound movement. It is therefore difficult to generalize previous imaging studies, based on horizontal movement only, to multidimensional auditory space perception. Using externalized virtual-space sounds in a functional magnetic resonance imaging (fMRI) paradigm to investigate this, we compared vertical and horizontal shifts in sound location. A common bilateral network of brain areas was activated in response to both horizontal and vertical sound movement. This included the planum temporale, superior parietal cortex, and premotor cortex. Sounds perceived laterally in virtual space were associated with contralateral activation of the auditory cortex. These results demonstrate that sound movement in vertical and horizontal dimensions engages a common processing network in the human cerebral cortex and show that multidimensional spatial properties of sounds are processed at this level.

## Results and Discussion

All experimental stimuli were delivered in free field before scanning took place (see Figure 1) and were recorded individually from each participant's ear canal. In

this way, stimuli were convolved with each subject's own pinna and head-related transfer function to produce the perception of sound externalized in space [9]. Such a recording method automatically takes into account individual differences in pinna and head transfer functions and results in better externalized percepts than those obtained with the use of generic head-related transfer functions [10, 11]. During playback, stereo stimuli were presented over headphones. All participants reported the perception of an externalized sound image for both stationary and moving stimuli, with the latter heard to move continuously. All stimuli were perceived as originating in front of the head and were lateralized to either the left or the right. Behavioral testing before scanning demonstrated that all subjects could also reliably distinguish between vertical and horizontal movement in a two-alternative forced-choice task. ("Vertical" or "horizontal" responses, regardless of stimulus hemifield, to 20 moving stimuli for each direction [vertical or horizontal] and side [left or right] were recorded. Percent accuracy across experiments was as follows: vertical movement left = 90%, vertical movement right = 80%, horizontal movement left = 85%, and horizontal movement right = 93%.) During scanning, participants were required to fixate a central white cross and pay attention to the auditory stimuli. A remote eye-tracker (ASL Model 504) did not detect any losses of fixation during the scanning session.

In the first fMRI study (experiment 1), participants were presented with seven auditory conditions: two stationary conditions (in the left or right hemifield), two vertical-movement conditions (in the left or right hemifield), two horizontal-movement conditions (in the left or right hemifield), and silence. When all sound conditions were compared with silence, bilateral activation was observed in the superior temporal plane. This involved Heschl's gyrus but also extended anteriorly into the planum polare and posteriorly into the planum temporale (Figure 2 and Table 1). In each hemisphere, a circumscribed area in the superior temporal plane was more active in response to contralateral than ipsilateral virtual stimuli. When the effect of the perceived hemifield of the stimulus was examined (left minus right stimuli or right minus left stimuli), increased activation was observed in the region of the primary auditory cortex (Heschl's gyrus [12, 13]) contralateral to the perceived side. As can be seen in the yellow and turquoise plots of Figure 2, although activation in these areas was predominantly driven by contralateral virtual sounds, some response to ipsilateral virtual sounds was also present.

Further analysis addressed the hypothesis that vertical and horizontal sound movement may activate similar areas. A conjunction analysis based on the common effect of vertical and horizontal movement versus stationary sound revealed a network of areas active for sound movement—regardless of its dimension (i.e., motion in azimuth and motion in elevation). This network involved the intraparietal sulcus, superior temporal plane, precentral gyrus, and cerebellum in both hemi-

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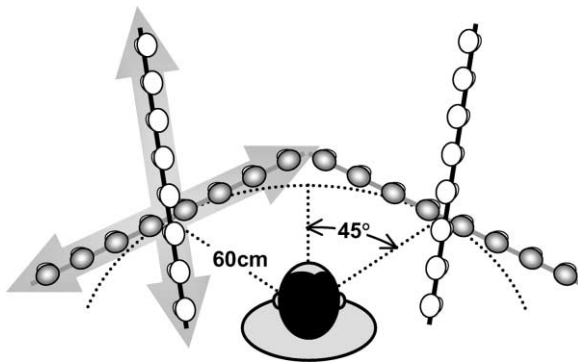


Figure 1. Schematic of the Free-Field Setup Used for Individual Recordings Prior to Scanning

Stimuli were delivered through an array of eight small speakers (Sony SRS-P3, 8  $\Omega$ , 0.4 W) mounted on a 150 cm straight plastic bar (neighboring speakers were separated by 20 cm). The bar was attached to a stand via a pivoting arm, so that it could be rotated into a vertical or horizontal position (all possible bar positions shown). For recording *horizontal-movement* stimuli, the loudspeaker array was horizontally aligned with the participant's ear level (it was tangentially oriented with respect to an imaginary 60 cm -radius circle centered on the subject's head; the center of the array was 45 degrees right or left, and the extension range was  $0^\circ$  to  $\pm 90^\circ$ ). Two directions of azimuthal motion were recorded: left to right and vice-versa. For recording *vertical-movement* stimuli, the loudspeaker array was rotated vertically and aligned so the third loudspeaker from the bottom was now at ear level. Two directions of vertical motion (range  $+60^\circ$  to  $-30^\circ$ ) were recorded: up to down and vice-versa. For the recording of *stationary* stimuli, the amplitude-modulated noise was delivered through a single speaker at ear level.

spheres (see Figure 3 and Table 1). As can be seen in Figure 3 (experiment 1, shown in yellow), activation in the superior temporal gyrus was posterior to Heschl's gyrus and extended medially into the planum temporale in both the left and the right hemisphere. This demonstrates that brain areas distinct from the primary auditory cortex, in parietal and frontal lobes as well as in the planum temporale, are activated by processing moving auditory objects *regardless* of their dimension (i.e., vertical or horizontal).

To investigate any possible differences in brain activation between sound movement in vertical and horizontal dimensions, we next contrasted the two movement conditions directly. Neither of the contrasts (horizontal movement minus vertical movement or vertical movement minus horizontal movement) showed activation at a corrected threshold of  $p < 0.05$ . However, when a less stringent threshold ( $p$ -uncorrected  $< 0.001$ ) was adopted, the vertical-minus-horizontal contrast revealed an area of activation in the left planum ( $[-62, -26, 4]$ ,  $Z = 3.59$ ); this area lay more laterally than the planum temporale activation in the conjunction analysis ( $[-46, -32, 6]$ ).

To further address the possibility of any differential activation between vertical and horizontal sound movement, we conducted a second fMRI study (experiment 2), in which we increased the number of trials in the vertical and horizontal conditions to obtain more power for their direct contrasts (see Experimental Procedures). Areas of activation in experiment 2 are listed in Table

1. No significant area of activation emerged when vertical and horizontal movement were directly contrasted (horizontal minus vertical movement or vertical minus horizontal movement). On the other hand, a conjunction analysis of the contrast between combined vertical and horizontal movement versus stationary sound essentially replicated the network of areas observed in the previous experiment (compare experiment 1 and experiment 2 in Figure 3). This network again comprised the intraparietal sulcus, superior temporal gyrus, precentral gyrus, and cerebellum. Unlike results from experiment 1, activations in the right superior temporal gyrus and left intraparietal sulcus no longer reached corrected significance.

Experiment 2 also allowed further tests for contralaterality effects in the auditory cortex. When the effect of the perceived hemifield for the virtual sound was examined (combined left minus combined right stimuli or combined right minus combined left stimuli), increased activation was again observed in the region of the contralateral primary auditory cortex (see Table 1).

Taken together, the results of these two experiments demonstrated a shared network for processing horizontal *and* vertical shifts of sound location in the human cortex. When compared to the stationary condition, sound-movement in both azimuth and elevation activated a common bilateral network of cortical areas beyond the primary auditory cortex; this network involved the planum temporale, superior parietal lobule, and prefrontal cortex. One possible interpretation of the activation due to horizontal motion in this experiment and in previous work [6] is that horizontal motion might produce activity in more neurons whose receptive fields are tuned in azimuth than the fixed control stimulus. However, the present results are based on a much more limited spatial "sweep" in azimuth than those of the previous experiment. Moreover, we found very similar activation for the vertical-motion condition, whereas the spatial tuning of auditory neurons can be broader in elevation than in azimuth (e.g., [14]). Our results may therefore be consistent with mechanisms specific to the computation of movement in acoustic space for the demonstrated network.

Activation in the parietal and prefrontal cortex during auditory spatial tasks has been previously demonstrated in imaging studies of sound movement confined to the horizontal dimension [4–7, 15, 16]. It has also been observed in imaging studies that required matching the azimuthal position of two sequential sounds (e.g., [17–19]). Our results extend this finding to sound movement in the vertical plane and suggest that parietal and prefrontal cortices are involved in perception of multidimensional spatial properties of sounds.

This conclusion is supported by lesion studies in humans. Several lines of evidence indicate that damage to the right parietal cortex produces auditory spatial deficits for contralesional sounds in the horizontal dimension (e.g., [3, 20–22]). One recent study has shown that right parietal lesions can result in contralateral deficits of sound localization in the vertical dimension also [23]. The results of the present study may shed new light on these neuropsychological findings and may indicate the parietal cortex as a common neural substrate for sound localization in both azimuth and elevation.

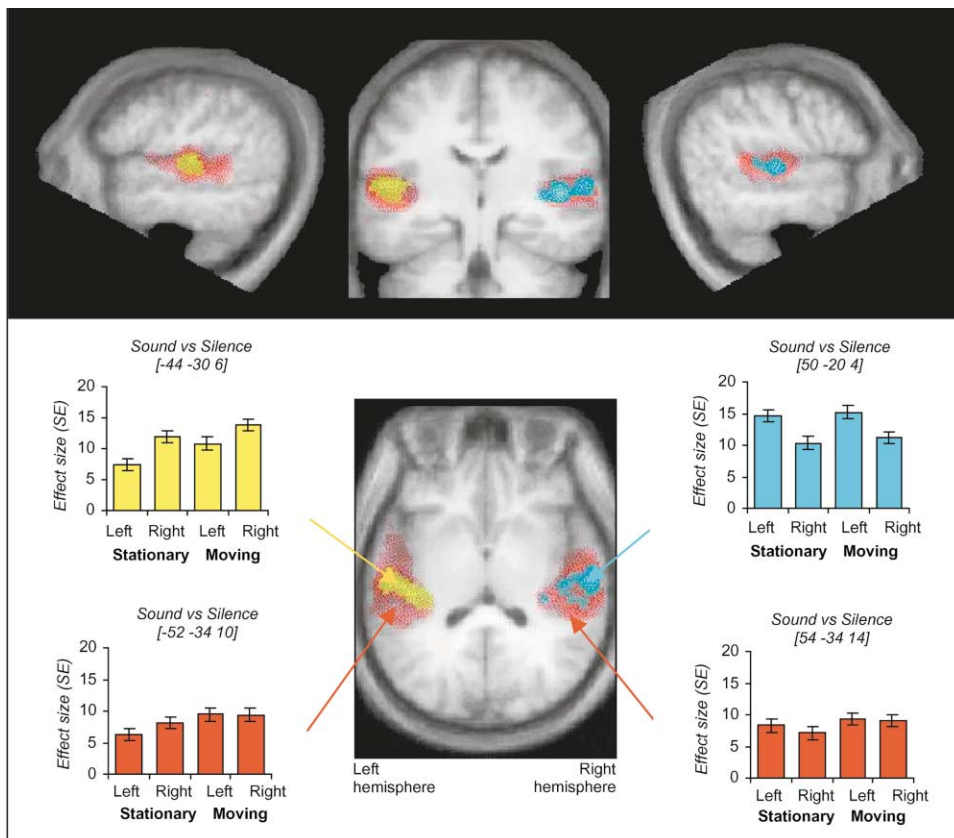


Figure 2. Main Effects of Sound and Perceived Stimulus Side

Main effects of sound versus silence (red, yellow, and turquoise); right sounds versus left sounds (yellow) or left sounds versus right sounds (turquoise) in experiment 1 were plotted on a mean structural image of the six subjects. The image is tilted in the pitch plane by  $-0.5$  radians so that the axial section is placed through the superior temporal plane. All activations shown are significant at  $p$ -uncorrected  $< 0.001$ . Effect sizes in the plots shown for the individual maxima are expressed with standard errors. Each plot shows that sound conditions are activated above silence (note the positive values in the red, yellow, and turquoise plots). Yellow and turquoise plots also display main effect of side, whereas red plots show more posterior regions that did not reveal any side-dependent effect.

The combined effects of vertical and horizontal sound movement, minus stationary sound, also produced activation in the planum temporale, the region of the superior temporal plane posterior to Heschl's gyrus. Although this cortical region has long been regarded as a language processor, there is increasing evidence of its involvement in processing a range of different sounds with complex spectrotemporal structures (for review, see [24]). Our results clearly confirm the role of the planum temporale in auditory spatial analysis during sound movement, consistent with previous functional imaging studies [6, 8]. Moreover, they further suggest that a generic spatial processing mechanism might exist in the planum temporale for auditory objects moving in either azimuth or elevation. It was beyond the scope of this study to establish whether such activation reflects similar processing in the planum temporale for both the spectral and binaural auditory cues contributing to sound movement perception. However, our approach of using virtual auditory space could be extended further to test whether differential activation in the planum temporale may emerge when sound movement can be encoded solely on the basis of purely monaural or purely binaural cues.

A final important aspect of the present results is the

strong contralaterality observed in the region of the primary auditory cortex. Although differential activation of the two auditory cortices has been observed previously with monaural stimuli [25], it has not been found with binaural stimuli that were heard as lateralized within the head on the basis of interaural time differences alone (ITD; [25]). The strong contralaterality observed with the externalized virtual binaural sounds used here is consistent with the representation of higher-order spatial properties of the acoustic stimulus in the primary auditory cortex as shown by animal work [26].

In conclusion, the results of the present study suggest common processing of auditory space in both azimuth and elevation, at and beyond the planum temporale, in a cortical network that has been proposed as the human homolog of the posterior/dorsal processing stream for auditory spatial information in the macaque ([27]; for evidence in humans, see [19, 28, 29]). Our findings suggest that this network may be involved in the perception of multidimensional sound movement.

#### Experimental Procedures

Six participants took part in experiment 1 (four men and two women, mean age 30 years, range 28–33 years, two left-handed by self

Table 1. Coordinates of Local Maxima and Z Scores for Experiments 1 and 2

| Anatomical Area                                       | Experiment 1     |         |        | Experiment 2     |         |        |
|---|------------------|---------|--------|------------------|---------|--------|
|   | Coordinates (mm) | Z Score | p-corr | Coordinates (mm) | Z Score | p-corr |
| <b>Effect of Any Sound</b>                            |                  |         |        |                  |         |        |
| Combined sound conditions > rest                      |                  |         |        |                  |         |        |
| Right superior temporal gyrus                         | 56               | -18     | 8      | Inf              | 0.0001  |        |
| Left superior temporal gyrus                          | -50              | -20     | 4      | Inf              | 0.0001  |        |
| Left precentral gyrus                                 | -50              | -4      | 52     | 5.14             | 0.008   |        |
| <b>Effect of Perceived Hemifield of Sound</b>         |                  |         |        |                  |         |        |
| Combined right sounds > combined left sounds          |                  |         |        |                  |         |        |
| Left superior temporal gyrus                          | -44              | -30     | 6      | 6.73             | 0.0001  |        |
| Combined left sounds > combined right sounds          |                  |         |        |                  |         |        |
| Right superior temporal gyrus                         | 50               | -20     | 4      | 7.41             | 0.0001  |        |
| Conjunction Vertical > Static and Horizontal > Static |                  |         |        |                  |         |        |
| Coordinates (mm)                                      |                  |         |        |                  |         |        |
| Z Score   |                  |         |        |                  |         |        |
| p-corr  |                  |         |        |                  |         |        |
| <b>Effect of Moving Versus Static Sounds</b>          |                  |         |        |                  |         |        |
| Left precentral gyrus                                 | -40              | -6      | 60     | 7.72             | 0.0001  |        |
| Left superior temporal gyrus                          | -46              | -32     | 6      | 5.85             | 0.0001  |        |
| Left superior parietal lobule                         | -30              | -54     | 64     | 7.53             | 0.0001  |        |
| Left cerebellum                                       | -14              | -76     | -44    | 4.98             | 0.03    |        |
| Right precentral gyrus                                | 40               | -4      | 62     | 5.23             | 0.009   |        |
| Right superior temporal gyrus                         | 64               | -8      | 0      | 4.48             | 0.03    |        |
| Right intraparietal sulcus                            | 48               | -40     | 56     | 5.98             | 0.0001  |        |
| Right cerebellum                                      | 22               | -64     | -46    | 6.13             | 0.0001  |        |
| Conjunction Vertical > Static and Horizontal > Static |                  |         |        |                  |         |        |
| Coordinates (mm)                                      |                  |         |        |                  |         |        |
| Z Score   |                  |         |        |                  |         |        |
| p-corr  |                  |         |        |                  |         |        |
| Left precentral gyrus                                 | -40              | -6      | 60     | 7.72             | 0.0001  |        |
| Left superior temporal gyrus                          | -46              | -32     | 6      | 5.85             | 0.0001  |        |
| Left superior parietal lobule                         | -30              | -54     | 64     | 7.53             | 0.0001  |        |
| Left cerebellum                                       | -14              | -76     | -44    | 4.98             | 0.03    |        |
| Right precentral gyrus                                | 40               | -4      | 62     | 5.23             | 0.009   |        |
| Right superior temporal gyrus                         | 64               | -8      | 0      | 4.48             | 0.03    |        |
| Right intraparietal sulcus                            | 48               | -40     | 56     | 5.98             | 0.0001  |        |
| Right cerebellum                                      | 22               | -64     | -46    | 6.13             | 0.0001  |        |
| Conjunction Vertical > Static and Horizontal > Static |                  |         |        |                  |         |        |
| Coordinates (mm)                                      |                  |         |        |                  |         |        |
| Z Score   |                  |         |        |                  |         |        |
| p-corr  |                  |         |        |                  |         |        |
| Left precentral gyrus                                 | -40              | -6      | 60     | 7.72             | 0.0001  |        |
| Left superior temporal gyrus                          | -46              | -32     | 6      | 5.85             | 0.0001  |        |
| Left superior parietal lobule                         | -30              | -54     | 64     | 7.53             | 0.0001  |        |
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| Right intraparietal sulcus                            | 48               | -40     | 56     | 5.98             | 0.0001  |        |
| Right cerebellum                                      | 22               | -64     | -46    | 6.13             | 0.0001  |        |
| Conjunction Vertical > Static and Horizontal > Static |                  |         |        |                  |         |        |
| Coordinates (mm)                                      |                  |         |        |                  |         |        |
| Z Score   |                  |         |        |                  |         |        |
| p-corr  |                  |         |        |                  |         |        |
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| Right superior temporal gyrus                         | 64               | -8      | 0      | 4.48             | 0.03    |        |
| Right intraparietal sulcus                            | 48               | -40     | 56     | 5.98             | 0.0001  |        |
| Right cerebellum                                      | 22               | -64     | -46    | 6.13             | 0.0001  |        |

In experiment 1, all p values were corrected for the entire brain volume. In experiment 2, all p values were corrected by small-volume correction [38] based on the loci of activation for the same contrasts in experiment 1.

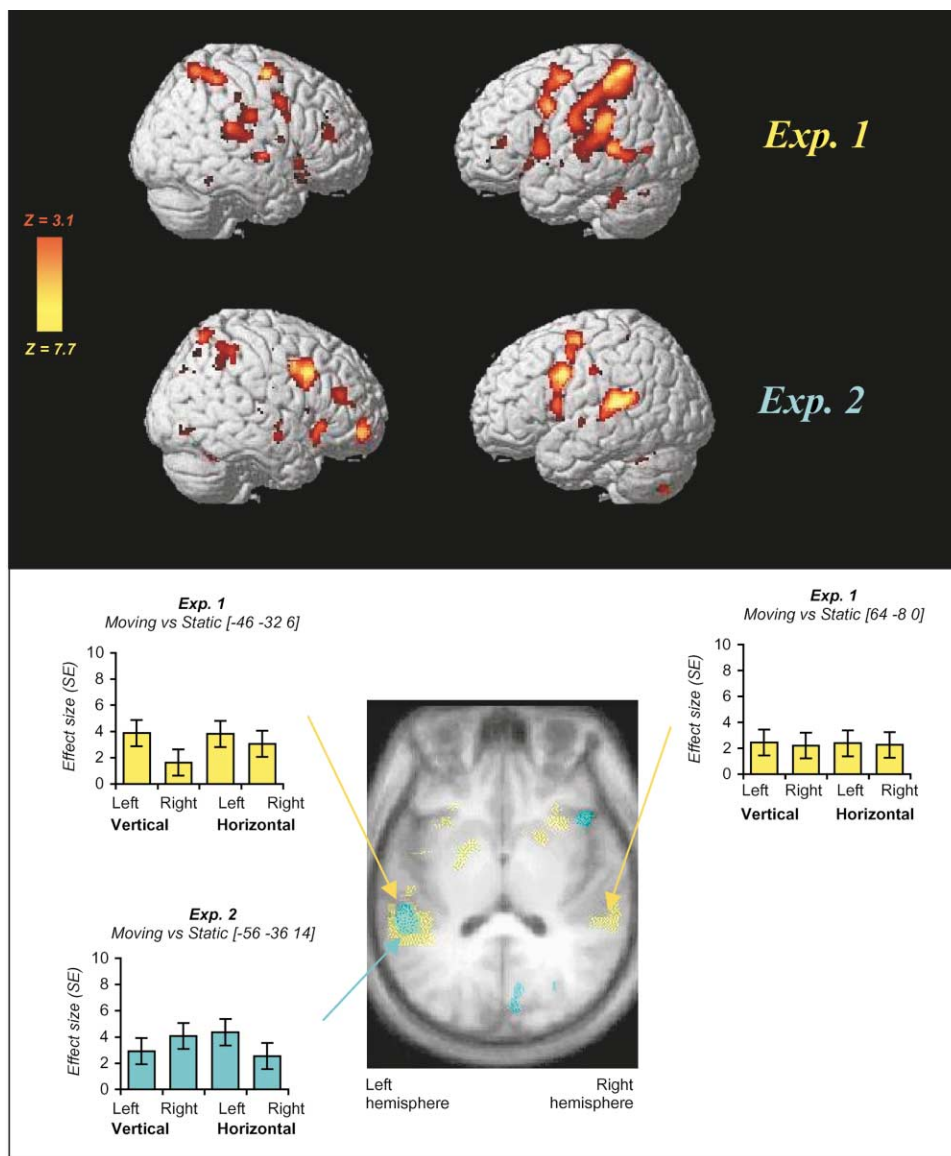


Figure 3. Combined Vertical and Horizontal Movement versus Stationary Sound

Combined vertical and horizontal movement, versus stationary sounds, in experiment 1 (upper row of lateral views and yellow plots) and experiment 2 (lower row of lateral views and turquoise plot). Activation was rendered on a lateral view of a standard brain. An axial slice was averaged from structural images of all subjects and tilted in the pitch plane by  $-0.5$  radians. All activations shown were significant at  $p$ -uncorrected  $< 0.001$ . Plots refer to activation in the planum temporale. Effect sizes in the plots shown for the individual maxima are expressed with standard errors. Note that they are all above zero.

report) and six in experiment 2 (six men and one woman, mean age 29 years, range 29–38 years, two left-handed by self report). None had any history of hearing loss or neurological disorder, and all had normal structural MRI scans. Experiments were carried out with the approval of the Ethics Committee of the National Hospital for Neurology and Neurosurgery. Each scanning session lasted approximately 1.5 hr.

The setup used for free-field recording is shown in Figure 1. Sound movement was simulated by sequential activation of each speaker in the array in strict spatial order for 50 ms (total duration of the resulting auditory object was thus 400 ms), while continuous broad-band noise was played (passband 1 Hz 20 KHz) at 60 dB sound pressure level (SPL). The noise was amplitude modulated, via 80% sinusoidal modulation at one of two rates (100 Hz or 200 Hz), to produce an extra cue for localization [30] and to prevent habituation

to the stationary stimulus. Loudspeakers were connected to a laptop computer (Dell Latitude LS) through a custom electronic interface (via DAQCard-6533, National Instruments). Timing of stimuli and generation of broad-band noise was controlled via the laptop computer with custom software developed with Cogent 2000 [31]. The acoustic waveform resulting from the free-field sound was recorded through miniature microphones (Knowles Electret) placed within each ear canal. The microphone output was amplified to a peak value of less than 1 V and recorded digitally at a sample rate of 44,100 Hz.

During scanning, individualized digital stimuli were played back to each subject on a custom electrostatic system [32] at 70 dB sound pressure level (SPL). In all sound conditions, subjects listened to 8 s of stimulation, in which eight sequential sound objects (each lasting 400 ms and followed by a 600 ms silence gap) were presented

in left or right virtual space. During sound-movement conditions, sound objects appeared subjectively to move smoothly in either a vertical or horizontal direction. Within these movement planes, direction of movement alternated every 1000 ms (upward or downward for elevation movements; leftward or rightward for azimuthal movements). During the stationary conditions, subjects listened to a sequence of stationary targets originating from an externalized virtual position of  $\pm 45$  degrees in azimuth.

Images were acquired with a VISION scanner operating at 2 Tesla (Siemens Erlangen, Germany) with gradient echo planar imaging. Each volume comprised 48 contiguous 1.8 mm slices with an in-plane resolution of 3 by 3 mm. In experiment 1, 160 scans were acquired for each participant in two sessions (40 volumes for each of the stationary conditions and 16 volumes for each movement condition and silence; more volumes were acquired for the stationary condition to allow orthogonality of the effect of interest in the conjunction analysis; see below). In experiment 2, 192 scans were acquired for each participant in four sessions (32 volumes for each of the six conditions).

In both experiments, to avoid stimuli being masked by the intense bursts of stray acoustic noise generated by the MR scanner, we adopted a "sparse" imaging paradigm [33] (TR/TE = 12000/40 ms; TA = 3.6 s).

For both experiments, preprocessing and analysis were carried out with SPM99 [34]. Scans were realigned and spatially normalized to the Montreal Neurological Institute (MNI) standard space [35]; the mean of the functional images was used for this purpose. Spatial smoothing was carried out with a gaussian filter with full width at a half maximum FWHM of 8 mm. In each experiment, data were fitted via multiple regression that modeled experimental conditions, sessions, and the interaction between the two. Linear contrasts were used for comparing the parameters of the multiple regression for the different conditions across sessions. For the critical comparison of the common effect of vertical and horizontal sound movement versus stationary sounds, we used a conjunction analysis [36, 37]. To ensure orthogonality of the effects of interest, we randomly assigned each of the stationary conditions to two separate covariates.

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