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ORIGINAL ARTICLE

Orienting and maintenance of spatial attention in audition and vision: multimodal and modality-specific brain activations

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Abstract We studied orienting and maintenance of spatial attention in audition and vision. Functional magnetic resonance imaging (fMRI) in nine healthy subjects revealed activations in the same superior and inferior parietal, and posterior prefrontal areas in the auditory and visual orienting tasks when these tasks were compared with the corresponding maintenance tasks. Attention-related activations in the thalamus and cerebellum were observed during the auditory orienting and maintenance tasks and during the visual orienting task. In addition to the supratemporal auditory cortices, auditory orienting, and maintenance produced stronger activity than the respective visual tasks in the inferior parietal and prefrontal cortices, whereas only the occipital visual cortex and the superior parietal cortex showed stronger activity during the visual tasks than during the auditory tasks. Differences between the brain networks involved in auditory and visual spatial attention could be, for example, due to different encoding of auditory and visual spatial information or differences in stimulus-driven (bottom-up triggered) and voluntary (top-down controlled) attention between the auditory and visual modalities, or both.

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Introduction

Recent functional magnetic resonance imaging (fMRI) studies have compared the brain mechanisms underlying orienting and maintenance of spatial attention within the auditory and visual modalities (Shomstein and Yantis 2006; Vandenberghe et al. 2001; Yantis et al. 2002). For example, Yantis et al. (2002) used a rapid serial visual presentation task, in which subjects were presented with two letter streams, one at the left and the other at the right from the point of fixation. In this experiment, the subjects were asked to press a button in response to two digits that occurred occasionally (every 3–5 s) among the letters. One of these digits designated that the subjects were to hold their attention at the current location (maintenance of attention), and the other that attention was to be shifted to the stream of letters at the opposite side (orienting of attention). Orienting of visual attention was found to be associated with transient activation in the superior parietal lobule (SPL) bilaterally, as compared with maintenance of attention. Recently, a similar rapid serial presentation study with speech stimuli (Shomstein and Yantis 2006) revealed activations associated with orienting of auditory attention mainly in the same SPL areas. Moreover, Yantis et al. (2002) and Shomstein and Yantis (2006) found activity associated with visual and auditory orienting of attention in the middle and superior frontal gyri (MFG and SFG, respectively), that were activated by visual orienting of attention also in previous studies (e.g., Corbetta et al. 1993; Coull and Nobre 1998; Giesbrecht et al. 2003; Hopfinger et al. 2000). Consistently, clinical studies have shown that dysfunctions of the SPL, MFG, and SFG can lead to deficits in visual orienting of spatial attention (for a review, see Mesulam 1981, 1999).

However, no previous brain imaging study compared auditory and visual orienting of attention. A direct within-subjects comparison of orienting and maintenance of attention in audition and vision might reveal differences between the brain areas involved in these functions that are not readily seen by comparing fMRI results from separate studies. Moreover, it is possible that the SPL, MFG, and SFG activations observed by Yantis et al. (2002) and Shomstein and Yantis (2006) were partly associated with linguistic processes required by these tasks involving written or spoken letters and numbers. Furthermore, as most of the other previous fMRI experiments on spatial attention (e.g., Giesbrecht et al. 2003; Hopfinger et al. 2000; Shomstein and Yantis 2006; Vandenberghe et al. 2001; Yantis et al. 2002), these studies used event-related experimental designs and analysis techniques. Event-related experiments effectively reveal transient activations associated with orienting of attention, but could be less effective than blocked designs for finding sustained attention-related activations.

Several fMRI and positron emission tomography (PET) studies have shown attention-related modulations also in thalamic and cerebellar activity, particularly in the pulvinar nucleus of the thalamus (LaBerge and Buchsbaum 1990) and in the posterior cerebellar cortex (Allen et al. 1997; Le et al. 1998). Furthermore, clinical studies have shown that like SPL and MFG dysfunctions, thalamic (Hugdahl et al. 1991; Mesulam 1981) and cerebellar (Townsend et al. 1999) abnormalities may lead to deficits in orienting of attention. However, only a few fMRI studies on orienting of attention have reported attention-related thalamic activations (Gitelman et al. 1999; Yantis et al. 2002), while no fMRI studies have shown cerebellar activations associated with orienting of attention (see, e.g., Giesbrecht et al. 2003; Gitelman et al. 1999; Hopfinger et al. 2000; Shomstein and Yantis 2006; Vandenberghe et al. 2001; Yantis et al. 2002). Attention-related thalamic and cerebellar activation is typically observed in experiments applying a block design (Allen et al. 1997; Gaab et al. 2003; LaBerge and Buchsbaum 1990; Le et al. 1998; Nitschke et al. 2004). It is possible that the lack of thalamic and cerebellar activation in the orienting of attention experiments is due to slow activation changes in these regions.

According to results of previous studies, the SPL, MFG, SFG, thalamus, and cerebellum could each contribute to both auditory (see, e.g., Gaab et al. 2003; Hugdahl et al. 1991; Shomstein and Yantis 2006) and visual (see, e.g., Allen et al. 1997; LaBerge and Buchsbaum 1990; Yantis et al. 2002) attention. However, the overlap and differences among the areas participating in different processes of spatial attention in audition and vision need to be identified. For example, it is possible that the brain processes involved in spatial attention differ between the two modalities due to fundamental differences in processing of auditory and visual spatial information. While visual information is spatiotopically organized from the retina to the visual cortex (Tootell et al. 1998), studies on animal models have found no evidence for spatiotopic organization in the cortical or subcortical auditory structures in primates or felines (Brugge et al. 2001; Furukawa et al. 2000; Stecker and Middlebrooks 2003). In keeping with the spatiotopic organization in the visual system, visual attention to a particular location results in location-specific attentional modulations (Heinze et al. 1994; Mangun et al. 1998; Tootell et al. 1998; Noesselt et al. 2002). In contrast, auditory studies have found small or no effects of attended sound location on the attention-related brain activity (Alho et al. 1994, 1999; Degerman et al. 2006; Petkov et al. 2004; Woldorff and Hillyard 1991; Woods et al. 1992; Zatorre et al. 1999). Direct comparison between orienting and maintenance of attention in audition and vision would make it possible to examine both multimodal and modality-specific features in the brain networks involved in spatial attention.

In the present fMRI study, we measured human brain activity during auditory and visual tasks in which the subjects selectively attended to non-speech sounds or pictures presented at a central location (maintenance task) or alternated the focus of their auditory or visual attention between opposite lateral locations (orienting task). In order to control for sensory and motor activations, similar series of sounds and pictures were delivered and the same number of responses were required in tasks that were compared with each other. Moreover, in each task, to-be-ignored stimuli were presented among the to-be-attended ones within the attended modality to decrease the predictability of the next stimulus location and increase the demands for attentional selection. In order to increase the reliability of comparisons within and between the modalities, a series of pilot studies was conducted to ensure that all tasks were equally difficult. A separate experiment was conducted to control for possible differences in activations related to auditory and visual attention to central versus lateral locations (Fig. 1).

Materials and methods

Subjects

Ten healthy right-handed subjects (five females; 24–35-year old, mean age 28 years) participated in the experiment. Data from one subject was discarded due to large

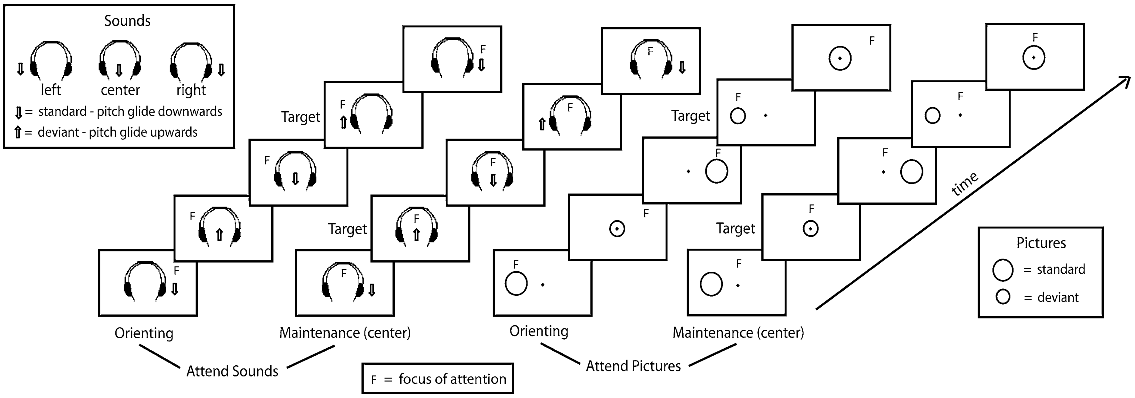

Fig. 1 Task design. Independent sequences of sounds and pictures were presented in three different spatial locations (*left*, *center*, or *right*). Left and right stimulus locations alternated both within the auditory and within the visual modality. In each modality, half of the stimuli appeared randomly in the center location. In the orienting tasks, subjects were required to focus their gaze on a fixation cross and to attend to the stimuli of the relevant modality appearing at the left or right locations (and to ignore the stimuli in the *center*). After a lateral stimulus had appeared, the subjects were to shift their attention to the opposite side and to wait for the next stimulus. In the maintenance tasks, the subjects were instructed to attend to the sounds or pictures at the center and to ignore the other stimuli. In the control experiment, the subjects maintained their auditory or visual attention either at the left, center, or right. In each task of both experiments, the subjects were required to respond to infrequent targets of the attended modality (upward pitch glides among downward glides or smaller *circles* among larger ones) appearing at the attended location. *F* indicates the focus of attention (*left*, *center*, or *right*) on each trial

movement artifacts (>1 mm, absolute movement) during fMRI data acquisition. All subjects gave a written informed consent prior to testing in accordance with the experimental protocol approved by the Ethical Committee of the Hospital District of Helsinki and Uusimaa.

Stimuli

Band-limited (–3 dB bandwidth of the sounds was at 120–180 Hz) normally distributed (bell-curve) noise bursts of 100 ms in duration (including 10 ms rise and fall times) were presented binaurally via headphones (UNIDES, ADU2a) and through earplugs applied for acoustic background noise reduction (see below). The center frequency of the noise bursts glided either downwards from 280 to 70 Hz (standards, $P = 0.88$) or upwards from 70 to 280 Hz (deviants, $P = 0.12$). Sounds with equivalent frequency distribution were used as standards and deviants to activate the same areas in the tonotopically organized auditory cortices. Band-limited noise was used because it is better than white noise in activating brain areas that are involved in the control of spatial attention (Zatorre et al. 2002). Moreover, sounds with a relatively low pitch were used in order to minimize interference with the fMRI scanner noise that has a relatively low sound energy at 100–500 Hz. Inter-aural intensity difference (25 dB) was used to produce left- and right-lateralized sounds. Central sounds had an effective intensity of about 70 dB sound pressure level (SPL) at the eardrum of each ear. The loudness of the lateralized sounds was matched with that of the central sounds according to judgments by three experienced listeners after which the effective intensities for the lateralized sounds were 75 dB SPL in the leading ear and 50 dB SPL in the other ear. Sounds were delivered through earplugs (Etymotic Research, ER3, Elk Grove Village, IL, USA). The noise of the scanner (~102 dB SPL, an A-weighted measurement inside the head coil) was attenuated by a viscoelastic mattress inside the headcoil, as well as the headphones and earplugs. Effective noise attenuation by the earplugs and viscoelastic mattress was ~30 and 5 dB, respectively.

Visual stimuli consisted of open thin-rimmed (large and small) circles presented on a black background for 100 ms. Diameter of the large circle was 4.2° (standard, $P = 0.88$) and the diameter of the small circle 3.1° (deviant, $P = 0.12$) projected on a mirror mounted on the head coil. The central circles were presented at the center of the screen and the lateralized circles on the horizontal meridian 5.1° to the left or right from the center of the screen. Based on the results of a pilot study, this was found to be the maximum distance allowing the subjects to perform the task without moving their eyes. Before the experiments, the subjects practiced the tasks with simultaneous eye-tracker recording until they could perform the tasks without moving their eyes.

The auditory and visual stimuli were presented in independent streams at random 400–1,400 ms (mean 660 ms) intervals (from offset to onset) between stimuli within each modality. The presentation order of the standard and deviant sounds and pictures was otherwise random except that there were never two deviants in a row. Half of the auditory and visual stimuli were central and the other half lateral (left or right). Within each modality, the lateral stimuli alternated (left, right, left, right...) and there could be one or more central stimuli between two successive lateral stimuli (Fig. 1). In the control experiment, the stimuli were otherwise similar to those of the main experiment, except that the left, center, and right stimuli were presented equiprobably in a fully random sequence, i.e., there was no regular left–right alternation. During auditory and visual tasks, and rest periods between them, the subjects were asked to focus on a small (size 0.7° × 0.7°) yellow fixation cross-presented at the center of the screen.

Procedure

Each block began with a 4-s bimodal centrally presented spoken (loudness matched with the auditory stimuli) and written instruction indicating the to-be-attended stimuli and the task. In the maintenance blocks of the main experiment, the subjects were instructed to selectively attend to the central stimuli of the designated modality (and to ignore all other stimuli). In half of the maintenance blocks of the main experiment, sounds and pictures were presented in concurrent independent streams, and in the rest of the maintenance blocks of the main experiment, only sounds or pictures were presented. In the orienting blocks of the main experiment, the subjects were instructed to focus their attention on the left or right stimuli of the designated modality and to shift their attention within the attended modality to the other side always after a stimulus had appeared in the attended location (Fig. 1). Thus, in the orienting blocks, the subjects continuously alternated the focus of their attention between the left and right locations. In each orienting block, sounds and pictures were presented in concurrent independent streams.

The control experiment consisted of maintenance blocks in which the subjects were instructed to attend selectively to stimuli either at the left, central, or right location of a designated modality (Fig. 1). In each block of the control experiment, both sounds and pictures were presented in concurrent independent streams.

In both experiments, the subjects were instructed to press a button with their right index finger whenever they detected a target stimulus, i.e., a deviant stimulus in the attended modality occurring at the to-be-attended location. The number of targets was balanced within each task over the whole experiment.

Duration of each block was 33.6 s followed by a 10-s period during which no stimuli were presented, except for a letter T for the Finnish word “tauko” (“break”), which replaced the fixation cross at the center of the screen. During the break, the subjects were required to focus on the letter T and to wait for the next task instruction. In both the main and control experiments, there were five blocks for each of the six tasks. The task was changed from block to block with auditory and visual tasks alternating in both the main experiment and the control experiment. For half of the subjects, the session was started with the main experiment, and for the other half the control experiment was conducted first.

Data acquisition and analysis

Functional brain imaging was carried out with a 3.0 T GE Signa MRI scanner (GE Medical Systems, Piscataway, NJ, USA) using a quadrature eight-channel head coil. The imaging area consisted of 28 functional gradient-echo planar (EPI) axial slices (thickness 4 mm, between-slices gap 1 mm, in-plane resolution 3.4 × 3.4 mm^2, voxel matrix 64 × 64, TE 32 ms, TR 2,800 ms, flip angle 90°). fMRI images were collected continuously during the experiment. Image acquisition was not time-locked to the beginning of the task blocks, that is, jittered acquisition was used (see, e.g., Price et al. 1999). A total of 1,050 functional volumes were acquired. Thus, fMRI data acquisition lasted for 49 min. In addition, a T1-weighted inversion recovery spin-echo volume was acquired for anatomical alignment (TE 1.9 ms, TR 9 ms, flip angle 15°). The T1 image acquisition used the same slice prescription as did the functional image acquisition, except for a denser in-plane resolution (matrix 256 × 256).

Data analysis was performed with fMRI Expert Analysis Tool software (Version 5.43), part of the Functional Magnetic Resonance Imaging of the Brain Center (FMRIB) software library (FSL, release 3.2, www.fmrib.ox.ac.uk/fsl, Smith et al. 2004). In order to allow for the initial stabilization of the fMRI signal, the first five volumes of the experiment were excluded from analysis. The data were motion corrected and spatially smoothed with a Gaussian kernel of 5 mm (FWHM), and high-pass filtered (cutoff 300 s; Woolrich et al. 2001). Statistical analysis was performed using the FMRIB Improved Linear Model (FILM; Woolrich et al. 2001). The hemodynamic response was modeled using a gamma-function (mean lag 6 s, SD 3 s) and its temporal derivative, and the high-pass filtering applied to the model was the same as that applied to the data. Explanatory variables were derived from timing (onset and duration of each block) in different tasks (main experiment: auditory and visual orienting and auditory and visual maintenance center tasks; control experiment: auditory and visual maintenance left, center, and right tasks) and instruction periods. Rest periods served as a baseline in the model. Individual level *Z*-statistic images were obtained by contrasting the activity in the auditory and visual orienting and maintenance tasks (only those with both auditory and visual stimuli) to each other within and between the modalities. For group analyses, *Z*-statistic images for each subject were transformed into a standard space (MNI152; Montreal Neurological Institute). The group analyses were performed using FMRIB's Local Analysis of Mixed Effects (FLAME; Beckmann et al. 2003) with a cluster threshold of $Z > 3.6$ and a cluster significance threshold of $P < 0.01$ (corrected for multiple comparisons). Conjunctions of the orienting and maintenance, and auditory and visual tasks were analyzed by inclusively masking the lower-level contrast *Z*-statistic images. For example, visual orienting versus visual maintenance was masked with auditory orienting versus auditory maintenance to reveal activity that was common to both modalities. In the conjunction analyses a corrected voxel-significance threshold of $P < 0.01$ was applied.

Based on previous studies (e.g., Gitelman et al. 1999; Shomstein and Yantis 2006; Townsend et al. 1999; Yantis et al. 2002), specific areas of the posterior cerebellum, thalamus, and cortex were selected for the region of interest (ROI) analysis. These areas were first identified in the high-resolution anatomical images of individual subjects. Corresponding ROIs were then defined in the space of the functional images. The size of the ROIs was $3 \times 3 \times 3$ voxels in the cortex and cerebellum and $2 \times 2 \times 2$ voxels in the thalamus. The posterior cerebellar ROI covered the areas crus I, crus II, and lobule VII of the lateral posterior cerebellar cortex (Schmahmann et al. 2000). The thalamic ROI covered mostly the pulvinar nucleus. The auditory-cortex and visual-cortex ROIs were located bilaterally in the posterior end of the superior temporal plane and in the lateral occipital cortex (extrastriate cortex), respectively. The SPL ROI was located adjacent to the intraparietal sulcus and the MFG ROI was located at the posterior end of the MFG.

Results

Performance

Mean hit rates and reaction times in the auditory and visual tasks are shown in Fig. 2. In the main experiment, there were no significant within-modality differences in hit rates or reaction times between the orienting and maintenance tasks, or between-modality differences in hit rates. In the control experiment, hit rates were lower during maintenance of visual attention at the right than during maintenance of visual attention at the center or left, while in the auditory modality, attention to the center location was associated with somewhat lower hit rates than attention to the lateral locations [two-factor repeated-measures ANOVA: modality (auditory, visual) * task type (left, center, right), interaction of modality and task type, $F(2, 18) = 7.9$, $P < 0.01$]. Moreover, in both experiments, reaction times were slower in the auditory tasks than in the visual tasks (main experiment: main effect of modality, $F(1, 9) = 47.7$, $P < 0.001$; control experiment: main effect of modality, $F(1, 9) = 24.2$, $P < 0.01$).

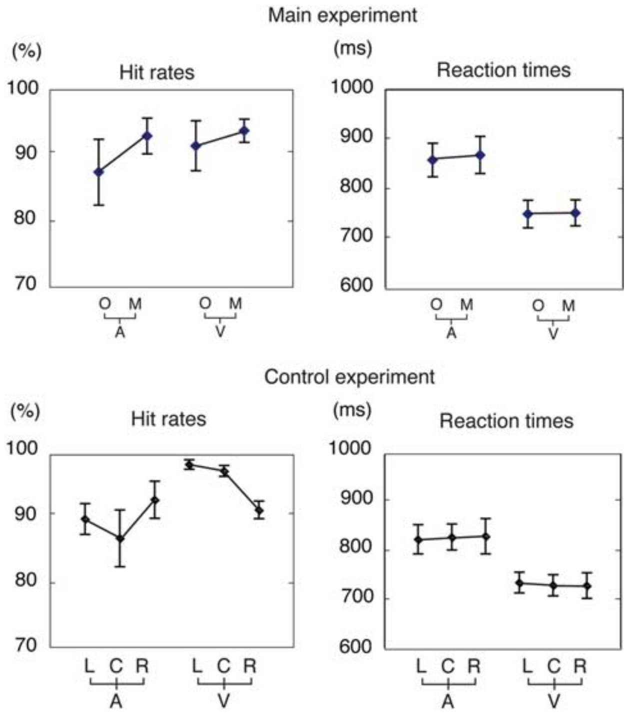

Fig. 2 Mean hit rates and reaction times in the main experiment and in the control experiment. *A* attend auditory, *V* attend visual, *O* orienting of attention, *M* maintenance of attention, *L* attend left, *C* attend center, *R* attend right. *Error bars* indicate SEM

Orienting-related activations

Within-modality comparisons of auditory and visual orienting task versus the respective maintenance task showed activations in parietal areas. These activations covered most of the SPL and areas of the temporo-parietal junction (TPJ; Fig. 3; Table 1). Also the conjunction of auditory and visual within-modality comparisons indicated that similar parietal activations are associated with both auditory and visual orienting (Fig. 3, bottom).

The posterior prefrontal cortex (MFG and SFG) and posterior cerebellum were also activated in both auditory and visual orienting tasks (Fig. 3, bottom left). Moreover, visual orienting versus maintenance revealed prominent thalamic activation (Fig. 3, middle right) not observed in the corresponding comparison of auditory tasks.

A comparison between the auditory and visual orienting versus maintenance contrasts [(auditory orienting versus maintenance) versus (visual orienting versus maintenance) and (visual orienting versus maintenance) versus (auditory

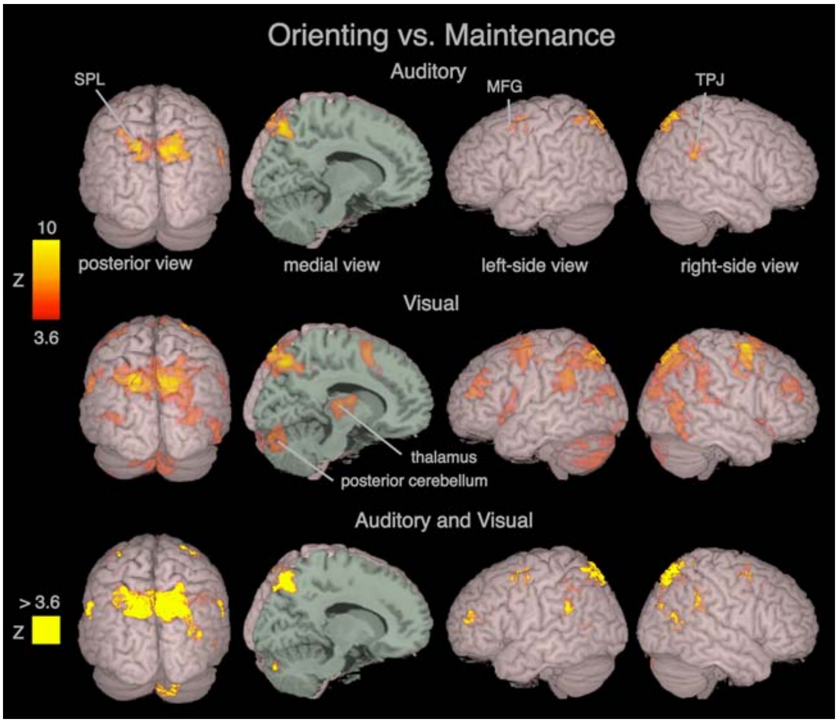

Fig. 3 Orienting-related brain activations. Results from comparisons of auditory and visual orienting tasks versus the respective maintenance tasks shown at the *top* and on the *middle row*, respectively, revealed auditory and visual orienting-related activations ($N = 9$, $Z > 3.6$ and cluster corrected $P < 0.01$). A conjunction analysis (*bottom*) revealed areas that were activated in both auditory and visual orienting tasks versus the respective maintenance tasks ($N = 9$, voxel corrected $P < 0.01$). *SPL* superior parietal lobule, *TPJ* temporoparietal junction, *SFG* superior frontal gyrus. Medial view is of the right hemisphere

orienting versus maintenance)] was conducted to reveal the differences in the auditory and visual orienting-related activations. Activations related to visual orienting were not significant even with a lenient threshold ($Z > 1.64$, cluster-corrected $P < 0.05$). Activations related to auditory orienting, in turn, were significant at this low threshold in the posterior cerebellum, ventral prefrontal cortex (VPFC), and TPJ. The modality-specific orienting-related activities were weak probably because similar activations occurred in both the auditory and visual orienting tasks (Fig. 3, bottom).

Modality-specific activations

Comparisons between auditory and visual maintenance (Fig. 4, top left; Table 2) and between auditory and visual orienting (Fig. 4, middle left; Table 2) revealed activations in the auditory areas of the left and right supratemporal cortex (STC). Moreover, activation associated with orienting and maintenance of auditory attention was detected in the MFG, SFG, TPJ, cerebellum, and several areas of the VPFC. A conjunction of auditory versus visual orienting and auditory versus visual maintenance comparisons suggested that modality-specific areas were activated both during orienting and maintenance of auditory attention (Fig. 4, bottom left).

Visual versus auditory maintenance (Fig. 4, top right; Table 2) and visual versus auditory orienting (Fig. 4, middle right; Table 2) comparisons, in turn, revealed prominent activations bilaterally in the striate and extrastriate visual cortices and in the SPL. No activations outside these areas were observed even when a more lenient threshold ($Z > 2.33$ and a cluster corrected $P < 0.05$) was applied. A conjunction of visual versus auditory maintenance and visual versus auditory orienting comparisons revealed also striate, extrastriate, and SPL activations (Fig. 4, bottom right).

There were no significant differences in STC activity between the auditory orienting and maintenance tasks or in the occipital visual-cortex activity between the visual orienting and maintenance tasks (Table 3).

Visual maintenance—bimodal versus visual maintenance—unimodal and auditory maintenance—bimodal versus auditory maintenance—unimodal contrasts were conducted to reveal the auditory and visual stimulus-dependent activations, respectively (see Petkov et al. 2004). Although these contrasts revealed weak stimulus-dependent activations in the auditory and visual areas, the activations were not statistically significant ($Z > 1.64$, cluster corrected $P < 0.05$).

Signal magnitudes in the thalamus and cerebellum

In contrast to visual conditions, a comparison between auditory orienting versus maintenance tasks revealed no posterior cerebellar and thalamic activity (Fig. 3). There are two possible explanations for this: (1) either these structures were activated in both auditory tasks or (2) they were activated in neither auditory task. To examine this

Table 1 Orienting-related brain activations

Brain region	*Z*-score	*x*	y	*z*
(a) Auditory orienting versus maintenance				
Right superior parietal lobule	6.09	18	–74	58
Left superior parietal lobule	5.59	–14	–70	58
Left middle frontal gyrus	4.74	–28	–6	66
Right supramarginal gyrus	4.72	62	–50	26
(b) Visual orienting versus maintenance				
Left superior parietal lobule (right superior parietal lobule)	8.94 (8.16)	–14 (16)	–70 (–74)	56 (52)
Right middle frontal gyrus	8.16	28	0	56
Left middle frontal gyrus	6.61	–24	–6	58
Left inferior frontal gyrus	5.95	–52	16	0
Left lingual gyrus (right lingual gyrus)	5.78 (5.61)	–4 (12)	–80 (–84)	–10 (–18)
Right thalamus	5.54	14	–8	12
Left precuneus	5.26	–28	–82	20
Right dorsolateral prefrontal cortex	5.21	40	38	22
Right temporoparietal junction	5.13	72	–40	18
Right inferior frontal gyrus	4.79	50	14	–4
Left posterior cerebellum	4.64	–32	–68	–38

MNI-coordinates and *Z*-score global maxima within activation clusters of significant ($Z > 3.6$ and cluster corrected $P < 0.01$) activations. Local maxima of the bilateral activity clusters in the other hemisphere in parenthesis

further, we analyzed the percent signal changes within the posterior cerebellar and thalamic ROIs (Fig. 5). Repeated measures ANOVA with factors ROI (thalamus, cerebellum), Hemisphere (left, right), and Condition (auditory orienting, visual orienting, auditory maintenance, visual maintenance) showed significant main effect for Condition [$F(1, 3) = 3.96$, $P < 0.05$] and significant interaction of ROI and Condition [$F(1, 3) = 5.36$, $P < 0.01$]. Activity in the left posterior cerebellum was significantly stronger in the auditory and visual orienting tasks (Tukey's post hoc test; $P < 0.01$ and 0.05, respectively), and auditory maintenance task ($P < 0.01$) than in the visual maintenance task. In the right posterior cerebellum activity also increased in the auditory and visual orienting tasks and in the auditory maintenance task, however, it did not differ significantly from the activity in the visual maintenance condition. Activity in the left thalamus, in turn, was stronger in the auditory orienting task ($P < 0.05$) and auditory maintenance task ($P < 0.1$) than in the visual maintenance task (Fig. 5a). Thus, ROI analysis suggests that the left posterior cerebellum and left thalamus were activated in both auditory tasks as compared with visual maintenance task. The time series of activation in each ROI revealed that attention-related activation started right after the beginning of the instruction and continued until the end of the task (Fig. 5b).

Control experiment

The control experiment aimed to reveal whether activation differences between the orienting and maintenance conditions of the main experiment were due to the fact that, in the orienting conditions, the attended stimuli occurred in lateral locations while in the maintenance tasks of the main experiment attention was focused on central auditory or visual stimuli. Comparisons between auditory or visual attend left, attend right, and attend center tasks of the control experiment revealed no significant differences in brain activity (threshold $Z > 1.64$, $P < 0.05$). ROI analyses for the SPL, MFG, posterior cerebellum, and thalamus, which showed higher activity in the orienting tasks than in the maintenance tasks of the main experiment, were conducted to examine more specifically the possible, subtle changes in these areas. These ROI analyses showed no significant differences between maintenance of auditory attention at the left, right, and center (Fig. 6). However, SPL and MFG activity during maintenance of visual attention at the left or right was slightly stronger than during maintenance of visual attention at the center (Fig. 6, top). Although this difference was not statistically significant, it may partly explain the more prominent difference in SPL and MFG activity in the main experiment between the visual orienting and visual maintenance tasks than between the auditory orienting and auditory maintenance tasks (Fig. 3). However, there were no differences in the posterior cerebellar or thalamic activity between maintenance of visual attention at the left, center, or right (Fig. 6, bottom). Therefore, the fact that the orienting tasks demanded attention to the left and right while the maintenance tasks demanded attention to central space (Fig. 1) probably did not affect the activity in the posterior cerebellum or thalamus in the comparison of orienting and maintenance tasks.

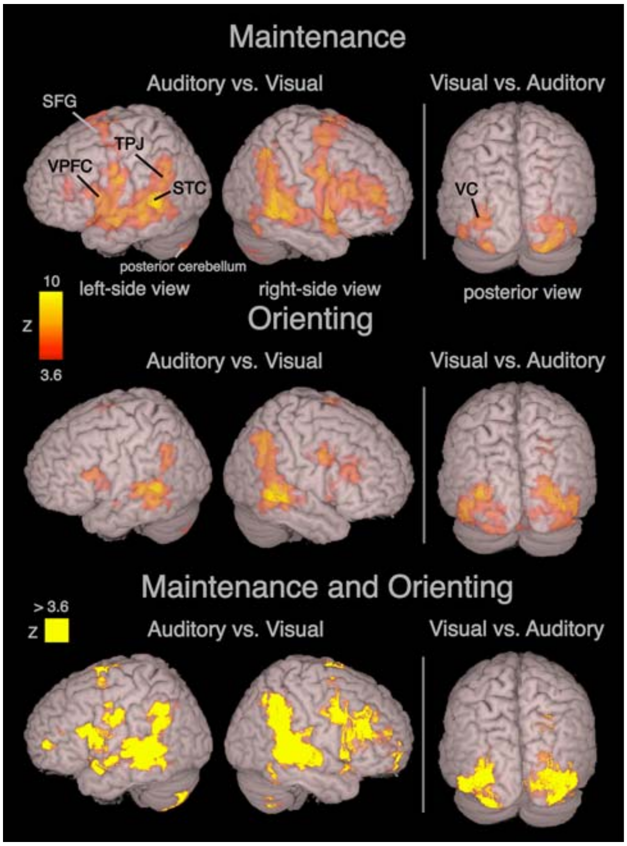

Fig. 4 Modality-specific brain activations. Comparison of auditory versus visual maintenance tasks (*top*), and auditory and visual orienting tasks (*middle*) revealed auditory and visual modality-specific attention-related modulations ($N = 9$, $Z > 3.6$ cluster corrected $P < 0.01$). Conjunction of the auditory orienting and maintenance tasks versus visual orienting and maintenance tasks, and vice versa (*bottom*), showed modality-specific activations associated with both auditory or both visual tasks ($N = 9$, voxel corrected $P < 0.01$). *MFG* middle frontal gyrus, *TPJ* temporoparietal junction, *VPFC* ventral prefrontal cortex, *STC* supratemporal cortex, *VC* visual cortex

Discussion

We investigated brain activity related to orienting and maintenance of spatial attention in audition and vision. We found multimodal orienting-related activations in the SPL, TPJ, MFG, SFG, and posterior cerebellum (Fig. 3, bottom). Moreover, the thalamus was activated by visual orienting of attention (Fig. 3, middle), and thalamic in activity in the left pulvinar was higher in both auditory tasks than in the visual maintenance task (Fig. 5, bottom). The posterior cerebellum and thalamus have been previously associated with visual orienting of attention (e.g., Gitelman et al. 1999; Townsend et al. 1999; Yantis et al. 2002) but their role in auditory spatial attention has remained unclear.

Activity was detected in the SPL bilaterally in the auditory and visual orienting tasks when compared to the respective maintenance tasks (Fig. 3). This result provides direct evidence that the SPL is involved in orienting of spatial attention both in audition and vision, as proposed by Shomstein and Yantis (2006). Moreover, our results indicate that also the TPJ is more strongly activated by orienting of attention than by maintenance of attention (Fig. 3). These findings are consistent with results of previous studies showing that lesions of parietal lobes have detrimental effects on auditory and visual spatial attention (Farah et al. 1989). In the auditory tasks, orienting-related activity in the TPJ was stronger in the right hemisphere than in the left hemisphere. Consistently, previous studies have shown that lesions in the right parietal cortex deteriorate spatial orienting of attention (see, e.g., Mesulam 1981). It is, however, unclear why there was a difference in the auditory orienting-related activity between the right and left TPJ, while no such difference was found in the visual orienting-related activity.

Consistent with the findings of Shomstein and Yantis (2006) and Yantis et al. (2002), our results indicate that also the MFG and SFG are involved in orienting of spatial attention both in the auditory and visual modalities (Giesbrecht et al. 2003; Hopfinger et al. 2000; Winkowski and Knudsen 2006; Wu et al. 2007). In the present study, MFG and SFG activity was also observed in the auditory maintenance of attention versus visual maintenance of attention condition (see also Degerman et al. 2006). The MFG/SFG activations encompassed the frontal eye field which is involved in the control of saccades (for a review see, Schall 2002). Therefore, it is possible that activity related to generation or inhibition of saccades (see Weissmann et al. 2004), although the participants were trained to perform the tasks without moving their eyes, contributed to the present activation of MFG/SFG especially in the visual tasks demanding attention to the lateral locations.

Another novel finding was that the posterior cerebellar cortex is activated during auditory and visual spatial attention (Figs. 3, 5). Based on previous studies (Allen et al. 1997; Gaab et al. 2003; Gottwald et al. 2003; Le et al. 1998; Nitschke et al. 2004; Townsend et al. 1999), it seems that the posterior cerebellum could be involved in tasks demanding active attentional control (for a review see, Akshoomoff et al. 1997). Like the present study, most previous fMRI studies reporting attention-related cerebellar activation, applied blocked experimental designs (Allen et al. 1997; Gaab et al. 2003; Le et al. 1998; Nitschke et al. 2004; see, however, Thoenissen et al. 2002). Yet, studies on spatial attention applying event-related designs did not find cerebellar activation (e.g., Giesbrecht et al. 2003; Gitelman et al. 1999; Hopfinger et al. 2000; Shomstein and Yantis 2006; Vandenberghe et al. 2001; Yantis et al. 2002).

We observed activation in the pulvinar during visual orienting of attention. Moreover, in both auditory orienting

Table 2 Modality-specific brain activations

Brain region	*Z*-score	*x*	*y*	*z*
(a) Auditory maintenance versus visual maintenance				
Left superior temporal gyrus	10.2	–54	–42	16
Right superior temporal gyrus	9.6	64	–36	4
Left posterior cerebellum	7.43	–26	–70	–36
Right posterior cerebellum	7.09	30	–68	–36
Right superior parietal lobule (left superior parietal lobule)	6.33 (4.81)	6 (–6)	–74 (–52)	40 (52)
Right posterior cerebellum	5.95	16	–72	–60
Left posterior cerebellum	5.91	–18	–74	–66
Left putamen	5.7	–24	0	2
Left middle frontal gyrus	5.55	–28	–2	52
(b) Auditory orienting versus visual orienting				
Right superior temporal gyrus	8.87	56	–28	–4
Left superior temporal gyrus	7.73	–64	–42	12
Left inferior frontal gyrus	6.32	–38	18	0
Left superior frontal gyrus (right superior frontal gyrus)	6.17 (4.64)	–2 (4)	–8 (2)	70 (66)
Right middle frontal gyrus	6.09	54	4	42
Right inferior frontal gyrus	5.43	34	26	2
Left posterior cerebellum	5.35	–26	–68	–36
Right medial frontal gyrus (right medial frontal gyrus)	5.26 (4.03)	4 (–4)	28 (14)	40 (54)
Left middle frontal gyrus	5.19	–50	4	16
Right precuneus	4.64	10	–76	28
(c) Visual maintenance versus auditory maintenance				
Right cuneus	8.88	28	–76	18
Right superior parietal lobule	6.7	26	–62	48
Left lingual gyrus	5.96	–44	–66	–18
(d) Visual orienting versus auditory orienting				
Right cuneus	9.69	30	–80	16
Left cuneus	8.35	–26	–82	18
Right superior parietal lobule	7.91	26	–62	48
Left superior parietal lobule	5.64	–24	–58	44
Right occipital gyrus	4.82	4	–94	–10

MNI-coordinates and *Z*-score global maxima within activation clusters of significant ($Z > 3.6$ and cluster corrected $P < 0.01$) activations. Local maxima of the bilateral activity clusters in the other hemisphere in parenthesis

Table 3 Percent signal changes ($N = 9$, SEM in parentheses) in the auditory cortex and visual cortex regions of interest (ROIs) during different tasks

	UAM	BAM	BAO	UVM	BVM	BVO
(a) Auditory cortex						
Left supratemporal plane	0.28 (0.2)	0.41 (0.2)	0.29 (0.18)	0.03 (0.13)	0 (0.11)	0.07 (0.17)
Right supratemporal plane	0.37 (0.14)	0.48 (0.12)	0.40 (0.11)	0.04 (0.07)	0 (0.07)	0.15 (0.1)
(b) Visual cortex						
Left occipital gyrus	0 (0.2)	0 (0.2)	0 (0.18)	0.22 (0.22)	0.20 (0.17)	0.38 (0.23)
Right occipital gyrus	0 (0.15)	0.04 (0.17)	0.02 (0.14)	0.16 (0.14)	0.09 (0.12)	0.34 (0.19)

U unimodal, *B* bimodal, *A* auditory, *V* visual, *M* maintenance, *O* orienting. During unimodal conditions, only the stimuli of the attended modality were presented while on the bimodal conditions there were concurrent streams of auditory and visual stimuli irrespective of the task. Baseline is set to the mean signal change across the entire study

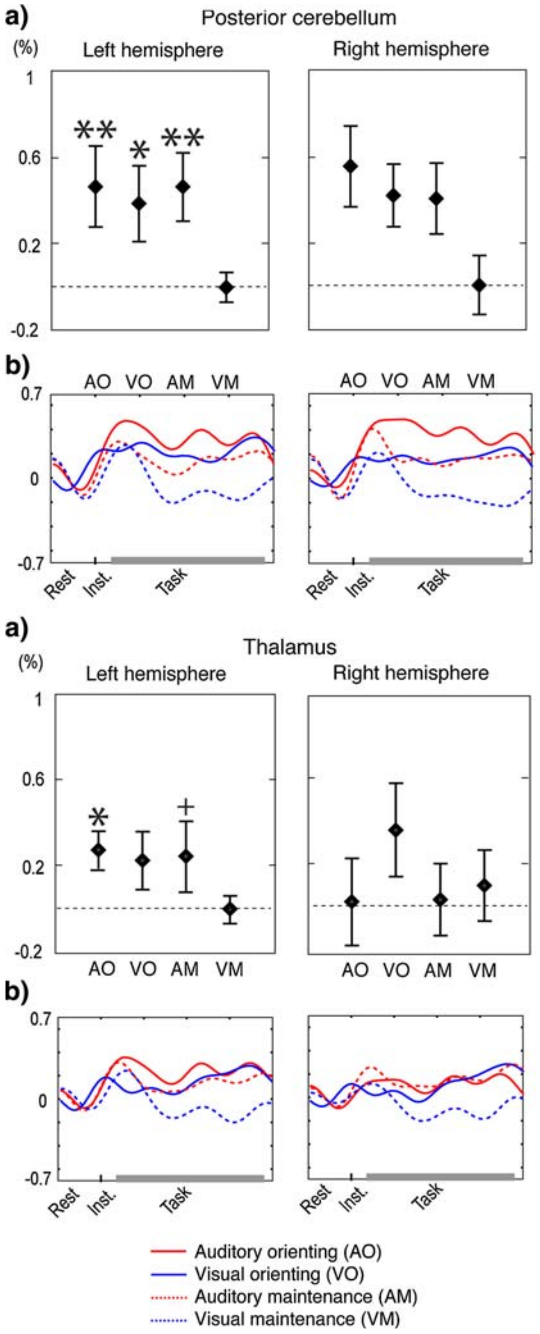

Fig. 5 **a** Mean percent signal changes, and **b** time series of the mean activation within the posterior cerebellar, and thalamic ROIs during each task ($N = 9$, $^{**}P < 0.01$, $^{*}P < 0.05$, $^{+}P < 0.10$; Tukey test, mean percent signal changes compared with visual maintenance task that served as a baseline condition). Each time series starts from the rest period and shows activity during the instruction (*inst.*) and task-performance (*horizontal gray bar*) periods. *Error bars* indicate SEM

and maintenance tasks, pulvinar activity was higher than in the visual maintenance task. The result that the pulvinar was activated during visual orienting task is consistent with the results of some previous fMRI studies (Gitelman et al. 1999; Yantis et al. 2002) and with attentional problems caused by thalamic lesions (Mesulam 1981; see also Hugdahl et al. 1991). Shomstein and Yantis (2006) did not observe thalamic activation when they compared activity during auditory orienting with activity during auditory maintenance of attention. Based on the present findings, the thalamus may have been activated on both auditory orienting and maintenance trials of their study and, therefore, no thalamic activation was observed when these trials were compared with each other. Furthermore, it is also possible that event-related fMRI used by Shomstein and Yantis (2006) is not as sensitive to thalamic attention-related activity as the block-design used in the present study.

Comparison of the results of the present and previous studies tentatively suggests that event-related and blocked designs are differently sensitive to attention-related activations in the thalamus and cerebellum. For example, it is possible that activations in these structures are not closely time-locked to stimulus presentation or that attention-related activity in these structures changes too slowly to be detected with an event-related design. [Note, however, that it is possible to detect sustained activity with event-related designs (Thoenissen et al. 2002; Toni et al. 2002)]. Possible differences in the regulation of blood flow in the cortex, thalamus, and cerebellum could further lead into systematically different hemodynamic response functions in these structures. It is also possible that the activation of the thalamus and cerebellum differ from cortical activation due to specific roles of these structures in control of attention. For example, it has been suggested that the posterior cerebellar cortex modulates the input that it receives from the parietal, temporal, and posterior frontal areas of the cerebral cortex and that it back-projects to the prefrontal cortex (Schmahmann 1996; Middleton and Strick 1997). Such modulation could be related, for example, to error correction (Fiez et al. 1992) or support function of cortical processing (Leiner et al. 1991) or implicit learning of motor and cognitive tasks (Ito 1990). The pulvinar nucleus of the thalamus, in turn, is commonly associated with attentional gating mechanisms regulating information that reaches conscious processing (LaBerge 1995). It is plausible that activity related to such sustained modulatory functions could be changing more slowly than, for example, activity in the SPL, MFG, and SFG that is related to transient shifts of attention (Yantis et al. 2002).

Taken together, our results suggest that a network consisting of the SPL, MFG, SFG, posterior cerebellum, and pulvinar is associated with spatial attention in audition and vision. The existence of such network is also strongly supported by neuroanatomical evidence. The superior and inferior parietal cortex receive the majority of their inputs from multimodal sensory brain areas via the medial pulvinar nucleus (Mesulam et al. 1977). In addition, a prominent output from the MFG and SFG goes to the pulvinar

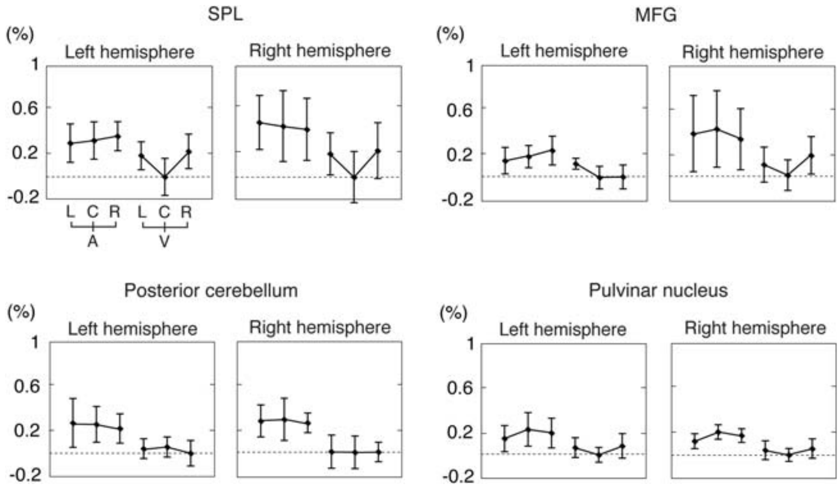

Fig. 6 Mean percent signal changes within the SPL, MFG, thalamic, and posterior cerebellar ROIs in the control experiment ($N = 9$). *A* attend auditory, *V* attend visual, *O* orienting of attention, *M* maintenance of attention, *L* attend left, *C* attend center, *R* attend right. *Error bars* indicate SEM

(Bos and Benevento 1975). Parietal cortical areas are connected to the MFG and SFG also via cortico-cortical projections (Mesulam 1981). The posterior cerebellum receives input from the MFG, SFG, and parietal areas via pontine nuclei (Brodal 1978; Allen et al. 1978; see also Ramnani et al. 2006). Furthermore, thalamic nuclei (the mediodorsal nucleus, the ventral lateral nuclei, and the ventral posterior nuclei) that are connected to the pulvinar via the reticular nucleus (LaBerge 1995) are the relay nuclei for the projections from the posterior cerebellum to the cerebral cortex (Middleton and Strick 1997).

The ROI analysis of the main experiment showed that the activations of the left posterior cerebellar cortex and left pulvinar were stronger during the auditory orienting and maintenance tasks than during the visual maintenance task (Fig. 5). Comparisons of the voxel-wise statistical maps between the auditory and visual tasks also suggested differences between the modalities. Consistent with previous studies (Alho et al. 1999; Degerman et al. 2006), the auditory tasks showed stronger activity than the visual tasks in the superior temporal gyrus, and in the prefrontal and inferior parietal cortex (Fig. 4, left). In contrast, visual modality-specific activations were observed only in the visual areas of the occipital and parietal lobes (Fig. 4, right; Table 2; cf. Alho et al. 1999; Degerman et al. 2006).

These differences between auditory and visual brain activations related to spatial attention could be partially explained by differences in the processing of spatial information in these modalities. It is possible that because spatial information is explicitly encoded in the visual cortical representations (Tootell et al. 1998), visual spatial attention does not result in activation of other brain areas as much as auditory spatial attention. Correspondingly, spatial attention may be more demanding for the auditory system because of the lack of spatiotopic organization (Furukawa et al. 2000; Brugge et al. 2001; Stecker and Middlebrooks 2003), and therefore leads to strong activation of several areas additional to auditory cortex, such as regions of the ventral prefrontal and inferior parietal cortices, and in the posterior cerebellum and thalamus. The posterior cerebellum, in particular, is activated when the cognitive load increases (e.g., Kirschen et al. 2005).

Previous studies on visual spatial attention indicate that the TPJ and VPFC participate in stimulus-driven attentional processes in the visual modality (see, e.g., Corbetta et al. 2000; Corbetta and Shulman 2002). These areas are also implicated in auditory (Molholm et al. 2005; Rinne et al. 2005; Downar et al. 2000), visual (Downar et al. 2000) and somatosensory (Downar et al. 2000) stimulus-change detection, and involuntary attention to novel auditory stimuli (Knight et al. 1989; Woods et al. 1993). Stronger activity in the TPJ and VPFC in the present auditory attention tasks than in the visual attention tasks might result from more frequent involuntary shifts of attention to irrelevant stimuli of the attended modality during the auditory tasks than during the visual tasks. Auditory stimulus changes (upward frequency glides among frequent downward glides) in irrelevant locations may have been more salient and therefore may have captured attention more easily during the auditory tasks than the subtle visual stimulus changes (small circles among large circles) in irrelevant locations during the visual tasks. Stronger VPFC activity during the auditory tasks than during the visual tasks might also be associated with suppressing processing of the salient irrelevant sound changes and/or inhibiting responding to them during attention to other sounds, as several studies have shown that these areas are involved in such inhibitory processes (Aron et al. 2004; Gemba and Sasaki 1989; Konishi et al. 1999; Menon et al. 2001). Modality-specific differences in involuntary attention may also have contributed to the MFG/SFG activity, because inhibition of involuntary attention to stimulus changes may have increased the MFG/SFG activity especially in the auditory maintenance tasks (Weissmann et al. 2004).

The current theories of attention are primarily based on either visual or auditory studies and do not predict differences between the modalities (e.g., LaBerge 1995; Näätänen 1990; Posner and Rothbart 2007; Mesulam 1981). However, our results showed differences between auditory and visual attention in frontal, inferior parietal, pulvinar and posterior cerebellar structures. This suggests either that attentional systems are partly different in audition and vision or that activation of a common attentional system is modulated differently by the present auditory and visual tasks.

Auditory modality-specific activations revealed by comparison of auditory and visual maintenance of attention in central space were distributed to broader areas than the activations revealed by comparison of auditory and visual orienting between lateral locations. This could be due to fundamental differences in visual attention to the central and lateral space: considerable neural resources are reserved, and therefore probably less effort is needed, for processing of foveal information than for extrafoveal processing (cf. Tootell et al. 1998). In the auditory modality, there appears to be no such differences between central and lateral processing. Note that the locations or within-modality location separations were not matched perceptually between the present auditory and visual stimuli and that this may have contributed to some extent to differences in performance and brain activity between the auditory and visual tasks.

Some of the frontal and parietal cortical areas activated here by spatial attention are also activated in spatial working memory tasks (Corbetta et al. 2002; Martinkauppi et al. 2000; Nitschke et al. 2004). Spatial working memory tasks involve complex cognitive functions including attentional processes. For example, in a typical spatial working memory task, such as the one applied by Martinkauppi et al. (2000), attention has to be constantly shifted to varying stimulus locations. Thus, it is possible that activity in spatial working memory tasks is partly related to orienting of attention. Alternatively, it is possible that working-memory load was increased in the present orienting tasks compared with the maintenance tasks leading into increased activity in the brain areas activated in working-memory studies, too. Thus, attention and working memory may be difficult to disentangle from each other. However, in the present study, there were no differences in the task performance between the auditory or visual orienting and maintenance tasks. Therefore, the present results are not easily explained by differences in attentional or working-memory load between the tasks.

In conclusion, our results indicate that a brain network consisting of the SPL, TPJ, MFG, SFG, thalamus, and posterior cerebellum is activated during both auditory and visual orienting of attention. Prefrontal areas were more strongly activated during auditory than visual spatial attention. Thus, our results provide evidence, on one hand on multimodal processes, and on the other, on differences in the control of spatial attention between audition and vision. In previous studies, SPL, TPJ, MFG, SFG, pulvinar, and posterior cerebellar activations have been associated with different kinds of attention-demanding auditory and visual tasks (Hyvärinen 1982; LaBerge 1995; Schmahmann 1997). It is likely that these areas are not only involved in orienting and maintenance of spatial attention, but also in several other attentional processes and generally are activated in tasks demanding goal-directed behavior (Corbetta and Shulman 2002) or reconfiguration of attention (Shomstein and Yantis 2006).

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