Right parietal cortex is involved in the perception of sound movement in humans

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Changes in the delay (phase) and amplitude of sound at the ears are cues for the analysis of sound movement. The detection of these cues depends on the convergence of the inputs to each ear, a process that first occurs in the brainstem. The conscious perception of these cues is likely to involve higher centers. Using novel stimuli that produce different perceptions of movement in the presence of identical phase and amplitude modulation components, we have demonstrated human brain areas that are active specifically during the perception of sound movement. Both functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) demonstrated the involvement of the right parietal cortex in sound movement perception with these stimuli.

The perception of movement in auditory space by humans depends on a number of cues. The movement of sounds in space produces changes in the sound considered at each ear alone[1] and changes in the relative phase and amplitude of the sound's spectral components between the two ears[2]. For broad spectrum sounds, the spatial filtering properties of the pinnae[3] provide another cue for the perception of spatial sound properties and are responsible for the external quality of the perception.

The neural basis for the perception of sound movement is not firmly established by animal work. The detection of differences in sound phase and amplitude at the two ears depends on the convergence of the inputs to each ear. This convergence first occurs in nuclei of the superior olive in the brainstem[4,5]. Neurons sensitive to changing sound phase or amplitude cues at the two ears have been described in the inferior colliculus[6] and primary auditory cortex[7]. The detection of cues based on the spectral shape of sound may depend on a different brainstem pathway. Neurons in the auditory cortex have also been shown to be selectively activated by the actual movement of sounds in space[8]. Animal lesions that involve the primary auditory cortex produce a deficit in the performance of tasks based on the detection of dynamic phase differences between the ears[9].

The auditory pathway described in animals from the cochlea to the auditory cortex is therefore necessary for the perception of sound movement. Human lesion work also suggests that the convergence of the inputs to the two ears in the brainstem is important for the detection of interaural cues that produce a perception of sound movement[10]. However, another human lesion study suggests that sound movement perception depends on processing beyond the auditory cortex in the right hemisphere[11], and that the pathway up to the auditory cortex is therefore not sufficient to underlie the perceptual process.

This study specifically addresses the question of which brain areas are responsible for the conscious perception of sound movement in humans, as opposed to the simple detection of the underlying cues. The study's hypothesis was that sound movement perception depends on processing in cortical areas beyond the primary auditory cortex. We have used novel stimuli that contain identical changes in the phase and amplitude at the two ears but produce different perceptions of sound movement. These stimuli allow us to identify brain areas where activity increases with the perception of sound movement. That activity has been measured in two separate experiments by BOLD (blood oxygen level-dependent) fMRI response and by regional cerebral blood flow as measured by PET.

Results

Psychophysical data

All subjects underwent psychophysical testing using a novel 500-Hz stimulus, presented over one second, containing a linear change in both the phase and the amplitude difference between the ears. Considered alone, both the phase and the amplitude change may be perceived as sound movement toward one side. When the directions of the perceived movements generated by these two cues are opposite to one another, cancellation or trading can occur; the stimulus is a dynamic extension for those used in static time-intensity trading experiments[12]. For all subjects, a point could be defined at which there was exact cancellation of the movement percept due to the two cues and a single static sound image was perceived in the midline (**Fig. 1**). The point of cancellation for the phase and amplitude ramps varied between subjects (**Table 1**). The mean amplitude/phase ratio at the point of trading was 0.86 (standard deviation 0.34).

During the PET and fMRI experiments, subjects were presented with two sound conditions (**Fig. 2**). The cancel condition represents the dynamic time-intensity-traded stimulus discussed above.

During the 'cancel' epochs, subjects listened to repeated stimuli containing phase and amplitude modulations, set at the point of cancellation so that there was no perceived movement. During the 'add' epochs, subjects listened to stimuli containing phase and amplitude changes of the same magnitude as in the cancel condition, but the direction of perceived movement due to either the phase or amplitude change was in the same direction, so that there was a strong resultant perception of movement. For the add condition, all subjects clearly perceived movement of the sound over one second to a point at least halfway between the midline and the maximum possible lateral displacement. In the add condition, the direction of perceived movement was randomized. Thus, the add and cancel conditions represent stimuli that produce different percepts despite containing the same component phase and amplitude cues. This allows the stimuli to reveal areas involved in the perception of sound movement, as opposed to the detection of the component cues.

At the start of each scanning session, subjects were played prolonged runs of either the add or cancel condition. All subjects reported single fused percepts corresponding to the individual sounds in either condition. For the add condition, all subjects performed at 100% level for the identification of the direction of movement under scanning conditions. For the cancel condition, all subjects scored at 50% (chance) level.

Table 1. Cancellation point for each subject.

Subject	Rate of interaural amplitude change at trade point, k_1 (s^{-1})	Rate of interaural phase change at trade point, k_2 (s^{-1})	Trading ratio amplitude/phase
1	0.10	0.22	0.43
2	0.10	0.17	1.43
3	0.15	0.12	1.25
4	0.10	0.16	0.62
5	0.15	0.10	1.50
6	0.10	0.14	0.71
7	0.15	0.16	0.94
8	0.10	0.14	0.71

One subject (subject 2) took part in both experiments. The rates of amplitude and phase changes have the dimensions of s^{-1} as the amplitude changes over the one second presentation (proportional change in sound pressure) and phase changes (radians) are both dimensionless.

fMRI STUDY

During the fMRI study, subjects listened to 40 second epochs of either the add or cancel condition, alternating with rest. Over the 40 seconds, subjects were presented with 33 stimuli. Figure 3a shows the comparison between the fMRI BOLD responses for the add (288 scans) and cancel (288 scans) conditions, based on a group analysis using statistical parametric mapping. Significant activation of posterior parietal cortex occurred in two areas in the right inferior parietal lobule (Brodmann area, BA40), in the right superior parietal lobule (BA 7), and in the left inferior and left superior parietal lobules. Analysis of the BOLD signal change between conditions for individual subjects showed a consistent increase in the three subjects in the more superior area in the right inferior parietal lobule (**Fig. 3b**). An increase in activation was also shown in the left and right prefrontal cortex, the cerebellum, and the right insula. Table 2 lists the areas of activation with their coordinates.

The comparison of the two sound conditions with rest showed significant bilateral activation of the primary auditory cortex (A1) in Heschl's Gyrus[13] (right co-ordinates 46 -24 10, Z = 6.9; left coordinates -50 -22 10, Z = 8.2). Therefore, A1 was active during both tasks, but was not differentially activated by sound movement. No differential activation in A1 was demonstrated even if this area was treated as a region of interest for which a prior hypothesis existed, in which case statistical correction for multiple comparisons does not need to be made.

PET STUDY

During the PET study, subjects were scanned over an 80- second acquisition period while they listened to the add or the cancel condition. Over a typical acquisition period of 80 seconds, subjects were presented with 66 stimuli. Figure 4 shows the comparison between the add (30 scans) and the cancel condition (30 scans) in the PET experiment. A single area of right parietal lobe activation was demonstrated, situated 18 mm from the superior area in the inferior parietal lobule demonstrated in the fMRI experiment (coordinates 24 -40 66, Z = 3.49). The comparison between the two sound conditions and silence demonstrated bilateral activation of A1 (right coordinates 50 -26 4, Z = 6.6; left coordinates -46 -26 8, Z = 6.0). Again, the comparison between the two sound conditions showed no significant difference at A1 even without correction for multiple comparisons.

Discussion

In this study we have used a novel psychophysical stimulus to demonstrate cortical areas where activity increases when sound movement is perceived. The use of stimuli with the same acoustic structure allows these areas to be interpreted in terms of perceptual and cognitive processing, rather than in terms of the earlier acoustic processing. Thus, this study addresses the question of how sound movement is perceived in general. The fMRI and PET studies converged to show right parietal lobe activation, and additionally are consistent with previous human lesion studies showing posterior right hemisphere involvement in auditory spatial perception[14,15].

A striking feature of this work is the demonstration of activity in areas in the fMRI experiment that are not shown by the PET study. Few previous studies have used the same stimulus in the same experiment with both techniques; the demonstration of additional

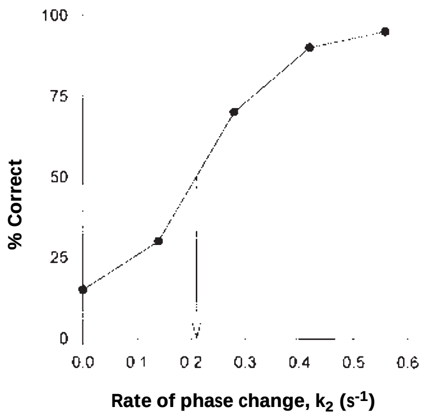

Fig. 1. Function used to calculate the point of trading between the linear amplitude and phase excursions for subject 1. The rate of amplitude change, k_1, is 0.1 s^{-1} (see Methods).

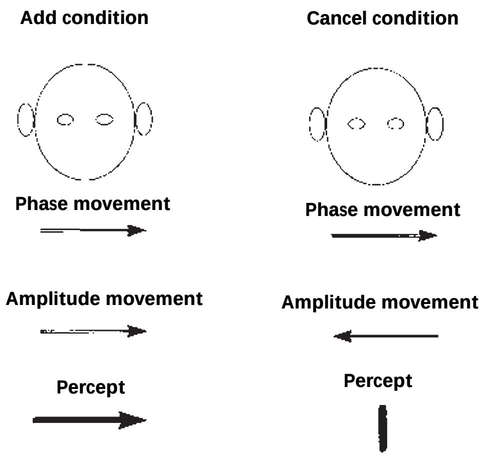

Fig. 2. Basis for the fMRI and PET paradigms. In the add condition, the percepts of movement due to amplitude and phase changes within the stimulus add to produce a strong resultant percept of movement. Stimuli for the cancel condition contain the same amplitude and phase changes in opposition, which results in no movement perception.

areas in the fMRI experiment may be based on methodological differences in the techniques, or due to biological differences in the nature of the task carried out.

DYNAMIC TIME-INTENSITY TRADING

The two conditions used in the imaging experiments produced different perceptions of movement in the presence of identical interaural phase and amplitude modulation. We have been able to quantify this different perception in terms of psychophysical performance. The variation between subjects in the trade point demonstrated for the dynamic time-intensity trades is notable and a phenomenon that is well etablished in static time-intensity trading[12]. No subject reported 'double images' in the cancel condition used, as have been reported in some studies of static time-intensity trading[12]. This may be because sustained perceptual adjustment of the auditory image is only possible in the static case, in which the stimulus is constant for a prolonged period.

COMMON ACTIVATION IN THE fMRI AND PET STUDIES

The fMRI and PET experiments both showed increased activation in the right parietal cortex during the perception of sound movement. The locations of the single area of significant activation in the PET experiment and the superior area in the inferior parietal lobule in the fMRI experiment are within the combined resolution of the two experiments, being situated 18 mm apart, with the use of a 5 mm filter in the fMRI experiment and 16 mm filter in the PET experiment. PET and fMRI are both indirect measures of regional brain activity; however the fMRI response and the regional cerebral blood flow obtained with PET are not identical. The fMRI response depends on blood oxygen level, whereas PET indicates local blood flow. It is possible that the maximum changes in blood oxygen level are not at the same position as the maximum changes in local blood flow.

The activation in the right parietal cortex is consistent with the idea that analysis of spatial sound properties, including movement, occurs beyond the primary auditory cortex in the right hemisphere, as suggested by human lesion experiments[14,15]. One study[14] used a lesion-mapping technique to identify the locus corresponding to a static lateralization deficit demonstrated by interaural amplitude testing. Subjects with deficits were found to have lesions in the posterior right hemisphere. Another study[15] demonstrated a dissociated deficit in sound movement detection due to a posterior right hemisphere lesion that was distinct from the auditory cortex. That lesion involved the right parietal cortex, in addition to the right insula, which was activated in a previous PET auditory movement study using an interaural phase paradigm[16].

We considered whether the areas differentially activated by the movement task might correspond to areas for the perception of sound movement, or whether they might have a less specific role in the perception of static auditory space. There is a longstanding psychophysical debate about whether sound movement perception depends on detection of velocity *per se* or sequential static perception [2,17]. The current experiment was not designed to distinguish between the two, but to demonstrate areas involved in sound movement perception, whatever the underlying mechanism. We have purposely used a low sound velocity (approximately half of the maximum possible lateral sound source displacement in one second); this velocity is clearly perceived as moving by all subjects and can be tracked. This is in contrast to the sudden changes in position that occur with the very rapid sound-movement velocities that have been used in some experiments[18], in which perceptual explanations based on sequential static perception become much more compelling. The low sound-movement velocity in the current experiment makes either velocity detection or sequential static detection mechanisms possible.

We also considered a possible attentional basis for the activation demonstrated in the movement condition, that is, an activation due to lateralized spatial shifts of auditory attention. In visuomotor attention tasks, parietal cortex is active when subjects have to make a response to a target presented at a location they do not expect[19,20]. However, this effect depends on the subject being required to make a speeded motor response to an unexpected target, and there is no evidence for such spatial cueing effects in auditory attention[21]. In the present study, the subjects did not make responses, and the loca-

Table 2. Areas of significant difference between the add and cancel condition (see Methods) in the fMRI experiment

Region	Area	Talairach Coordinates	Z Score
Parietal	Right LPs [7]	26 -72 60	5.5
	Right LPi [40]	32 -42 50	5.4
	Right LPi [40]	66 -26 26	5.4
	Left LPi [40]	-52 -38 32	6.7
	Left LPs [7]	-20 -48 76	6.1
	Left postcentral	-44 -32 62	5.6
Frontal	Right [6/8]	58 8 46	7.4
	Right Gfi/insula	34 24 -8	4.5
	Left [6]	-36 0 58	6.5
	Left Frontal	-54 4 44	5.7
	Left Gfi	-38 8 22	4.9
	Left [6]	-22 2 68	5.1
	Anterior Cingulate	-4 10 50	5.6
Cerebellar	Right hemisphere	28 -46 -36	6.1
	Right hemisphere	-26 -64 -18	4.9
	Midline/vermis	4 -78 -18	5.6

The abbreviations for the individual areas are as in Talairach[40] and are given with the Brodmann area based on that atlas in brackets. LP, parietal lobule. LPi, inferior parietal lobule. LPs, superior parietal lobule. Gfi, inferior frontal gyrus.

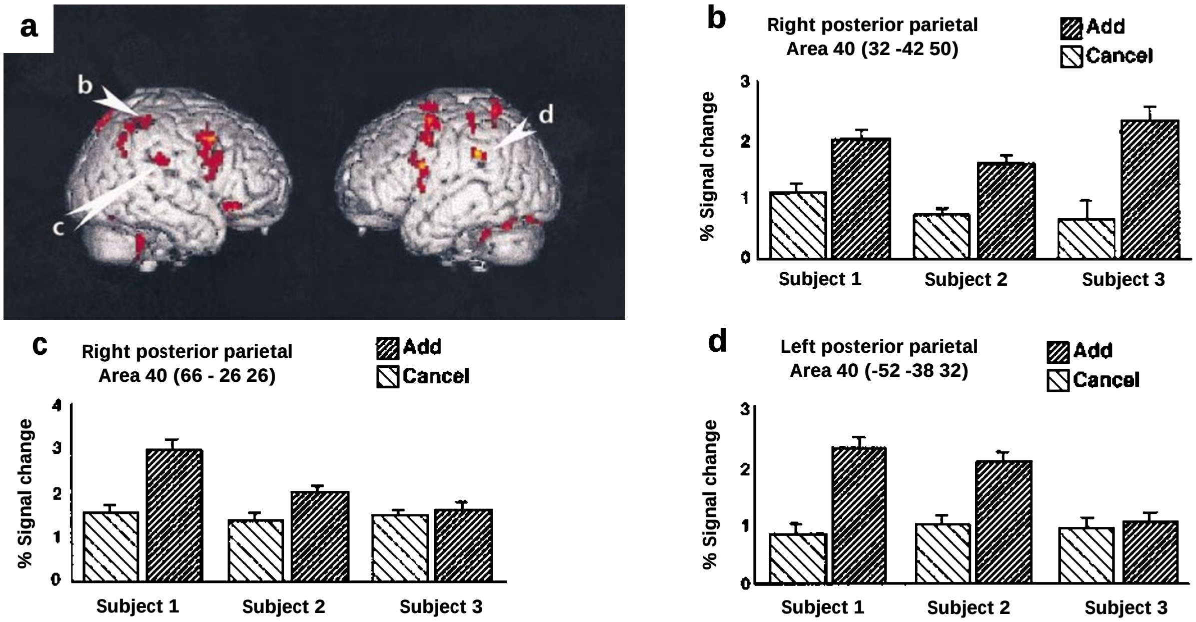

Fig. 3. Areas of increased activation using the add condition compared to the cancel condition in the fMRI experiment (see Methods). **(a)** Group comparison for three subjects superimposed on a T1-weighted template. The posterior parietal areas of maximal signal change are highlighted by arrows. **(b)** Percentage change in BOLD signal measurements for individual subjects from the superior right posterior parietal areas in (a). **(c)** Percentage change in BOLD signal measurements for individual subjects from the inferior right posterior parietal areas in (a). **(d)** Percentage change in BOLD signal measurements for individual subjects from the left posterior parietal area in (a). The BOLD signal bars are relative to an arbitrary origin, and the figure can only be used to compare the blood flow between the conditions. Error bars correspond to one standard error.

tions of the stimuli, although randomized within a run, included only three spatial positions (right, left or center), known in advance by the subject. We therefore suggest that the posterior parietal activation we observe is due to perceptual processing of movement, rather than attention. Specifically, we hypothesize that a perceived representation of the stimulus movement exists in the posterior parietal cortex. This is in accord with neurophysiological studies suggesting a role for the posterior parietal cortex in the representation of abstract spatial information[22].

Abstract spatial representations in the posterior parietal cortex can be produced by several sensory modalities[22], and the area of activation shown therefore does not represent an auditory analogue of the specific visual area for the perception of motion in the anterolateral occipital cortex[23]. Neurophysiological work suggests a role for the posterior parietal cortex in the planning of motor and oculomotor action[22,24], in addition to the representation of the space within which those actions are performed. Although subjects performed no output task and maintained visual fixation (and electro-oculogram recordings did not show eye movements when subjects listened to the stimuli), a possible additional role of the parietal area demonstrated here in the planning of eye movements cannot be excluded.

THE AUDITORY CORTEX IN SOUND-MOVEMENT PERCEPTION

Neither the fMRI nor the PET experiments showed any increase in activation in auditory cortex during sound-movement perception. This is contrary to what might have been predicted from single-unit recordings in animals, showing neurons in the auditory cortex with selective responses to spatial sound cues[7,8,25,26]. However, the actual differences in firing rate of neurons in the auditory cortices that show spatial selectivity are subtle. If neurons in human auditory cortex behaved similarly, such subtle responses might not be apparent using a technique based on the detection of local summated activity, especially under fMRI scanning conditions where saturation effects in the BOLD response are possible[27]. Thus, the absence of a differential response in auditory cortex to the two sound stimuli does not exclude its involvement in the task.

ADDITIONAL ACTIVATION IN THE fMRI STUDY

The fMRI experiment showed areas of activation in the left parietal cortex and in bilateral frontal areas that were not seen with PET. This may be because the contrast between the two sound conditions in the fMRI experiment was based on 288 scans per condition, compared to 30 scans per condition in the PET experiment. The stimuli used for the two functional imaging experiments were identical and presented at the same sensation level relative to background noise, and the psychophysical performance of the subjects under scanning conditions was the same. However, despite the acoustic isolation in the fMRI experiment, the subjects did hear considerable background noise generated by the scanner. The task might then have additionally included an element of auditory streaming[28] in order for the subject to separate the stimulus from the noise. This is the process of separating auditory perceptual objects, analogous to Gestalt processing in the visual system, when the objects would be called figure and ground. This process, and the shorter fMRI epochs, may have increased the attentional load in the fMRI experiment, and thus have engaged attentional mechanisms that may not have been activated to the same degree in the PET experiment.

Frontal and parietal activation have been described in studies of auditory selective attention[21,29]. A PET study of auditory selective attention, using a paradigm based on pitch change, suggests the existence of an anterior cingulate and predominantly right frontal net-

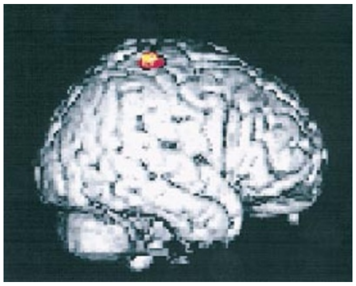

Fig. 4. Statistical parametric map showing area of increased activation using PET for add compared to the cancel condition (see Methods). Group comparison for 6 subjects are superimposed on a T1-weighted template.

work, which is supramodal[29]. That study incorporated lateralization to disengage stimulus-dependent and independent effects. However, it cannot be compared directly with the present study, which explored the detection of spatial cues without a specific lateralized attention task. Another study of selective attention by fMRI in consonant-vowel discrimination[21] used binaural and dichotic listening conditions to vary the attentional load (again requiring lateralized attention in the dichotic condition), and showed bilateral increased parietal activation in the task demanding greater selective attention.

The prefrontal activation demonstrated in the present experiment might also be related to spatial monitoring, which has been shown to involve the prefrontal areas in a visual spatial monitoring task[30]. Spatial monitoring refers to the active checking of the incoming spatial auditory information. There was no spatial search strategy or output task required in this experiment, but activation of spatial working memory by a random sequence of moving tones with different directions is also possible. The areas of frontal activation we describe are not within the accepted limits for the frontal eye fields[31], but a role for these areas in spatial attention linked to eye movements[32] cannot be excluded.

A PERCEPTUAL AND ATTENTIONAL NETWORK

Whatever the mechanism, the additional activation seen in the frontal cortices cannot be explained in terms of abstract spatial representation in the same way as the parietal activation. The frontal activation is hypothesized to be a post-perceptual phenomenon. The activation of both frontal and parietal areas in the movement task represents a form of functional connectivity for which there is an established anatomical basis. The prefrontal areas receive projections from both ventral parietal cortex (area 7)[33] and from area 7a/LIP in the monkey[33,34]. We suggest that the parietal areas, in conjunction with the prefrontal areas that we have demonstrated in the fMRI experiment, form a network involved in sound spatial perception and selective attention.

Methods

Subjects. Three subjects participated in the fMRI experiment and six subjects in the PET experiment. All subjects were right handed, with no hearing or neurological disorder and normal structural MRI scans. All subjects gave informed written consent, and the study was approved by the local hospital ethics committee and conducted under certification from the Administration of Radioactive Substances Advisory Committee (Department of Health, London, UK).

Stimuli. Stimuli for all experiments were 500-Hz tones containing changes in both phase and amplitude between the ears. The mean sensation level was 50 dB in all experiments. The sounds were all one second long. This duration was chosen to ensure that subjects clearly perceived the movement of the sound, as opposed to a sudden change in position. In all sounds, the phase was linearly advanced at one ear as it was simultaneously retarded at the other, as occurs when a sound moves in the horizontal plane around the head. This change in the instantaneous phase at either ear is identical to a frequency modulation, but subjects are much more sensitive to the phase cue when there is a reference tone in the other ear[15,35]; subjects perceived the lateral movement but not the monaural frequency change with the modulation depths used here. The amplitude in all sounds was also linearly increased in one ear and decreased in the other. Considered alone, both the phase and amplitude changes produce a perception of sound movement from the midline to one side. When the perceptions due to the phase and amplitude changes are in the same direction, they add to each other (add condition). When the perceptions due to the phase and amplitude changes are to opposite sides, they can cancel (cancel condition), so that subjects perceived a single stationary sound image in the midline. The add and cancel pressure waveforms, x (t), at either ear for a given subject are represented below for the case of (1) an add stimulus producing perceptual movement to the right and (2) a cancel stimulus:

$$\text{(1)}\quad \text{left } x(t) = A_0 (1 - k_1 t) \sin(2\pi f t + k_2 t),$$

$$\text{right } x(t) = A_0 (1 + k_1 t) \sin(2\pi f t - k_2 t)$$

$$\text{(2)}\quad \text{left } x(t) = A_0 (1 + k_1 t) \sin(2\pi f t + k_2 t),$$

$$\text{right } x(t) = A_0 (1 - k_1 t) \sin(2\pi f t - k_2 t)$$

f = carrier frequency (500 Hz for all stimuli), A_0 = starting amplitude, k_1 = constant determining the rate of amplitude change, k_2 = constant determining the rate of phase change. k_2 generated the rate of phase change necessary to cancel the movement due to the amplitude cue in the cancel condition. The values of k_1 and k_2 were fixed for all stimuli presented to any given subject. The waveforms were smoothed on and off over 20 ms using a cosine squared function. The add and cancel conditions represent stimuli that contain identical magnitudes of component amplitude and phase modulations, but which produce different perceptions of movement. This allows their use in categorical functional imaging paradigms to investigate sound-movement perception.

Psychophysical testing. All subjects underwent psychophysical testing in a quiet environment, using headphones. In addition, the subjects for the fMRI experiment were tested using the fMRI sound delivery equipment immediately before the scanning session. For all subjects, a point was defined for the cancel condition where the perceived movement was cancelled by varying the interaural phase modulation for a fixed change in interaural amplitude. The rate of interaural amplitude change, k_1, was fixed at either $0.10\ s^{-1}$ or $0.15\ s^{-1}$ for each subject; some subjects required the greater amplitude change because the amplitude change of 0.1, when presented alone, was subthreshold and did not produce a perception of movement. A two-alternative, forced-choice procedure was used with two intervals that both contained the fixed amplitude change. The direction of amplitude change was opposite in the two trials, and the order of trials randomized. The sound also contained ramp phase changes, which produced a perception of movement in the opposite direction to the movement due to the amplitude ramp alone. The stimulus length was one second, and the interstimulus interval was one second. The rate of interaural phase change, k_2, was randomly varied between zero and a value that always produced a perception of movement in the direction of the phase change. Five levels of phase change were used with at least 20 trials per level. Subjects were required to identify the trial in which the sound appeared to move to the right. A response was counted as correct if the subject chose the interval containing the phase change producing a perception of movement to the right. The percentage of correct trials was determined as a function of phase change to allow a 50% trade point to be defined for each subject. This function is shown in Fig. 1 for subject 1. When the phase cue was insufficient to cancel the amplitude change, the subject chose the interval in which the amplitude signal moved to the right, and therefore scored less than 50%. When the phase cue was more than sufficient to cancel the amplitude change, the subject scored above 50%. The trade point, marked with an arrow on Fig. 1, represents the point where phase and amplitude cancelled each other, and subjects did not perceive movement in either interval and therefore performed at chance. This value of k_2 was used in the imaging experiments.

fMRI experiment. Stimuli based on the add or cancel condition were delivered over an acoustically isolated system of speakers and graduated tubes at a sensation level of 50 dB, set when the scanning sequence was running. A combination of external ear defenders and ear plugs around the final tubes within the ear canal was used for passive attenuation of the scanner noise.

All stimuli contained identical phase and amplitude modulations, determined psychophysically prior to the scan. During the movement epochs, subjects were presented with stimuli in which the movement perception added, to give a perception of movement to the left or the right in random order. All subjects were able to correctly identify the correct direction of movement with 100% accuracy, and perceived movements from the midline to a point more than halfway between the midline and the maximum possible excursion toward one ear. In the control epochs, the stimulus with cancellation was used. Epochs of either sound condition were presented alternating with silence. The epochs were approximately 40 s long, and subjects were presented with 33 stimuli during the sound epochs. There was no output task, and subjects were instructed to listen for any changes in the position of the sound and required to fixate a visual cross-piece placed at the midpoint of the visual axis. Electro-oculogram recording, carried out during a separate session with stimulus presentation but no scanning, demonstrated no eye movements.

fMRI SCANNING AND ANALYSIS. BOLD contrast image volumes were acquired at 2.0 T (Siemens VISION, Erlangen) with gradient-echo echo-planar imaging (TR/TE = 6000 ms/40 ms). Each volume comprised sixty-four contiguous 3-mm slices, with an in-plane resolution of 3 x 3 mm. Each subject underwent three consecutive imaging sessions comprising 384 such volumes. The first six volumes of each session were discarded to discount T1 saturation effects. The movement and control conditions were presented in a fixed order alternating with rest (baseline). Each epoch lasted for seven volumes (approximately 40 s). For each subject separately, the T2* time series was realigned to the first image, stereotactically normalized and smoothed with an isotropic Gaussian kernel of 5 mm FWHM [36,37]. The entire imaging time-series for each subject was used for a group analysis, representing 1134 image volumes in total. Condition-specific effects were estimated using the general linear model and theory of Gaussian fields as implemented in SPM96. A high-pass filter with a cut-off frequency of 0.19 cycles per min modelled and excluded low-frequency confounding effects in the time-series. A fixed-response, box-car model was used to characterize condition effects, using linear contrasts to test hypotheses about regionally specific condition effects. The SPM{Z} for the add minus cancel comparison was thresholded at a Z value of 3.09 ($p = 0.001$ uncorrected for multiple comparisons), and the resulting foci were characterized in terms of both spatial extent and peak height corrected for multiple comparisons[38,39] at the five percent level.

PET SCANNING. Identical stimuli to those used in the fMRI experiment were delivered over insert earphones at a sensation level of 50 dB. Thus, subjects would attend to approximately 66 stimulus sounds during a typical acquisition period of 80 s. Subjects fixated a cross-piece and carried out no output task, as in the fMRI experiment. Twelve scans were carried out on a Siemens scanner in 3D mode, five with the add condition, five with the cancel condition, and two with silence. The order of scans was randomized across subjects. Statistical parametric mapping[36,38,39] implemented in SPM96 software (http//:www.fil.ion.ucl.ac.uk/spm) was used to compare regional cerebral blood flow between conditions. The data were smoothed with an isotropic Gaussian kernel of 16 mm FWHM.

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