

# High Binaural Coherence Determines Successful Sound Localization and Increased Activity in Posterior Auditory Areas

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## Summary

Our brain continuously receives complex combinations of sounds originating from different sources and relating to different events in the external world. Timing differences between the two ears can be used to localize sounds in space, but only when the inputs to the two ears have similar spectrotemporal profiles (high binaural coherence). We used fMRI to investigate any modulation of auditory responses by binaural coherence. We assessed how processing of these cues depends on whether spatial information is task relevant and whether brain activity correlates with subjects' localization performance. We found that activity in Heschl's gyrus increased with increasing coherence, irrespective of whether localization was task relevant. Posterior auditory regions also showed increased activity for high coherence, primarily when sound localization was required and subjects successfully localized sounds. We conclude that binaural coherence cues are processed throughout the auditory cortex and that these cues are used in posterior regions for successful auditory localization.

## Introduction

In everyday life we are presented with complex sound signals that often originate from different sources and convey competing information. In order to select relevant information for further processing and to guide behavior, the brain must group together signals relating to the same event and location, and it must segregate signals that are unrelated. A classical example of this is the cocktail party effect, when many voices are heard at once, but we are able to select one speaker and listen to the content of one specific message (e.g., [Cherry, 1953](#)). In an analogy with processing in the visual system, it has been suggested that “sound-objects” might be formed and that segregated processing for sound recognition and sound localization takes place in auditory regions anterior and posterior to Heschl's gyrus, respectively (see [Rauschecker, 1997, 1998](#); [Rauschecker and Tian, 2000](#); [Alain and Itzenberg, 2003](#); see also [Zatorre et al., 2004](#)). The selection of relevant sounds from background might rely on several cues. These would include the spectral and temporal characteristics of the sensory event, as for recognition of complex harmonic sounds (e.g., [Zatorre et al., 2004](#); [Alain and Itzenberg, 2003](#)) or speech sounds (e.g., [Vouloumanos et al.,](#)

[2001](#)). Another important cue for selection is the position of the sound sources in space. Two separate auditory events will typically originate from different locations, and thus identification of source location can be exploited to distinguish between competing auditory events ([Blauert, 1997](#)). The localization of sound sources in the horizontal plane relies, mainly on binaural cues. The two principal binaural cues that the brain can use to localize sounds are timing differences (interaural time difference [ITD]) and sound pressure differences (interaural level difference [ILD]) between the two ears ([Wright and Fitzgerald, 2001](#)). However, for the brain to successfully interpret these cues, the inputs to the two ears must have similar spectrotemporal characteristics (i.e., high binaural sound coherence). Thus, only sounds presented with high binaural coherence will result in the perception of a single source that can be localized in space and selected as a relevant sound object (e.g., [R.I. Chernyak and N.A. Dubrovsky, 1968](#), Sixth International Congress on Acoustics, Tokyo; [Blauert and Lindemann, 1986](#); [Blauert, 1997](#)).

Psychophysically, if subjects are asked to localize the position of sound-sources, the localization performance decreases as the input to the two ears becomes more and more different (i.e., decreasing levels of binaural sound coherence). [Jeffress and colleagues \(Jeffress et al., 1962\)](#) used bursts of white noise with different levels of binaural sound coherence during an auditory localization task. Lateralized sound positions in the horizontal plane were produced with varying interaural time differences (ITD). The results demonstrated that the deviation between perceived and real sound position increased with decreasing level of coherence. Perceptually, decreasing levels of binaural coherence also results in a “smearing” of the sound source (i.e., increased spatial width) that may underlie the difficulty in precisely localizing the sound source ([R.I. Chernyak and N.A. Dubrovsky, 1968](#); [Blauert and Lindemann, 1986](#)). Thus, the ability to successfully localize sound sources in space requires high levels of coherence between the inputs presented to the two ears ([Jeffress et al., 1962](#)).

The neural basis for processing of binaural sound coherence in humans has been studied by presenting auditory noise with different levels of binaural coherence during fMRI ([Budd et al., 2003](#)). In this experiment, all sounds were presented with a constant ITD equal to zero, and subjects passively listened to the sounds. The comparison of all sounds versus silence revealed the expected activation in and around Heschl's gyrus. A region in the lateral extent of Heschl's gyrus showed a linear relationship between activity and the level of binaural coherence ([Budd et al., 2003](#)). It should be noted that in this study all sound conditions were presented with ITD = 0. Therefore, binaural cues were not actively used for sound localization (cf. [R.I. Chernyak and N.A. Dubrovsky, 1968](#)), and changes of brain activity could not be linked with changes in behavioral performance. Thus, the question arises if the level of binaural coherence might modulate other regions within

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auditory cortex when binaural cues become task relevant, influencing the subject's ability to actively discriminate sound positions.

Previous neuroimaging studies on sound localization exclusively used sounds with full binaural coherence (e.g., Krumbholz et al., 2005; Zatorre et al., 2002; Maeder et al., 2001). Overall, these data indicate that the active localization of stationary sounds (Krumbholz et al., 2005; Zatorre et al., 2002; Maeder et al., 2001; Alain et al., 2001), or the perception of moving sounds (Krumbholz et al., 2005; Hart et al., 2004; Warren et al., 2002; Pavani et al., 2002) activate auditory regions in the posterior superior temporal gyrus (STG), posterior to Heschl's gyrus. Further, this pattern of brain activation was found irrespective of whether ITD and/or ILD was used to produce the spatial auditory percept (e.g., Krumbholz et al., 2005; Hart et al., 2004; see review, Arnott et al., 2004). These findings confirm the hypothesis, formulated on the basis of studies in nonhuman primates, that a dorsolateral "where" pathway exists for the auditory modality (Rauschecker, 1998; Romanski et al., 1999; Rauschecker and Tian, 2000; Tian et al., 2001; see also Maeder et al., 2001; Alain et al., 2001, for related imaging studies in humans). Thus, areas in posterior auditory cortex (i.e., posterior STG) appear to use binaural cues to extract and represent spatial features of the auditory input.

The question arises whether the level of binaural sound coherence, and thus the ability to localize sounds in space, modifies activity in these posterior regions. During fMRI, we asked subjects to localize the horizontal position of sounds that were presented with different levels of binaural sound coherence. Coherence levels were calculated according to Blauert (1997) and are expressed in  $k$  values. Five different  $k$  values were used:  $k = 1$ ,  $k = 0.6$ ,  $k = 0.4$ ,  $k = 0.2$ , and  $k = 0$  (from full coherence to null coherence; see also [Experimental Procedures](#)). Five ITDs were used to produce lateralized perception of sounds (ITDs =  $-400$ ,  $-200$ ,  $0$ ,  $200$ , and  $400$   $\mu$ s, for sound positions from left to right). The level of binaural coherence and the ITDs were randomized on a trial-by-trial basis. The subjects' task was to report the perceived sound position on each trial (left or right to the head mid-line: two-alternative forced-choice [2-AFC]). For each level of sound coherence, we determined the subject's ability to localize sound by fitting the behavioral responses with a sigmoidal psychometric function as a function of ITD. We expected that decreasing binaural coherence would result in poorer sound localization (see Jeffress et al., 1962) and a reduction of the coefficients of best fit for the psychometric function.

Localization performance was indexed, using the coefficients of sigmoidal best fit for each level of sound coherence, and then parametrically correlated with the fMRI data. Note that because our design orthogonally assessed the effect of coherence at five different ITDs, we could study how coherence affects spatial localization for different azimuths (e.g., central versus peripheral sounds). Furthermore, in a second experiment we compared brain activity for full coherence ( $k = 1$ ) versus null coherence ( $k = 0$ ) during passive listening and ITD equal to zero. This allowed us to assess whether any effect of coherence depends on active localization of

sounds (Experiment 1), or if these depend solely on the coherence characteristics of sensory input instead (Experiment 2). Finally, a third experiment manipulated the subject's ability to detect frequency-modulated tones of different amplitudes embedded in white noise (ratio of the tone-to-noise amplitude = 0.60:1; 0.23:1; 0.21:1; 0.19:1; and 0.10:1). This should provide additional evidence concerning the specificity of any activation for successful sound localization (Experiment 1), over and above mere changes of behavioral performance and/or attentional demands.

## Results

### Psychophysical Data during fMRI Scanning

In the localization experiment (Experiment 1), subjects made left-right judgments about sound positions (2-AFC procedure) at five different levels of binaural coherence. For each coherence level, the group mean percentage of "right" responses was plotted as a function of ITD and was fitted with a sigmoidal function (Figures 1A–1E). Good localization performance (e.g., see Figure 1A, with  $k = 1$ ) resulted in a good fit of the psychometric function and high coefficients of determination ( $r^2$ ). With decreasing  $k$  values, localization became less accurate and the corresponding fit coefficients also decreased (see Figure 1F). A repeated-measures ANOVA revealed a highly significant effect of binaural sound coherence on localization performance ( $F[4,60] = 28.59$ ,  $p < 0.001$ ), demonstrating an impairment of sound localization with decreasing levels of coherence during fMRI.

### fMRI Data

The fMRI analyses first identified brain regions implicated in the sound localization task and then tested for any modulation by sound coherence within these areas (Experiment 1: parametric modulation associated with localization performance). An analogous approach was used to analyze the data from the second experiment, first identifying areas responding to sounds and then assessing any modulation by sound coherence within these (Experiment 2: full versus null coherence during passive listening). Finally, for the third experiment, we also highlighted areas responding to all types of sounds (irrespective of the tone-to-noise ratio) and then tested for any changes of brain activity correlated with the subject's ability to detect the frequency-modulated target tone within these regions (Experiment 3: parametric modulation associated with tone detection performance).

#### *Experiment 1: Active Spatial Localization*

The effect of sound coherence during spatial localization was investigated by testing for any parametric modulation of brain responses by  $r^2$  coefficients derived from psychophysical data (see Figure 1F). Thus, we looked for brain regions in which activity covaried with localization performance. The parametric analysis was constrained within brain regions showing an overall activation for the localization task, irrespective of behavioral performance (Table 1; see Figure 2, cyan outlines). This overall effect revealed bilateral activation of auditory areas in the superior temporal cortex and

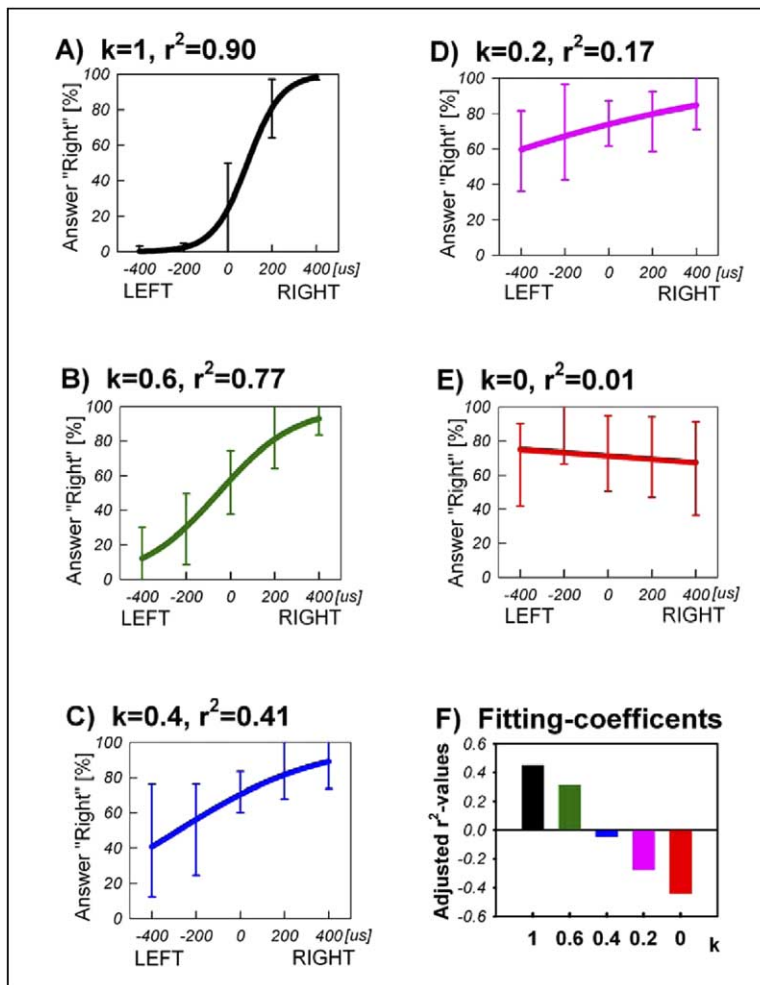


Figure 1. Psychophysical Data for Sound Localization with Different Levels of Binaural Sound Coherence

(A–E) The group mean percentage of “right” responses as a function of ITD is shown for each coherence level. For each level of binaural coherence, the data were fitted with a sigmoidal function. This showed that sound localization performance decreased with decreasing sound coherence, with correspondingly decreasing coefficients of determination ( $r^2$ ) for the sigmoidal fit. (F) Localization performance (expressed as  $r^2$  values) as a function of  $k$ . In order to orthogonalize the coherence effect from any overall effect of sound, the fitting coefficients were adjusted to a mean of zero before parametric analyses of fMRI data. Error bars represent SD.

contralateral motor cortex, as expected, given that subjects responded to every stimulus with a right-hand button press (Table 1). In addition, several premotor, parietal, and subcortical regions, plus a cluster in the lingual gyrus, also showed increased activation during active sound localization (see Table 1). The activation in the superior temporal cortex included the Heschl’s gyrus (likely to contain the primary auditory cortex) (see yellow outlines in the central panel of Figure 2; also, Penhune et al., 1996; Morosan et al., 2001; Rademacher et al., 2001) and extended posteriorly into the posterior STG (also see cyan outlines in Figure 2).

Within these regions we tested for any modulatory effect of binaural sound coherence. This demonstrated that activity in auditory cortex increased with increasing binaural coherence and subjects’ localization performance (Figure 2, central panel, red; Table 2). The modulation extended from Heschl’s gyrus posteriorly into the posterior part of the STG and the middle temporal gyrus. In addition, increasing the  $k$  level significantly modulated activity in the right caudate nucleus. Our analyses also suggested that binaural coherence affected activity in the inferior parietal lobule (see Table 2, italics). Although this activation did not fully meet our criteria for statistical significance (i.e., no overall effect

of localization task minus rest was detected there), we noted that involvement of the inferior parietal cortex in auditory space perception would be consistent with previous reports on the localization of stationary sounds (Bushara et al., 1999; Weeks et al., 1999; Maeder et al., 2001) and processing of sound movement (Pavani et al., 2002; Griffiths et al., 1998).

The signal plots for Heschl’s gyrus (Figures 2A and 2B) and posterior auditory regions (Figures 2C and 2D) show that activity decreased with decreasing coherence, thus mirroring subjects’ localization performances (cf. Figure 1F). Note that the effect of coherence was observed irrespective of the ITD. Figure 3 shows the level of activity in Heschl’s gyrus (Figures 3A and 3B) and posterior auditory regions (Figures 3C and 3D), according to coherence level and ITD. The data indicate that the progressive decrease of activity with decreasing binaural coherence was present for all ITDs. This implies that the effect of coherence on brain activity does not depend on sound position and can be observed both for lateralized sounds (ITD different from 0) and central sounds (ITD = 0; red lines in Figure 3). In summary, high binaural sound coherence resulted in better localization performance and was associated with increased activity both in Heschl’s Gyrus (possibly

Table 1. Overall Effect of the Sound Localization Task in Experiment 1: Active Sound Localization

	Main Analysis			Fixation Controlled			
	Cluster Size	p Corrected	MNI Coordinates	z Value	MNI Coordinates	z Value	
Right Hemisphere							
R	Anterior STG	5349	<0.001	56, 10, -8	3.73	56, 6, -8	3.48
	Heschl's gyrus			56, -14, 0	7.61	64, -8, -2	4.47
	Posterior STG			56, -38, 8	4.33	54, -26, 4	4.49
	Middle temporal gyrus			64, -32, -4	5.38	68, -28, 0	6.38
	Caudate			12, 6, 4	4.11	18, 18, -2	3.46
R	Supramarginal gyrus	327	<0.001	36, -46, 32	4.37	38, -44, 32	4.02
R	Middle frontal gyrus	128	0.025	38, 30, 24	4.48	38, 30, 24	4.04
R	Lingual gyrus	184	0.004	4, -80, 0	4.75	- - -	-
Left Hemisphere							
L	Anterior STG	11015	<0.001	-52, 4, -2	6.25	-50, -4, 6	3.89
	Heschl's gyrus			-50, -24, 4	>8	-56, -20, 2	5.07
	Posterior STG			-60, -42, 8	6.5	-58, -38, 8	4.60
	Middle temporal gyrus			-54, -60, 0	5.27	-56, -46, 8	4.79
	Precentral gyrus			-38, -12, 64	>8	-38, -14, 64	4.13
	Postcentral gyrus			-54, -20, 50	>8	-54, -22, 50	5.62
L	Middle frontal gyrus	1886	<0.001	-4, -4, 60	7.59	-8, -8, 52	5.18

Anatomical location, cluster size, corrected p values, peak coordinates, and z values for the overall effect of localization task. The anatomical labeling of Heschl's gyrus (and any region anterior or posterior to it) was inferred from the functional responses observed in Experiment 2 (sound minus rest; see also main text and cf. [Penhune et al., 1996](#); [Morosan et al., 2001](#)). p values are corrected for multiple comparisons at cluster level (cluster size estimated at  $p = 0.001$ , uncorrected). Because activation clusters extended over large areas of the brain (see also [Figure 2](#)), we report multiple peaks within these clusters. The rightmost columns show coordinates and z values for the same overall effect of localization task in a subgroup of four subjects, with trials containing losses of fixation removed.

including the primary auditory cortex; see also [Budd et al., 2003](#)), and in posterior auditory regions that are thought to process the spatial characteristics of sounds (e.g., [Maeder et al., 2001](#); [Pavani et al., 2002](#); see also [Arnott et al., 2004](#), for review).

**Experiment 1: Subanalysis with Exclusion of Eye Movements during Localization**

To exclude any possible influence of eye movements during auditory localization, we performed additional analyses for the four subjects for whom we had eye position data recorded during fMRI. For each subject, the new analyses modeled separately any trials containing losses of central fixation. These new subanalyses confirmed all of our results. The localization task was found to activate Heschl's gyrus and posterior auditory regions, contralateral motor cortex, plus premotor and subcortical areas (see [Table 1](#), rightmost columns). Critically, the level of binaural sound coherence modulated activity in both Heschl's gyrus and the posterior part of the superior temporal gyrus (see [Table 2](#), rightmost columns), validating the results of our main analyses, with central fixation confirmed.

**Experiment 2: Passive Listening to Central Sound with Different Levels of Binaural Sound Coherence**

One aspect of our results for the localization experiment (Experiment 1, see above) was that binaural sound coherence modulated brain activity both in auditory regions in Heschl's gyrus and auditory regions in the posterior part of the STG. The question arises whether these effects depend on the current task requiring use of binaural cues, as in the localization task, or if, instead, the modulation by coherence was purely driven by the binaural characteristics of sensory input. We addressed this issue in a second fMRI experiment when subjects passively listened to bursts of white noise with either full binaural coherence ( $k = 1$ ) or null coherence

( $k = 0$ ). To minimize any covert, automatic attempt to localize a single sound source in the horizontal plane, all sounds were presented with ITD equal to zero. First we compared both types of sounds (coherent and incoherent) versus rest. This revealed bilateral activation of Heschl's gyrus (see [Figure 2](#), yellow outlines in central panel; and [Table 3A](#)). Unlike Experiment 1 (localization task), during passive listening the auditory activation was confined to a more central region and did not extend posteriorly into the posterior part of the STG (compare yellow and cyan outlines in [Figure 2](#), central panel). Within these central regions, we directly compared full versus null coherence, revealing the modulation of brain activity there ([Table 3B](#)). These results indicate that binaural coherence cues affect activity in Heschl's gyrus and that processing of these cues in central auditory areas does not depend on sound localization being currently task relevant (see also [Budd et al., 2003](#)).

**Experiment 3: Active Detection of Frequency-Modulated Tones**

A third experiment assessed whether activations reported in Experiment 1 (active sound localization) are specific for successful sound localization or instead might relate to more general mechanisms of successful processing of auditory features. In Experiment 3, subjects were asked to detect frequency-modulated tones embedded in white noise (2-AFC: "tone-present"/"tone-absent"). Using a procedure conceptually analogous to Experiment 1, we manipulated the maximal amplitude of the tone, thus parametrically changing the tone-to-noise ratio (tone-to-noise ratio = 0.60:1; 0.23:1; 0.21:1; 0.19:1; 0.10:1). Behavioral data collected during fMRI showed that the subjects' ability to discriminate the target tone from the white-noise background decreased with decreasing tone-to-noise ratio (see [Figure 4](#); top

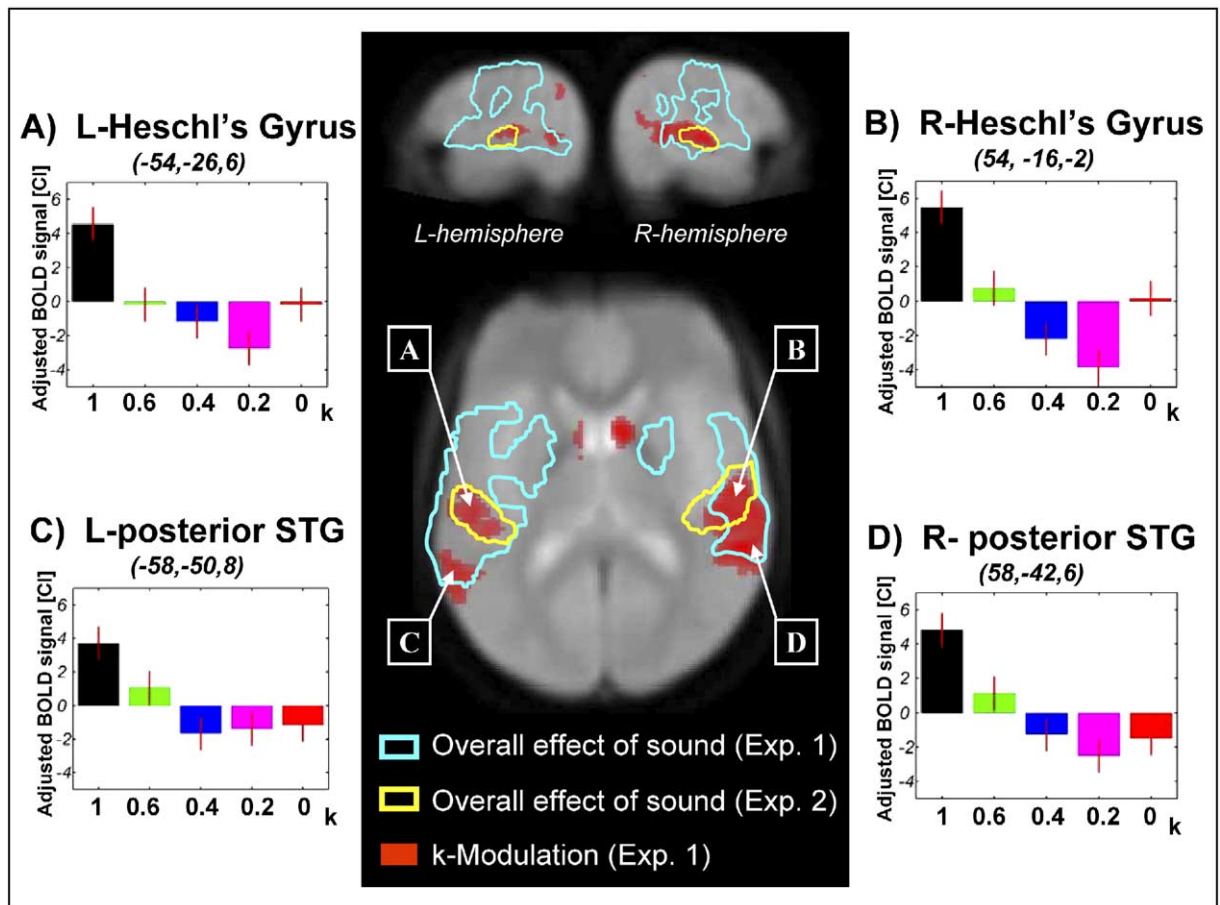


Figure 2. Modulatory Effect of Binaural Coherence during Active Localization in Experiment 1

(Central panel) This shows areas where activity decreased with decreasing binaural coherence (in red). The modulatory effect extended from Heschl's gyrus posteriorly into the posterior STG (with further extension into the middle temporal gyrus). The anatomical sections also show the overall effect of localization task (Experiment 1; cyan outlines). This included Heschl's gyrus plus other regions on the superior temporal gyrus, and, in particular, regions posterior to Heschl's gyrus, where an effect of coherence was also detected (see regions "C" and "D"). For display purposes, the statistical threshold for the modulatory effect of binaural coherence was set to  $p < 0.001$ , uncorrected (voxel level), thus showing some cluster that was not statistically significant according to our statistical criteria (e.g., see inferior parietal activation in the left hemisphere visible in the sagittal section; top left). (Side panels) The signal plots in Heschl's gyrus (A and B) and posterior STG (C and D) show that activity decreased with decreasing coherence, thus mirroring the subjects' localization performance (cf. Figure 1F). The level of activation displayed here is adjusted to a mean of zero, and it is expressed in confidence interval (CI = 10%) units. Error bars in CI units.

central panel). As for Experiment 1, we used the psychophysical data for the analysis of fMRI data. The parametric analysis was constrained within brain regions activated by the overall effect of sound in Experiment 3 (see Table A in the Supplemental Data available with this article online). We found that activity in Heschl's gyrus and the anterior STG increased with the subjects' tone detection performance (Figure 4, central panel, in green; and Table 4A). Despite the fact that the activation of the anterior region in the right hemisphere did not fully reach statistical significance (see Table 4A), the involvement of areas anterior to Heschl's gyrus during successful processing of nonspatial sound features is consistent with a role of these regions in auditory object recognition (e.g., Arnott et al., 2004; Maeder et al., 2001; Alain et al., 2001).

Critically, the modulatory effect related to tone detec-

tion performance did not extend to regions posterior to Heschl's gyrus, where Experiment 1 demonstrated modulation of brain activity according to sound localization performance (Figure 4, red outlines in central panel). We formally tested for commonalities and differences across the two experiments, which showed that in Heschl's gyrus behavioral performance covaried with brain activity in both Experiments 1 and 3 (see Figures 4A and 4B and Table 4B). In posterior auditory regions, we found significant differences between the two experiments (Table 4C), with brain activity covarying selectively with localization performance, but not with tone detection performance (see Figures 4C and 4D). Figures 4A and 4B show the level of activity in Heschl's gyrus decreasing both with k level (Experiment 1, red lines) and with decreasing tone-to-noise ratio (Experiment 3, green lines). On the other hand, in the posterior

Table 2. Modulatory Effect of Binaural Sound Coherence during Active Sound Localization in Experiment 1

		Main Analysis		Fixation Controlled		
		p Corrected	MNI Coordinates	Z Value	MNI Coordinates	Z Value
R	Heschl's gyrus	<0.001	54, -16, -2	5.51	58, -20, 0	5.76
R	Posterior STG	<0.001	58, -42, 6	5.85	52, -26, 4	4.59
R	Middle temporal gyrus	<0.001	68, -32, 0	6.2	68, -30, -2	3.82
L	Heschl's gyrus	0.029	-54, -26, 6	4.46	-48, -32, 4	3.14
L	Posterior STG	0.013	-58, -50, 8	4.67	-56, -50, 8	3.43
L	Middle temporal gyrus	0.029	-58, -56, 0	4.47	- - -	-
R	Caudate	0.001	12, 8, 0	5.33	- - -	-
R	Inferior parietal lobule	<i>n.a</i>	56, -46, 48	3.10	64, -42, 40	2.81
L	Inferior parietal lobule	<i>n.a</i>	-56, -50, 36	3.63	-64, -48, 30	3.28

p values are corrected at a voxel level, considering as the volume of interest regions that were activated for the overall effect of the localization task (see Table 1). The parietal areas reported in italics did not show an overall effect of the localization task and are reported here for completeness only. (L/R, left/right hemisphere; n.a., not applicable, because not in the volume of interest)

STG, activity was modulated according to k level (and localization performance; red lines in Figures 4C and 4D), but not by changes of tone-to-noise ratio (see green lines in Figures 4C and 4D). Thus, while both changes of binaural coherence (Experiment 1) and changes of tone-to-noise ratio (Experiment 3) lead to similar effects on overt behavioral performance (cf. Figure 1F and Figure 4, bar plot at the top of the central panel), only the former yielded to modulation of brain activity in the posterior auditory cortex. This suggests a selective role of posterior auditory regions in successful sound localization.

**Discussion**

The influence of the level of binaural coherence on sound localization was investigated using dichotic stimu-

lation with five different levels of coherence between the two ears. Orthogonally to this we manipulated the ITD to produce lateralized perception of sounds. Psychophysical data demonstrated that the subjects' ability to localize sounds in the horizontal plane decreased with decreasing binaural sound coherence (see Figure 1F). Concurrently, fMRI data showed that the level of activity both in central auditory regions (i.e., Heschl's gyrus) and in the posterior STG also decreased with decreasing binaural sound coherence and declining localization performance (see Figure 2). A second experiment showed that coherence cues still affected activity in the central auditory regions when subjects passively listened to coherent versus incoherent sounds. Further, the successful discrimination of frequency-modulated tones from background white noise also revealed modulation in Heschl's gyrus (see Figures 4A and 4B), as

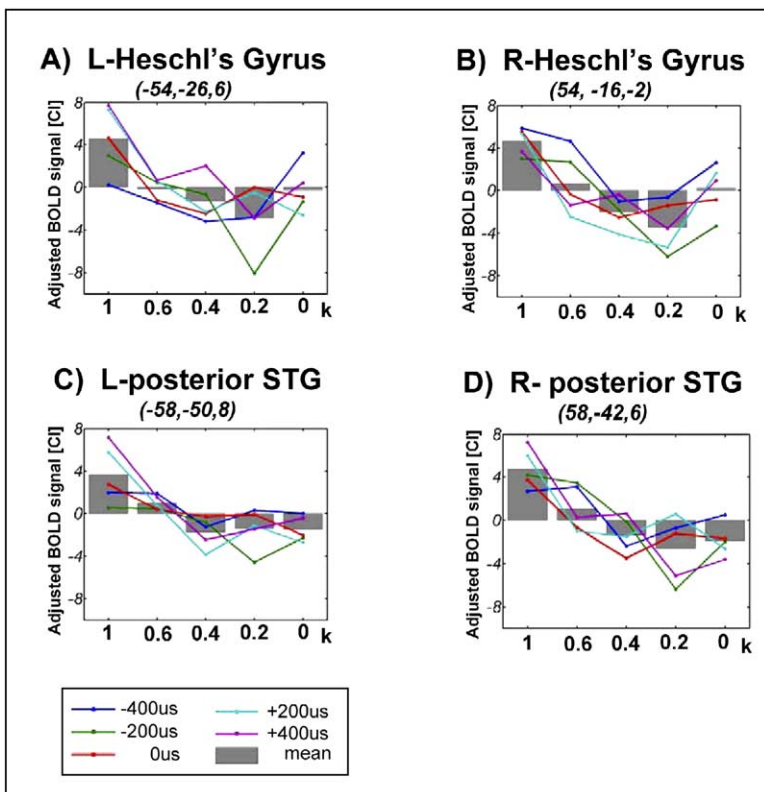


Figure 3. Modulatory Effect of Binaural Coherence Shown Separately for Each ITD  
Activity in Heschl's gyrus (A and B) and posterior STG (C and D) decreased with decreasing coherence. The level of brain activity for the different ITDs is plotted as lines in different colors and superimposed on the mean effect (gray bars). The data indicate that the progressive decrease of activity with decreasing binaural coherence was present irrespective of the ITD.

Table 3. Overall Effect of Sound and Modulatory Influences of Binaural Sound Coherence during Passive Listening in Experiment 2

	Size of Cluster	p Corrected	MNI Coordinates	z value
A. Overall Effect of Sound				
R Heschl's gyrus	676	<0.001	50, -22, 4	5.58
L Heschl's gyrus	532	<0.001	-40, -30, 4	4.82
B. Coherent minus incoherent sounds				
R Heschl's gyrus	v.c.	0.043	52, -10, -8	3.8
L Heschl's gyrus	v.c.	0.063	-36, -36, 12	3.66
R <i>Posterior STG</i>	<i>n.a.</i>	<i>n.a.</i>	<i>68, -40, 8</i>	<i>3.17</i>
L <i>Posterior STG</i>	<i>n.a.</i>	<i>n.a.</i>	<i>44, -54, 8</i>	<i>2.62</i>

(A) Coherent and incoherent sounds versus rest. P values are corrected for multiple comparisons at cluster level (cluster size estimated at  $p = 0.001$ , uncorrected). (B) Coherent minus incoherent sounds. p values are corrected at voxel level, considering the regions activated by the overall effect of sound minus rest as the volume of interest (A). The posterior STG values reported in italics did not show an overall effect of sound minus rest and are reported here for completeness only. L/R, left/right hemisphere; v.c., voxel level, corrected; n.a., not applicable, because not in the volume of interest.

well as in anterior auditory regions. However, neither passive listening to high binaural coherence sounds (Experiment 2) nor active processing of nonspatial sound features (here, frequency-modulated tones; Experiment 3) resulted in the activation of posterior auditory areas. We conclude that posterior auditory areas are primarily activated during successful auditory spatial localization (Experiment 1 only).

Our psychophysical data confirmed that the subjects' ability to localize sounds in the horizontal plane decreased with decreasing binaural sound coherence (see Figure 1F). Previous studies indicated that sounds presented with high binaural coherence will result in the perception of a single source that can be localized in space and selected as a relevant sound object (e.g., R.I. Chernyak and N.A. Dubrovsky, 1968; Blauert and Lindemann, 1986; Blauert, 1997). Decreasing binaural coherence results in a progressive "blurring" of the spatial source, increasing the difficulty of identifying a precise position of sound sources in space (e.g., R.I. Chernyak and N.A. Dubrovsky, 1968; Jeffress et al., 1962; Blauert and Lindemann, 1986; Blauert, 1997). Thus, decreasing binaural coherence results in poorer sound localization (Jeffress et al., 1962), as also observed in the current study.

Here we show that this change of localization performance as a function of binaural coherence correlates with changes in brain activity in auditory regions posterior to Heschl's gyrus. The involvement of the posterior STG in the present study is consistent with single-cell recordings (Rauschecker and Tian, 2000; Tian et al., 2001), anatomical tracer studies (e.g., Romanski et al., 1999), and previous imaging data in humans (e.g., Krumbholz et al., 2005; Pavani et al., 2002; Maeder et al., 2001) that highlighted the importance of this region in spatial perception for the auditory modality. Single-unit recordings in monkeys suggest that sound localization involves a dorsolateral "where" pathway including the caudal part of STG (Rauschecker and Tian, 2000; Tian et al., 2001; see also Romanski et al., 1999 for related anatomical tracer studies). In humans, auditory localization of stationary sounds was investigated using fMRI and PET (Alain et al., 2001; Maeder et al., 2001; Zatorre et al., 2002; Warren and Griffiths, 2003). These studies consistently demonstrated activation of the posterior parts of the STG for sound localization. Further, lateralized sound percepts have been pro-

duced either by internal ITD or ILD (sounds delivered through headphones [Maeder et al., 2001; Hart et al., 2004] or by external sound sources [Alain et al., 2001; Zatorre et al., 2002]). The posterior/superior part of the human temporal lobe was consistently found to be active, irrespective of the specific methods used to produce spatial sounds (see also Arnott et al., 2004, for review).

However, unlike typical daily life situations in which the auditory system receives concurrent inputs from multiple sound sources, previous localization studies used exclusively coherent stimulation at the two ears, thus investigating sound localization for unambiguous perception of one single sound source (but see also Zatorre et al., 2002). Here, we studied sound localization while manipulating the level of binaural sound coherence. Consistent with the previous literature (e.g., Maeder et al., 2001; Pavani et al., 2002; Zatorre et al., 2002), we found activation of posterior auditory areas when subjects engaged in sound localization. However, here we demonstrate that the engagement of these brain regions was contingent on the subjects being able to use binaural cues to successfully estimate stimulus location (i.e., for high levels of binaural sound coherence and good localization performance; e.g., see Figure 2).

Furthermore, the present study showed that the effect of binaural coherence during sound localization was independent of ITD (see Figure 3), extending previous findings concerning the role of ITD in auditory space perception. While localization of lateralized sounds (ITD different from zero) leads to consistent activation in the posterior STG (e.g., Maeder et al., 2001), little evidence exists for segregated representations of specific ITDs in auditory cortex (Woldorff et al., 1999; Krumbholz et al., 2005). Zatorre et al. (2002) studied source localization for sounds that included combinations of ITD, ILD, and head-related parameters during PET scanning. While overall, spatial sounds produced activation of primary and posterior auditory areas, this study found no specific activation for one or another source location. Thus, even external spatial sound signals, which add ILD and head-related transfer cues to ITD information, typically do not result in activation of specific regions of auditory cortex as a function of source location. At the single-cell level, studies in monkeys and cats showed that the vast majority of neurons

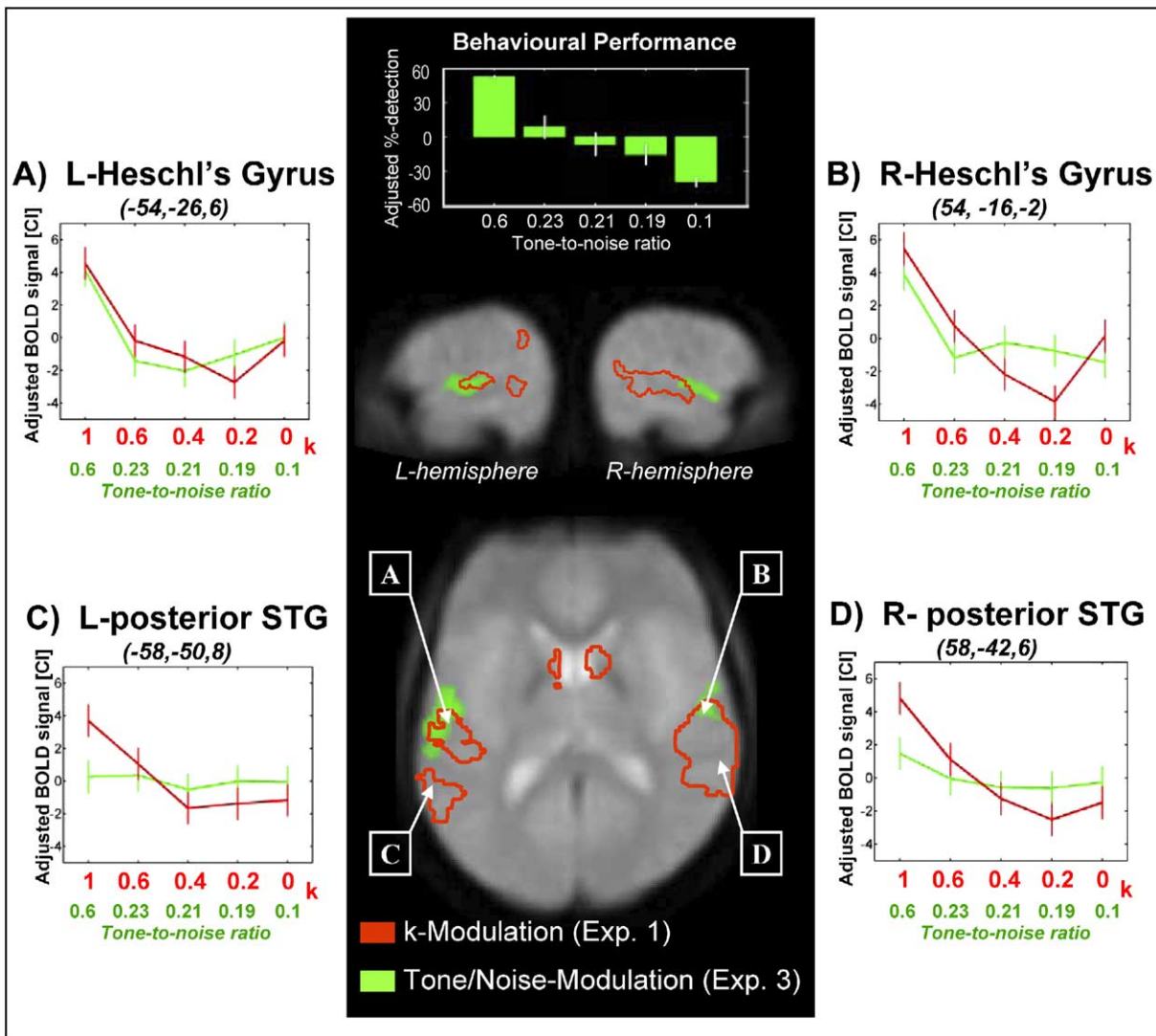


Figure 4. Modulatory Effect of Tone-to-Noise Amplitude Ratio during Active Tone Detection in Experiment 3

(Central panel) Behavioral performance (% detection of the target tones) as a function of the tone-to-noise ratio, demonstrating a progressive decrease of the subjects' ability to detect the target tones with decreasing tone-to-noise ratio. Middle and bottom of this panel show areas in which brain activity decreased with decreasing detection performance (in green). The modulatory effect extended from Heschl's gyrus anteriorly into the anterior STG. The red outlines on the anatomical section also show the modulatory effect of localization performance, as observed in Experiment 1. These panels indicate that performance during sound localization and tone detection commonly affected activity in a central region (Heschl's gyrus), while posterior areas were selectively modulated according to localization performance only (Experiment 1; red outlines). For display purposes, the statistical threshold for the modulatory effect of tone detection was set to  $p < 0.001$ , uncorrected (voxel level). (Side panels) The signal plots in Heschl's gyrus (A and B) show that activity decreased with both decreasing tone-to-noise ratio (green lines) and with decreasing binaural coherence (red lines). Thus, the subjects' performance was mirrored irrespective of task (sound localization and tone detection). In contrast, posterior auditory regions (C and D) showed no modulation for changes in the tone-to-noise ratio. Thus, activity in the posterior STG mirrored the subjects' performance only during active sound localization. The level of activation displayed is adjusted to a mean of zero and it is expressed in confidence interval (CI = 10%) units. Error bars in CI units.

in the posterior auditory cortex are spatially selective (e.g., preferring sounds of the contralateral hemisphere; see Stecker et al., 2005; Tian et al., 2001). However, these neurons often display broad tuning curves (e.g., responding to azimuthal differences of  $40^\circ$  to  $60^\circ$ ; see Tian et al., 2001; cf. Stecker et al., 2005, 2003; Recanzone, 2000) and their topological organization does not reflect positions in external space (Recanzone, 2000; Stecker et al., 2003; Stecker and Middlebrooks, 2003).

The lack of any such topographical organization at the neuronal level might explain why fMRI techniques that rely on the engagement of large populations of neurons with similar response characteristics have generally failed to detect any location-specific activation (e.g., Bushara et al., 1999; Woldorff et al., 1999; Zatorre et al., 2002; but see also Krumbholz et al., 2005 for interhemispheric differences). In the present study, we orthogonally manipulated ITD and binaural coherence, showing



Table 4. Effects of Tone-to-Noise Ratio in Experiment 3 and Direct Comparisons with Experiment 1

	p Corrected	MNI Coordinates	z Value
<b>A. Modulatory Effect of Tone-to-Noise Ratio during Active Tone Detection (Experiment 3)</b>			
R Heschl's gyrus	<0.001	68, -24, -4	5.48
L Anterior STG	0.005	-50, 0, -8	4.96
L Heschl's gyrus	0.004	-52, -20, 2	5.03
R Anterior STG	0.056	56, 6, -12	4.95
<b>B. Common Effect of Sound Localization (Experiment 1) and Tone Detection (Experiment 3)</b>			
R Heschl's gyrus	0.015	56, -12, 0	4.07
L Heschl's gyrus	0.032	-56, -26, 8	3.85
<b>C. Areas Activated More for Sound Localization (Experiment 1) than for Tone Detection (Experiment 3)</b>			
R Heschl's gyrus	0.001	52, -16, -2	4.81
R Posterior STG	0.008	60, -42, 2	4.24
L Heschl's gyrus	0.026	-52, -32, 8	3.91
L Posterior STG	0.002	-58, -58, 8	4.69

(A) Modulatory effect of tone-to-noise ratio during active tone detection (Experiment 3). p values are corrected at voxel level, considering as the volume of interest regions that were activated for the overall effect of detection task (see Table SA). The anterior STG in the right hemisphere (in italics) did not show an overall effect of detection task and that data are reported for completeness only. (B) Common effect of performance during tone detection (Experiment 3) and sound localization (Experiment 1); see also Figures 4A and 4B. p values are corrected at voxel level, considering as the volume of interest regions that were activated for the modulatory effect of binaural coherence in Experiment 1 (see Table 2). (C) Areas showing better correspondence between brain activity and behavioral performance during sound localization (Experiment 1) than tone detection (Experiment 3); see also Figures 4C and 4D. p values are corrected at voxel level, considering as the volume of interest regions that were activated for the modulatory effect of binaural coherence in Experiment 1 (see Table 2). L/R, left/right hemisphere.

that responses in auditory cortices were modulated by the latter, but not by the former (see also Figure 3).

The question arises whether the modulation of posterior auditory cortex reported here might depend on the active process of sound localization. Using PET, Zatorre and colleagues compared brain activity during passive listening of spatial sounds versus silence (Zatorre et al., 2002). This revealed activation of both Heschl's gyrus and the posterior STG, suggesting that active localization might not be necessary to engage the posterior STG. Using fMRI, Maeder and colleagues presented subjects with either lateralized bursts of white noise (ITD between 0 and 681  $\mu$ s) for sound localization or environmental sounds for sound recognition. Direct comparison between the two tasks/stimuli showed selective activation of the posterior STG plus the inferior parietal cortex for sound localization (Maeder et al., 2001). In a second experiment, the same stimuli were presented, but during passive listening. Again, posterior temporal and inferior parietal cortices activated selectively for spatial sounds (i.e., bursts of white noise with variable ITDs; see Maeder et al., 2001). Accordingly, the authors suggested that a posterior "where" pathway (see also Arnott et al., 2004) is engaged by spatial sounds irrespective of current task requirements and attentional or motor biases. However, it should be noted that both of these studies compared

auditory stimuli containing ITD information versus stimuli with no ITD information (silence [Zatorre et al., 2002] or ITD = 0 [Maeder et al., 2001]); therefore, it could be argued that the posterior effects still relate to the presence of ITD in the auditory input.

Here, we performed two control experiments to determine the specificity of our posterior modulatory effects for successful spatial localization. First, we assessed whether the modulatory effects of binaural coherence that we observed during sound localization depends on the active task requirement of localizing sounds or on the lower-level automatic processing of binaural cues. We compared brain activity for full coherence ( $k = 1$ ) versus null coherence ( $k = 0$ ) during passive listening with a constant ITD of zero, revealing binaural coherence effects only in Heschl's gyrus (Experiment 2). A previous fMRI study (Budd et al., 2003) that presented subjects with different levels of sound coherence and ITD equal to zero, also found that binaural coherence modulated activity in regions confined to Heschl's gyrus. As in the present study, the posterior STG was not significantly activated. The finding that regions in Heschl's gyrus showed an effect of binaural sound coherence irrespective of task requirement (i.e., modulation observed in both Experiments 1 and 2; see also Budd et al. [2003]) suggests that these cues are processed automatically at earlier stages of the auditory pathway. Indeed, electrophysiological studies in the owl indicated that the spike pattern in the optic tectum depends on the level of sound coherence (Saberi et al., 1998). Fully coherent binaural bursts of white noise resulted in firing patterns characterized by a high average spike activity and a well-defined tuning curve depending on ITDs. However, lowering the level of binaural coherence resulted in reduced average activity and an overall loss of ITD tuning (Saberi et al., 1998). Thus, it seems likely that the cortical effects that we report here may also result from early binaural processing in subcortical structures (see also Budd et al. [2003]).

A second control experiment assessed whether mere changes in attentional demands (e.g., see Hall et al. [2000]) and/or changes in overall performance (e.g., successful sound recognition; see Arnott et al. [2004]) might explain the modulatory effects observed in posterior auditory regions during sound localization (Experiment 1), or whether these are specific for successful sound localization instead. Thus, we asked subjects to detect frequency-modulated tones embedded in a white noise background. Decreasing the ratio of tone-to-noise amplitudes we obtained a progressive decrease of the subjects' ability to detect the target tone (see Figure 4, top central panel). This change of detection performance affected activity in Heschl's gyrus (see Figures 4A and 4B, green lines) and in auditory areas anterior to it, but it did not affect posterior auditory areas where only changes in localization performance resulted in modulation of brain activity (see Figures 4C and 4D; cf. red and green lines). We should, however, note that the lack of any modulatory effect according to tone detection performance (with a statistically significant difference between Experiments 1 and 3) should not be taken as conclusive evidence that posterior areas never process nonspatial sound fea-

tures. Had we used a different task, target stimuli and/or masking procedure, we might have found some effect of task performance in posterior auditory areas, even if no sound localization is required (see also Hall et al. [2000] and Arnott et al. [2004]). Nevertheless, the results of both of our control experiments suggest that the modulatory effects in posterior auditory areas are primarily associated with changes in localization performance. This is also consistent with the hypothesis that posterior auditory areas are selectively engaged in the representation of auditory space (e.g., Rauschecker, 1997, 1998; Rauschecker and Tian, 2000; Alain et al., 2001; Maeder et al., 2001; Zatorre et al., 2004; and also Arnott et al., 2004).

In conclusion, our study revealed that the level of binaural sound coherence modulates activity throughout the human auditory cortex and that in posterior regions, this correlates positively with the subject's ability to localize sound sources. Accordingly, modulation of brain activity in Heschl's gyrus was found during both active sound localization (Experiment 1) and during passive listening to central sounds (Experiment 2). Binaural sound coherence modulated activity in the posterior STG, particularly when subjects successfully used interaural information (here, ITD) to localize sound positions in the horizontal plane (Experiment 1). An additional control experiment showed that these modulatory effects in the posterior auditory cortex correlated specifically with changes in localization performance, but not with changes in tone detection performance (Experiment 3). These findings suggest that coherence cues are automatically processed in or before primary auditory areas and that the results of these neural computations are exploited by later stages in the auditory pathway along a posterior processing stream to localize sounds. Binaural coherence cues may play an important role in the analysis of complex auditory scenes, allowing for selection of relevant sound sources on the basis of their location in space.

## Experimental Procedures

### Subjects

Sixteen healthy, right-handed subjects (aged 18–35 years; eight males) participated in Experiment 1 (active localization). Fourteen of them took part in Experiment 2 (passive listening). Nine healthy, right-handed subjects (aged 18–35 years; five males) participated in Experiment 3 (tone detection); four of them had already taken part in Experiments 1 and 2. After receiving an explanation of the procedures, all subjects gave written informed consent. The study was approved by the independent Ethics Committee of the Fondazione Santa Lucia (Scientific Institute for Research Hospitalization and Health Care).

### Paradigm

In Experiment 1 (active localization), functional MRI data were acquired using an event-related design. Twenty-five event types were organized in a  $5 \times 5$  factorial design. The first factor was the level of binaural coherence, and the second factor was the interaural time difference. Each sound event lasted for 2 s with a subsequent silent phase of 1 s. The 25 possible combinations of sound coherence and ITDs were presented in randomized and unpredictable order. The task of the subject was to localize each sound in the horizontal plane, pressing one of two buttons with the right hand (2-AFC procedure). All subjects underwent five separate fMRI runs, each lasting approximately 5.2 min.

Experiment 2 (passive perception) used a block design with two

types of sound stimuli: full binaural coherence ( $k = 1$ ) and null coherence ( $k = 0$ ), both presented with ITD equal to zero. The stimulus duration was 20.8 s, and blocks of stimulation alternated with rest periods (no sound stimuli) also lasting 20.8 s. The subjects listened passively to the stimuli and did not produce overt responses. All subjects underwent two fMRI runs, each lasting approximately 6.9 min. Of the two fMRI runs of Experiment 2, one was presented before and one after Experiment 1.

In Experiment 3 (tone detection), functional MRI data were acquired using an event-related design. The five event types consisted of a frequency-modulated tone with five different amplitudes, embedded in white noise. Each sound lasted for 2 s with a subsequent silent phase of 1 s. The five event types were presented in randomized and unpredictable order. The task of the subject was to decide if the frequency-modulated tone was "present" or "absent" and to indicate that decision by pressing one of two buttons with the right hand (2-AFC procedure). All subjects underwent five separate fMRI runs, each lasting approximately 5.2 min.

### Prescanning Tests

Prior to fMRI scanning in Experiments 1 and 2, subjects were trained briefly to perceive differences of binaural sound coherence. Subjects were presented with fully coherent stimuli and fully incoherent stimuli (ITD = 0) and they were made aware of the perceptual difference between the two: "central inside the head" for coherent sounds or "sounds on both ears" for incoherent sounds (see R.I. Chernyak and N.A. Dubrovsky, 1968; Blauert and Lindemann, 1986). After this, subjects were presented with ten coherent stimuli and ten incoherent stimuli in a randomized order, and they were asked to indicate verbally what they perceived. All subjects gave at least 70% correct answers. Also, prior to fMRI scanning, subjects were presented with fully coherent white noise with ITD = 0  $\mu$ s. The perceived horizontal position of the sound was aligned to the subjective head-midline, by adjusting the balance on the amplifier. Note that the balance adjustment does not change the sound pressure level overall.

### Experiment 1: Localization Task

The level of binaural sound coherence was varied during an auditory localization task. White noise stimuli were used for dichotic stimulation (band-pass filtered white noise; cutoff frequency, 0.6 kHz and 22 kHz; duration 2 s; rise and fall times, 20 ms). As indicated by fast Fourier transformation, a white noise signal consists of uniformly distributed  $N$  frequencies with normally distributed amplitudes ( $-36 \pm 5$  dB [mean  $\pm$  SD]). Two stereo channels are independent if the amplitudes of the  $N$  frequencies are determined separately. To generate binaural stimuli with different levels of coherence, two independent white noise signals were mixed to varying degrees for one ear channel, while the other ear received one unchanged white noise signal. The mixing of the two independent white noises is expressed as follows:  $WN_2 = WN_1 \cdot \sqrt{k/(1-k)}$ , where  $WN_2$  and  $WN_1$  are the percentage rate of the two independent white noises and  $k$  is the desired value of coherence level (cf. Blauert, 1997).  $WN_1$  was set to 100% and five different  $k$  values of sound coherence were used:  $k = 1$ ,  $k = 0.6$ ,  $k = 0.4$ ,  $k = 0.2$ , and  $k = 0$ . Note that all sound stimuli were adjusted for equal sound pressure levels to exclude any confounding effect due to dB differences.

The different sound positions in the horizontal plane were produced using interaural time differences. Each of the five different coherence levels was presented with five different ITDs:  $-400 \mu$ s and  $-200 \mu$ s (sound leading at the left ear),  $0 \mu$ s (equal arrival time at both ears), and  $+400 \mu$ s and  $+200 \mu$ s (sound leading at the right ear). Accordingly, the auditory stimuli are perceived as intracranial sound images, along a line joining the two ears (cf. Blauert, 1997). Irrespective of the level of binaural coherence, subjects made left-right judgments about sound positions (2-AFC procedure). Subjects indicated the perceived intracranial position of the sound by pressing one of two buttons ("left" or "right") with the right thumb immediately after each sound. During sound localization, subjects were required to maintain central gaze on a fixation point (see section below on eye tracking).

### Experiment 2: Passive Listening

Experiment 2 comprised only fully coherent sound stimuli ( $k = 1$ ) and fully incoherent stimuli ( $k = 0$ ). Both white noise stimuli were

presented with an ITD = 0 and a duration of 20.8 s. Blocks of stimulation alternated with blocks of equal duration, but without any sound stimuli. During blocks of stimulation, sounds were presented continuously (band-pass filtered white noise; cutoff frequency, 0.6 kHz and 22 kHz; duration 20.8 s; rise and fall times, 20 ms). During fMRI scanning, subjects listened passively to blocks of fully coherent or fully incoherent sounds while maintaining central fixation.

#### **Experiment 3: Detection of Frequency-Modulated Tones Embedded in a White Noise Background**

In Experiment 3, we manipulated the ratio of tone-to-noise amplitude to obtain different levels of detection performance for the target tones. The parameters of the frequency-modulated sinus tone (900 Hz; frequency modulated by 6 Hz; modulation depth, 12%) were chosen to match those in previous work by Hall et al. (2000). Sinus tones had a duration of 2 s and were embedded in white noise stimuli. The ratio of tone-to-noise maximal amplitude was set to five different values: 0.60:1; 0.23:1; 0.21:1; 0.19:1; and 0.10:1. All sound stimuli were adjusted for equal overall sound pressure level to exclude any confounding effect due to dB differences. On each trial, subjects reported whether or not they perceived the target tone by button press (2-AFC procedure).

#### **Image Acquisition**

All three experiments employed identical parameters of image acquisition. Imaging was carried out in a 3T Siemens Allegra head scanner (Siemens, Erlangen, Germany). BOLD (blood oxygenation level-dependent) contrast was obtained using echo planar T2\*-weighted imaging (EPI). The acquisition of 32 transverse slices provided coverage of the whole cerebral cortex. Repetition time was 2.08 s and in-plane resolution was 3 × 3 mm; slice thickness and gap were 2.5 mm and 1.25 mm, respectively.

#### **Data Analysis**

##### **Psychophysical Data for Experiment 1**

On each trial, subjects responded “right” or “left” by button press to indicate the perceived sound position (localization task). For each level of binaural coherence, the group average frequency of “right” responses was determined as a function of ITD. Data were fitted to the sigmoidal equation:  $f(\text{ITD}) = 100 / (1 + e^{-(K(\text{ITD} - \text{ITD}_{50\%}))})$  where  $f$  is the percentage frequency of “right” responses,  $\text{ITD}_{50\%}$  is the ITD where  $f$  is 50%, and  $K$  is the slope of the function at  $\text{ITD}_{50\%}$  (cf. Zimmer et al., 2003). The coefficients of determination ( $r^2$ ) obtained from the fit were used as a measure of the subjects’ ability to estimate the sound position. For the parametric analysis of fMRI data, the  $r^2$  values were mean adjusted to orthogonalize the modulatory effect of coherence with respect to the overall effect of sound (see below).

##### **Psychophysical Data for Experiment 3**

On each trial, subjects responded “present” or “absent” by button press, to report whether they perceived the frequency-modulated target tone. For each tone-to-noise ratio, the group average for “present” responses was determined as a mean percentage value. For the parametric analysis of fMRI data, these five percentage values were mean adjusted to orthogonalize the modulatory effect of correct detection with respect to the overall effect of sound.

##### **fMRI Data**

Data were analyzed using SPM2 (<http://www.fil.ion.ucl.ac.uk>). The first four image volumes of each run were discarded to allow for stabilization of longitudinal magnetization (leaving 740 volumes for Experiment 1, 400 volumes for Experiment 2, and 740 volumes for Experiment 3, per subject). Preprocessing included rigid-body transformation (realignment) and slice timing to correct for head movement and slice acquisition delays. The images were normalized to the MNI space, using the mean of the functional volumes, and then smoothed with a Gaussian filter of 6 mm full-width at half maximum (FWHM) to increase the signal-to-noise ratio and to facilitate group analyses.

For all three experiments, statistical inference was based on a random effects approach (A.P. Holmes and K.J. Friston, 1998, Fourth International Conference on Functional Mapping of the Human Brain), which comprised two steps. First, for each subject the data were best fitted at every voxel, using a combination of effects of interest. In Experiment 1, the effects of interest were the timing

of the 25 event types (given by crossing of the two stimulus factors: five levels of binaural coherence and five ITDs). In Experiment 2, the effects of interest were the timing of the two event types (full coherence and null coherence; block length = 20.8 s). In Experiment 3, the effects of interest were the timing of the five event types (five tone-to-noise ratios). All stimulus functions were convolved with the SPM2 standard hemodynamic response function.

In Experiment 1, linear compounds (contrasts) were used to determine responses for the five coherence levels, averaging across ITDs and fMRI runs. This resulted in five contrast images per subject. In Experiment 2, the linear compounds determined the effects of the two conditions ( $k = 1$  and  $k = 0$ ) across the two fMRI runs, thus producing two contrast images per subject. In Experiment 3, linear compounds were used to determine responses for the five tone-to-noise ratios. This resulted in five contrast images per subject. The contrast images then underwent the second step, comprising a within-subject ANOVA that modeled the mean of each effect (five levels of coherence in Experiment 1; two levels in Experiment 2; five tone-to-noise ratios in Experiment 3) and the mean effect of subject. Finally, linear compounds were used to compare these effects, now using between-subjects variance (rather than between-scans variance). Correction for nonsphericity (Friston et al., 2002) was used to account for possible differences in error variance across conditions and any nonindependent error terms for the repeated measures analysis.

The aim of Experiment 1 was to test whether brain regions engaged during sound localization showed some modulation according to binaural coherence and localization performance. Thus, we first highlighted the overall (mean) effect of the localization task ( $p < 0.05$ , corrected, at cluster-level; cluster size estimated at  $p = 0.001$ , uncorrected). Then, we tested for any parametric modulation of brain activity by binaural coherence. The effect of binaural coherence and changing localization performance was assessed using a linear compound consisting of the five mean-adjusted  $r^2$  coefficients derived from the behavioral data (see Figure 1F). Note that the mean adjustment orthogonalizes the effect of localization-performance with respect to the overall effect of task, making our analyses unbiased. For this comparison the SPM threshold was set to  $p = 0.05$ , corrected; considering all voxels showing an overall effect of the localization task as the volume of interest (see Table 1; Worsley et al., 1996).

An analogous procedure was used to analyze Experiment 2 (passive listening). Again we determined the overall (mean) effect of stimulation ( $p < 0.05$ , corrected, at cluster level; cluster size estimated at  $p = 0.001$ , uncorrected), and we tested for any effect of binaural coherence within the activated regions. For this comparison the SPM threshold was set to  $p = 0.05$ , corrected, considering all voxels showing an overall effect of the two stimulation conditions versus rest as the volume of interest (see Table 3A; Worsley et al., 1996).

The aim of Experiment 3 was to assess whether any modulatory effect of binaural coherence during spatial localization observed in Experiment 1 was specific for changes in localization performance, or whether comparable changes in performance for nonspatial sound features (here, discrimination of a target tone from background white noise) would also result in similar modulation of brain activity. We first determined the overall (mean) effect of auditory stimulation in Experiment 3 ( $p < 0.05$ , corrected, at cluster-level; cluster size estimated at  $p = 0.001$ , uncorrected; Table SA). Next, we tested for any effect of detection performance using mean-adjusted % correct detection for the five tone-to-noise ratios (see Figure 4, top central panel), within these regions.

Furthermore, we statistically compared performance-related modulations in Experiment 1 and Experiment 3, using a between-groups ANOVA. Note that all contrast images (i.e., the effect sizes for each subject) were scaled to normalize the performance indices measured in the two experiments (i.e., the  $r^2$  coefficient for  $k = 1$  and the % detection for tone-to-noise ratio = 0.6 were set to equal one). This allowed us to compare the effect of performance (normalized and mean-adjusted) on brain activity in the two experiments. We tested for common effects of performance using conjunction analyses (<http://www.sph.umich.edu/~nichols>), and we directly compared the two experiments highlighting performance-related modulations that were specific for the localization task. Be-

cause the aim of Experiment 3 was to provide a control for the performance-related modulations observed in Experiment 1, corrected *p* values were assigned, using regions activated in Experiment 1 as the volume of interest (see Table 2; Worsley et al., 1996).

#### Eye Tracking

For four subjects, the gaze direction was monitored during fMRI using an ASL eye tracking system that was adapted for use in the scanner (Applied Science Laboratories, Bedford, MA; Model 504, sampling rate 60 Hz). For these subjects additional analyses of the localization data (Experiment 1) were carried out to confirm our results with central fixation verified. Eye-position traces were examined in a 2000 ms window, beginning with the sound onset and lasting for the duration of the sound event. Losses of fixation were identified as changes in horizontal eye position greater than  $\pm 2^\circ$  of visual angle. This revealed that, on average, subjects lost fixation in 13.3% of the trials. New fMRI analyses explicitly modeling trials containing losses of fixation were carried out for each of the four subjects. Due to the small pool of subjects and the consequent reduction in degrees of freedom for statistical inference, we tested for the overall effect of localization task and any modulation by coherence using between-runs variance (i.e., a total of 20 runs, five per subject), rather than between-subjects variance. Therefore, statistical inference for these additional analyses cannot be extended to the population; instead it concerns the four subjects tested here. However, this would be beyond the aim of these additional analyses that seek solely to confirm our main results (population inference) with central fixation controlled.

#### Supplemental Data

Supplemental Data include one table and can be found with this article online at <http://www.neuron.org/cgi/content/full/cgi/47/6/893/DC1>.

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