BRAIN RESEARCH 1286 (2009) 155–164

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Research Report

Brain networks of bottom-up triggered and top-down controlled shifting of auditory attention

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ARTICLE INFO

Article history:
Accepted 25 June 2009
Available online 3 July 2009

Keywords:
Attention
Auditory
Dorsal/ventral attention system
fMRI
Human brain

ABSTRACT

During functional magnetic resonance imaging (fMRI), our participants selectively attended to tone streams at the left or right, and occasionally shifted their attention from one stream to another as guided by a centrally presented visual cue. Duration changes in the to-be-attended stream served as targets. Loudness deviating tones (LDTs) occurred infrequently in both streams to catch attention in a bottom-up manner, as indicated by their effects on reaction times to targets. LDTs activated the right temporo-parietal junction (TPJ), posterior parts of the left inferior/middle frontal gyrus (IFG/MFG), ventromedial parts of the superior parietal lobule (SPL), and left frontal eye field/premotor cortex (FEF/PMC). In addition, LDTs in the to-be-ignored sound stream were associated with enhanced activity in the ventromedial prefrontal cortex (VMPFC) possibly related to evaluation of the distracting event. Top-down controlled cue-guided attention shifts (CASs) activated bilateral areas in the SPL, intraparietal sulcus (IPS), FEF/PMC, TPJ, IFG/MFG, and cingulate/medial frontal gyrus, and crus I/II of the cerebellum. Thus, our results suggest that in audition top-down controlled and bottom-up triggered shifting of attention activate largely overlapping temporo-parietal, superior parietal and frontal areas. As the IPS, superior parts of the SPL, and crus I/II were activated specifically by top-down controlled attention shifts, and the VMPFC was specifically activated by bottom-up triggered attention shifts, our results also suggest some differences between auditory top-down controlled and bottom-up triggered shifting of attention.

1. Introduction

In everyday life, attention is dynamically allocated depending on the events in the external environment and current behavioral goals. A sudden sound in the environment, for example, a cough heard during a conversation, may trigger in a bottom-up manner an involuntary attention shift from the currently attended speaker to the person who coughs. In this case, the event triggering bottom-up attention shift may be evaluated as irrelevant and one may continue following the conversation. However, if attention is triggered by a relevant sound (e.g., a cell phone ringing in your pocket; Roye et al., 2007), it is likely that the original task is replaced with a new one (answering the phone or thinking who might be calling you). Attention may also be shifted voluntarily in top-down control, for example, from one speaker to another during a conversation, according to the current behavioral goals.

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0006-8993/$ – see front matter
doi:10.1016/j.brainres.2009.06.083

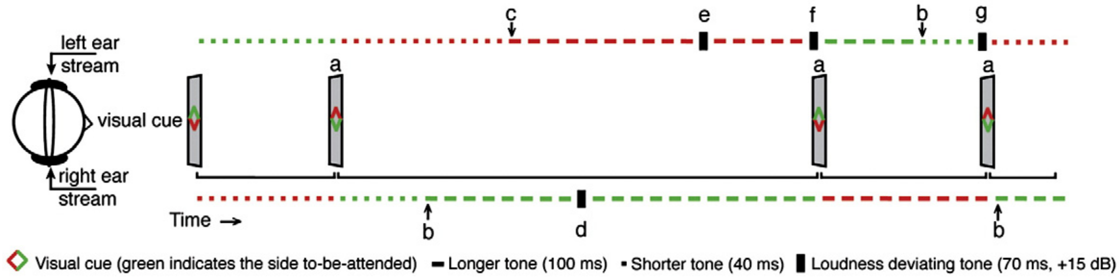

Fig. 1 – Participants selectively attended to tones at the left or right as indicated by a visual cue composed of green and red arrowheads and occasionally shifted their attention between the two tone streams when the cue color changed (a, cue-guided attention shift, CAS). Performance was measured as reaction times of correct responses and rate of missed responses to a change in duration of the to-be-attended tones (b, Target) during sustained attention and after a CAS. Duration changes occurred also in the to-be-ignored stream (c, Irrelevant duration change). Loudness deviating tones (LDTs) occurred occasionally among to-be-attended and to-be-ignored tones during sustained attention to tones at one side (d, LDT at the to-be-attended side; e, LDT at the to-be-ignored side), or just before a CAS (f, CAS preceded by LDT at the side to-be-ignored before the shift; g, CAS preceded by LDT at the side to-be-attended before the shift). The onset of one block is shown. A foveal fixation cross that was presented throughout the experiment is not shown.

Corbetta and Shulman (2002) suggested that partially segregated areas of the cerebral cortex are involved in bottom-up triggered and top-down controlled shifts of visual attention. In their model, the temporo-parietal junction (TPJ, i.e., inferior parts of the inferior parietal lobule and posterior parts of the superior and middle temporal lobe) and posterior parts of the inferior/middle frontal gyrus (IFG/MFG) constitute "the ventral attention system" involved in bottom-up triggered (or stimulus-driven) visual attention. Superior parietal areas, i.e., the intraparietal sulcus (IPS) and superior parietal lobule (SPL), and the frontal eye field (FEF) in the posterior prefrontal cortex, in turn, constitute "the dorsal attention system" involved in top-down controlled (or goal-directed) visual attention. In contrast to this model of two distinct attention systems, however, many functional magnetic resonance imaging (fMRI) studies have reported substantial overlap between the brain areas associated with bottom-up triggered and top-down controlled visual attention (e.g., Kim et al., 1999; Rosen et al., 1999; Peelen et al., 2004; Serences and Yantis, 2007). Recently, Serences and Yantis (2007) suggested that both bottom-up triggered and top-down controlled shifting of visual attention activates areas within the suggested dorsal attention system. They also found that during top-down controlled sustained attention this activity was specific for attended spatial location (activity in the hemisphere contralateral to the attended location was stronger than activity in the ipsilateral hemisphere), while the activity associated with bottom-up triggered attention was transient. Other studies have suggested that areas within the ventral attention system are also modulated by both bottom-up triggered and top-down controlled shifting of visual attention (Kim et al., 1999; Peelen et al., 2004). Thus, these results appear to be at least partly inconsistent with Corbetta and Shulman's (2002) model. Further, previous fMRI studies on visual attention have not made a distinction between involuntary change detection and bottom-up triggered attention shifting studied extensively in the auditory modality (Escera et al., 2000; Näätänen et al., 2007). It is therefore unclear, whether the ventral attention system is involved in detection of salient stimulus changes per se or whether this activity actually reflects bottom-up triggered shifting of attention.

Only a few previous auditory fMRI studies have investigated brain activity underlying top-down controlled shifting of spatial attention (Shomstein and Yantis, 2006; Salmi et al., 2007a; Wu et al., 2007). We recently showed that such shifting of spatial auditory and visual attention activates the same areas in the IPS/SPL and FEF/premotor cortex (PMC, Salmi et al., 2007a). Further, results of other previous studies suggest that the posterior IFG (Doeller et al., 2003; Rinne et al., 2005) and TPJ (Knight et al., 1989; Woods et al., 1993; Molholm et al., 2005) are involved in bottom-up induced auditory attention. However, some auditory studies report that the TPJ and posterior IFG/MFG are also activated during top-down controlled shifting of auditory attention or active sound localization (Alho et al., 1999; Maeder et al., 2001; Alain et al., 2008; Salmi et al., 2007a) and that distracting auditory events catching attention in a bottom-up manner during focused attention activate also the IPS/SPL and FEF (Rinne et al., 2007; Watkins et al., 2007).

In the present study, we compared within the same experiment brain activations associated with bottom-up triggered and top-down controlled shifting of auditory attention (see Fig. 1). A challenge in a study on top-down controlled auditory attention is to trigger attention shifting in a controlled manner (see Mayer et al., 2009) without activating the areas involved in auditory bottom-up triggered attention (Molholm et al., 2005; Rinne et al., 2005; Schönwiesner et al., 2007). As an auditory cue for attention shifting would unavoidably activate bottom-up processes, we chose to use visual cues to instruct the participants to shift their auditory attention (cue-guided attention shift, CAS). This allowed us to control for auditory attention without activating auditory bottom-up processes but with the downside that visual cue changes may modulate visual attention, too. However, since a visual cue was presented throughout the experiment and thus visual attention was constantly required, we assumed that activations associated with the visual cue changes and visual attention would be

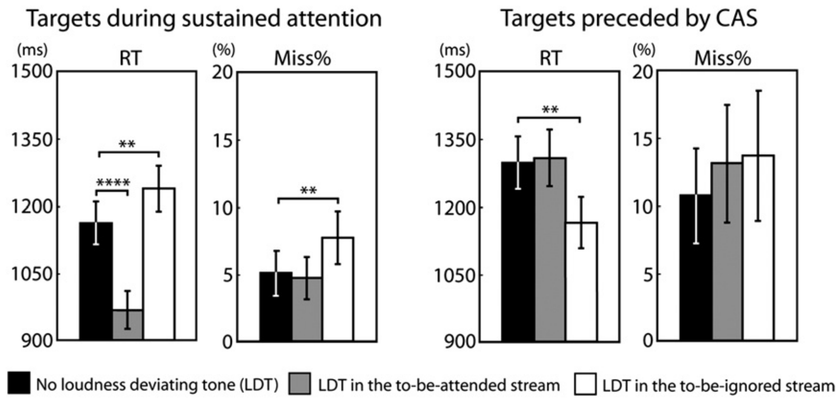

Fig. 2 – RTs and Miss%s for target tones during sustained attention (left) and following immediately a CAS (right) when they were not preceded by an LDT, when they were preceded by an LDT in the to-be-attended stream, and when they were preceded by an LDT in the to-be-ignored stream ($p<0.0001$, **; $p<0.01$, **).**

negligible in comparison with modulations of brain activity related to auditory attention in the present paradigm. Bottom-up triggered auditory attention shifts were initiated by task-irrelevant physically deviant sounds (loudness deviating tones, LDTs) occurring both in the to-be-ignored and to-be-attended locations. LDTs occurred either independent of the CASs or immediately before the CASs. Throughout the experiment, the participants were required to fixate on a cross at the center of a screen, direct their auditory attention as indicated by the visual cue around the fixation cross, and to respond to target duration changes occurring among the attended sounds.

Based on earlier fMRI studies that investigated separately either bottom-up triggered (Rinne et al., 2007; Watkins et al., 2007) or top-down controlled attention (Shomstein and Yantis 2006; Salmi et al., 2007a; Wu et al., 2007), we hypothesized that bottom-up triggered shifting of auditory attention caused by LDTs and top-down controlled shifting of auditory attention associated with CASs would activate overlapping brain networks in the parietal and frontal areas. LDTs in the to-be-ignored location were expected to be more distracting than the LDTs in the to-be-attended location, as LDTs in the to-be-ignored location would probably trigger spatial attention shifting. Further, we expected that by comparing brain activity associated with LDTs in the to-be-ignored and to-be-attended location, we could reveal the brain network of bottom-up triggered shifts of auditory spatial attention. Finally, we hypothesized that LDTs in a to-be-ignored location would facilitate subsequent top-down controlled CASs to that location, while LDTs in the to-be-attended stream of sounds right before a CAS might distract top-down controlled shifting of attention to the other stream. These effects of LDTs on top-down controlled attention were also expected to modulate brain activity associated with CASs.

2. Results

2.1. Behavioral results

Behavioral results are shown in Fig. 2. During sustained-attention (left panel, black bar), the mean reaction time (RT) to targets not preceded by an LDT was 1161 ms (s.e.m. 47 ms) and percentage of missed responses to the targets (Miss%) was 5.1% (s.e.m. 1.6%). The relatively long RTs and occurrence of response errors indicates that the present task was difficult even for targets not preceded by an LDT or a CAS. This was also our intention, because such demanding task forces participants to focus their attention strongly on the to-be-attended input.

As expected, during sustained attention, RTs became longer (paired samples *t*-test, $t(18)=2.9$, $p<0.01$) when a target was preceded by an LDT in the to-be-ignored stream (left panel, white bar), as compared with targets not preceded by an LDT. LDTs in the to-be-ignored stream also increased Miss% ($t(18)=2.9$, $p<0.01$) for the subsequent targets as compared with targets not preceded by an LDT during sustained attention. These results indicate that the LDTs indeed caught participants' attention in a bottom-up manner. However, somewhat unexpectedly, during sustained attention, RTs to the targets became shorter ($t(18)=6.8$, $p<0.0001$) when a target was preceded by an LDTs in the same, to-be-attended tone stream (left panel, grey bar). This suggests that bottom-up triggered auditory attention may facilitate performance if the triggering event occurs among to-be-attended sounds.

Also CASs affected participants' performance. For targets not preceded by an LDT but by a CAS, the mean RT was 1297 ms (s.e.m. 57 ms; right panel, black bar), which was significantly longer ($t(18)=3.9$, $p<0.001$) than the RT for targets during sustained attention. As expected, LDTs catching attention in a bottom-up manner facilitated performance after a CAS if they occurred in a stream that was to be attended after a subsequent CAS: RTs became significantly shorter ($t(18)=3.7$, $p<0.01$) for targets preceded by a CAS, if the CAS was preceded by an LDT in the stream that was to be ignored before the CAS (right panel, white bar), as compared with targets following a CAS not preceded by an LDT. However, unlike we expected, LDTs in the to-be-attended stream preceding a CAS to the other stream did not have a significant effect on target detection following such CAS (right panel, gray bar) as compared with target detection after a CAS not preceded by an LDT in either stream.

2.2. fMRI results

2.2.1. Brain activations induced by LDTs and CASs

Comparison of brain activity associated with LDT events with brain activity associated with sustained attention without

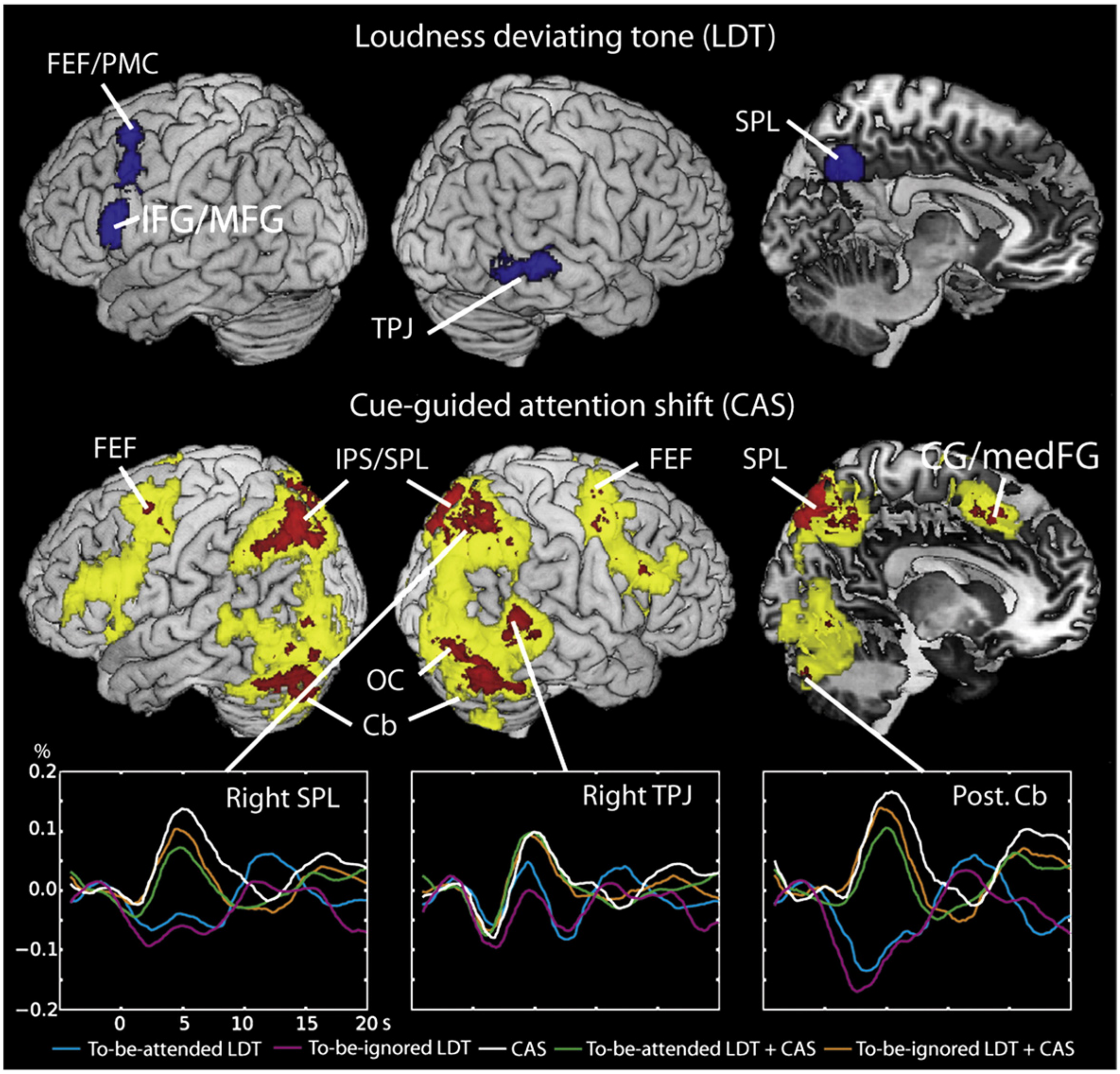

Fig. 3 – Top: Bottom-up influences on brain activity caused by LDTs during auditory sustained attention (blue, $Z>3.0$, $p<0.01$). Middle: Top-down controlled CAS contrasted with auditory sustained attention (red, $Z>5.0$, $p<0.01$, and yellow, $Z>3.0$, $p<0.01$). Bottom: Activation time-series in the right SPL, right TPJ and posterior cerebellar (Post. Cb) ROIs during different events. Note that figure at the top middle shows activity at the posterior temporal cortex. However, below the brain surface this activity cluster reached TPJ.

LDTs revealed activity ($Z>3.0$, cluster-corrected $p<0.01$) related to processing of LDTs and bottom-up attention to them in the right TPJ, ventromedial parts of the bilateral SPL, posterior parts of the left IFG/MFG, and left FEF/premotor cortex (PMC; Fig. 3, top). Top-down controlled attention shifts, in turn, activated ($Z>3.0$, cluster-corrected $p<0.01$) the IPS/SPL, FEF/PMC, TPJ, IFG/MFG, cingulate/medial frontal gyrus (CG/medFG), lateral and ventromedial occipital cortex (OC), and crus I/II of the posterior cerebellum (Post. Cb; middle), bilaterally, as indicated by comparison of brain activity following CASs with activity during sustained attention. Thus, bottom-up triggered shifting of attention associated with LDTs and top-down controlled shifting of attention associated with CASs activated overlapping areas in the ventromedial SPL, left IFG/MFG, left FEF/PMC, and right TPJ.

Effects of LDTs on CAS-related brain activity were studied in regions of interest (ROIs) defined based on the activity clusters revealed by the comparison of CASs and sustained attention (see, previous paragraph). A repeated-measures ANOVA for activation time-series (Fig. 3, bottom) with factors Event Type (CAS with no LDT and CAS preceded by an LDT in the to-be-attended stream) and Time from Event Onset (4–6, 6–8, 8–10 s) suggested that activity in the right SPL ($F(1,18)=8.6$, $p<0.01$) and posterior cerebellum ($F(1,18)=6.9$, $p<0.05$) ROI was lower when a CAS was preceded by an LDT in the stream that was to be attended before the CAS (Fig. 3, bottom, green line) as compared with CASs with no preceding LDT (white line). In other brain regions, LDTs did not cause significant modulations on activity associated with CASs.

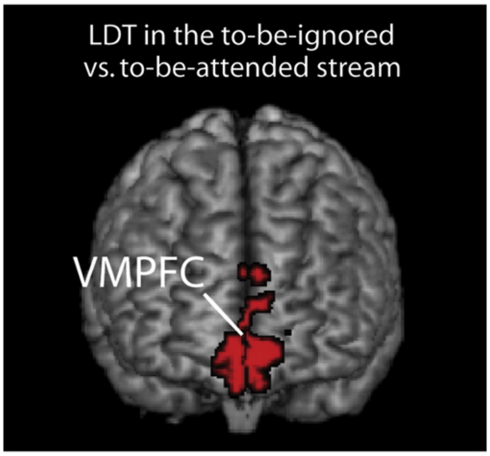

Fig. 4 – Comparison of activations following LDTs in the to-be-ignored stream and to-be-attended stream showed significant differences ($Z > 1.64$, $p < 0.05$) in the VMPFC. The brain is viewed from the front.

2.2.2. *The effect of locus of attention on LDT activations during sustained attention and attention shifting*

The effects of locus of attention on LDT activations were first examined using ROIs defined based on the activity clusters revealed by the comparison of LDTs and sustained attention and on the comparison of CASs and sustained attention (see, above). No differences in these ROIs were observed between activations to LDTs in the to-be-attended and to-be-ignored streams (Fig. 3, blue and red lines, respectively).

However, the locus of attention modulated LDT activations ($Z > 1.64$, cluster-corrected $p < 0.05$) outside these ROIs in the ventromedial prefrontal cortex (VMPFC). This was revealed by a conjunction of two contrasts: LDTs in the to-be-ignored stream during sustained attention vs. LDTs in the to-be-attended stream during sustained attention and LDTs in the to-be-ignored stream followed by a CAS vs. LDTs in the to-be-attended stream followed by a CAS (Fig. 4). Conjunction of contrasts is reported as the separate contrasts showed no significant differences possibly due to relatively low number of repetitions. The opposite contrasts (LTDs in the to-be-attended stream vs. LTDs in the to-be-ignored stream) and conjunction of these contrasts revealed no significant differences in any brain region.

2.2.3. *Activations associated with duration changes in the to-be-attended and to-be-ignored stream during sustained attention*

Brain activity associated with target duration changes occurring without a preceding LDT or CAS was significantly higher ($Z > 5.0$, cluster-corrected $p < 0.01$) than brain activity during periods of sustained auditory attention without duration changes or LDTs in either stream in distributed areas of the superior temporal cortex (Fig. 5, top, red/yellow). Outside the superior temporal cortex, target duration changes activated areas in the posterior IFG/MFG, IPS, CG/medFG, left precentral

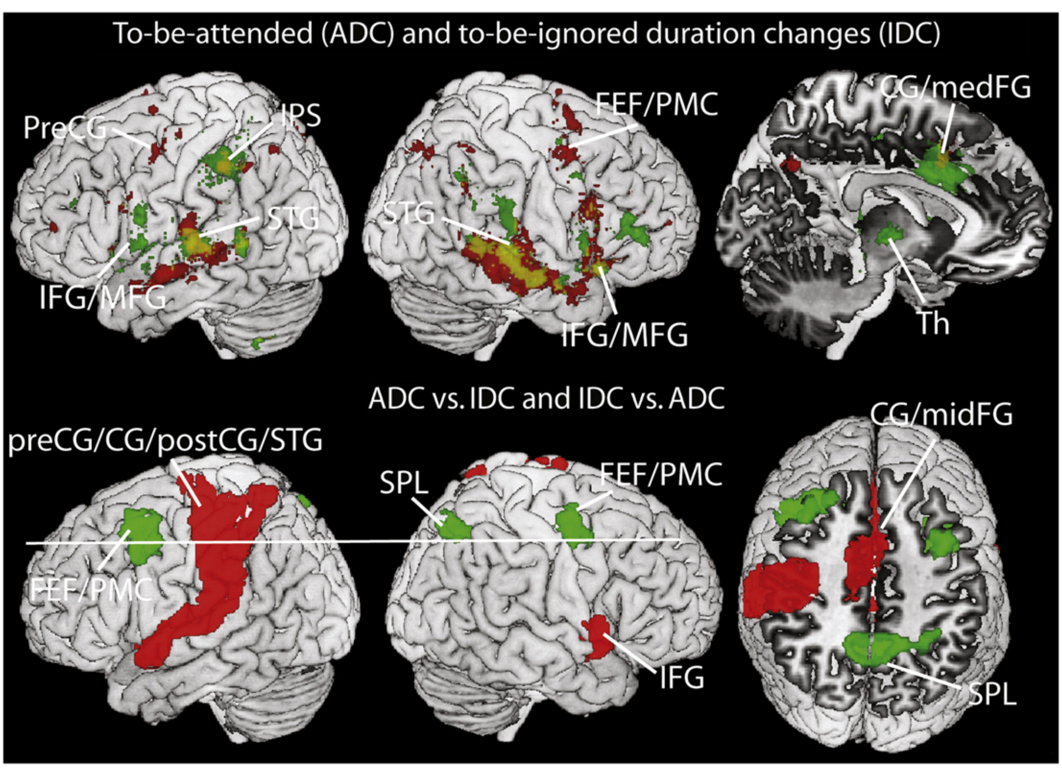

Fig. 5 – Areas activated ($Z > 5.0$, $p < 0.01$) by to-be-attended (red) and to-be-ignored (green) duration changes during sustained attention as compared with sustained attention with no duration changes (top) or with each other (bottom). Areas that overlap between to-be-ignored and to-be-attended duration changes are shown in yellow. At top right the section is from the medial surface and white horizontal line at the bottom left mark the level of the section shown at the bottom right.

gyrus, and FEF/PMC, bilaterally (top, red/yellow). Activity in the left precentral gyrus, central sulcus, and postcentral gyrus (contralateral to the hand of response), right IFG, and CG/medFG was observed when target duration changes were compared with duration changes in the to-be-ignored stream ($Z>3.0$, cluster-corrected $p<0.01$, bottom, red). Duration changes in the to-be-ignored stream, in turn, enhanced brain activity significantly ($Z>5.0$, cluster-corrected $p<0.01$) in the STG, IPS, CG/midFG, TPJ, posterior IFG/MFG, and thalamus in comparison with brain activity during sustained-attention periods without duration changes or LDTs in either stream (Fig. 5, top, green/yellow). Contrasting brain activity associated with to-be-ignored duration changes to activity associated with target duration changes revealed that to-be-ignored duration changes elicited activity ($Z>3.0$, cluster-corrected $p<0.01$) in the SPL and FEF/PMC bilaterally (Fig. 5, bottom, green).

3. Discussion

The present auditory task was made difficult intentionally to ensure strongly focused auditory attention. Therefore, as expected, even RTs to targets without a preceding CAS or LDT were relatively long and the participants also omitted some responses. The effects of LDTs on RTs to subsequent targets suggested that LDTs captured attention in a bottom-up manner: LDTs in the to-be-ignored stream most likely caused spatial attention shift to the to-be-ignored stream (i.e., to the wrong direction) as RTs to subsequent targets were prolonged during sustained attention (Doeller et al., 2003; Grimm et al., 2008) and shortened when a target was preceded by a CAS to the stream where the LTD had just occurred. Thus, an LDT in the stream that was to be ignored before a CAS and attended after it served as an additional exogenous cue for attention shifting. Moreover, LDTs in the to-be-attended stream during sustained attention shortened RTs to subsequent targets. This effect was probably caused by facilitation of the sensory or motor processes, or both, needed in target processing due to enhanced alertness for events in the attended stream (Hackley and Valle-Inclán, 2003). Finally, RTs to targets preceded by a CASs were longer than RTs to targets during sustained attention probably because of the cost associated with attention shifting right before the target (see Salmi et al., 2007b).

In keeping with the previous studies that have separately examined auditory bottom-up triggered (Doeller et al., 2003; Rinne et al., 2005; Molholm et al., 2005; Rinne et al., 2007; Watkins et al., 2007) or top-down controlled shifts of attention (Shomstein and Yantis 2006; Salmi et al., 2007a; Wu et al., 2007), we observed activity in the STG/MTG, TPJ, SPL, IFG/MFG and FEF/PMC for bottom-up triggered attention shifts, and activity in the IPS/SPL, FEF/PMC, STG/MTG, TPJ, IFG/MFG, CG/medFG, and crus I/II of the posterior cerebellum for the top-down controlled attention shifts. In contrast to previous studies of auditory top-down controlled attention, we found activity also in the lateral and ventromedial OC for top-down controlled attention shifts. This OC activity was probably related to processing of the visual cue.

In contradiction with our hypothesis, LDTs in the to-be-attended location preceding a CAS did not distract this CAS according to the lack of significant difference in RTs and response accuracy between targets following such CASs and those following CASs not preceded by an LDT (Fig. 2). However, CAS-related activity in the right SPL and posterior cerebellum ROI was lower when a CAS was preceded by an LDT in the stream that was to be attended before the CAS to the other stream (Fig. 3). Thus, these LDTs indeed appeared to suppress subsequent top-down controlled CASs in a bottom-up manner although this suppression was not observable in task performance.

3.1. *Activity in the areas corresponding to the ventral attention system*

Based on studies of visual attention, Corbetta and Shulman (2002) suggested that the ventral attention system is specialized in detection of salient or unexpected stimuli. Consistently, in the present study, the posterior IFG/MFG and TPJ were activated by LDTs. Activity in the right TPJ and posterior IFG/MFG was observed also for the CASs in the present study, even when they were not preceded by an LDT. This result is in line with the findings of some previous studies reporting activity in the TPJ and posterior IFG/MFG during top-down controlled auditory attention (e.g., Alho et al., 1999; Salmi et al., 2007a). However, these findings are discrepant with the visual-attention model of Corbetta and Shulman suggesting that the ventral attention system is specific for bottom-up triggered attention. The discrepancy might be due to differences between auditory and visual attention or between the auditory and visual experimental designs, or both. Still, as described in Introduction, several previous studies using trial-by-trial cueing have also suggested an overlap between the brain networks of top-down controlled and bottom-up triggered attention in the visual modality (Rosen et al., 1999; Peelen et al., 2004), implying that the posterior IFG/MFG and TPJ are not specialized in bottom-up triggered attention, but are activated also by top-down controlled attention. The present results provide further support to the view that the areas within the suggested ventral (visual) attention system are involved in both bottom-up triggered and top-down controlled attention in audition.

In addition to the LDTs and CASs, the posterior IFG/MFG was activated by duration changes in the to-be-attended and to-be-ignored streams during sustained attention. This is consistent with previous studies investigating brain activations to infrequent duration, pitch and location changes in tones (Rinne et al., 2000; Opitz et al., 2002; Molholm et al., 2005; Rinne et al., 2005; Tse et al., 2006; Deouell, 2007; Schönwiesner et al., 2007). The present IFG/MFG activity to to-be-ignored duration changes was probably associated with auditory change detection and bottom-up triggered attention shifting (Rinne et al., 2000; Deouell, 2007).

3.2. *Activity in the areas corresponding to the dorsal attention system*

In keeping with the model of visual attention by Corbetta and Shulman (2002) and recent studies of top-down controlled auditory attention shifting (Shomstein and Yantis

2006; Salmi et al., 2007a; Wu et al., 2007), the present activations in the IPS/SPL and FEF support the involvement of these areas in top-down controlled attention shifting. In the parietal cortex, especially in the IPS and dorsal parts of the SPL enhanced activity was observed for the CASs, but not for the LDTs. Moreover, our results show that activity in the dorsal attention system, especially in the right SPL, is modulated by events that trigger bottom-up attention (see, Fig. 3, bottom). The activity in the IPS and FEF/PMC observed in a comparison of brain activity elicited by to-be-ignored duration changes during sustained attention with activity associated with target duration changes (Fig. 5, bottom) might also be related to interaction of dorsal and ventral attention systems, as the to-be-ignored duration changes may have been followed by active suppression of attention shifting to the to-be-ignored stream and/or suppression of motor responses that the participants were prepared to make to duration changes.

However, some of our results concerning the dorsal attention system argue against full segregation of the brain networks of bottom-up triggered and top-down controlled attention: (1) the ventromedial parts of SPL (see, Fig. 3) showed activity also when trials associated with LDTs and to-be-ignored duration changes were compared with sustained attention with no duration changes or LDTs, (2) enhanced bilateral FEF/PMC activity was observed when to-be-ignored duration changes were compared with to-be-attended duration changes, and (3) enhanced left FEF/PMC activity was observed when LDTs were compared with sustained attention. The results showing that the ventromedial SPL was activated by both the CASs and LDTs, while the superior parts of SPL were activated specifically by the CASs, suggest that different regions of the SPL might serve different functions in auditory attention. The activity in the ventromedial SPL and FEF/PMC associated with LDTs and to-be-ignored duration changes might be related to the involvement of these areas in bottom-up triggered attention (Serences and Yantis, 2007; Watkins et al., 2007), such as initiation of involuntary attention shifts. The effects of top-down control in processing of the LDTs and to-be-ignored duration changes cannot be ruled out, however, as voluntary reorienting of attention back to the task after an involuntary attention shift to the LDTs or to-be-ignored duration changes, or active suppression of bottom-up processing of the LTDs and to-be-ignored duration changes might be required.

3.3. *Activity in the CG/midFG and cerebellum*

As many previous studies of visual attention (Kim et al., 1999; Rosen et al., 1999; Peelen et al., 2004; Kincade et al., 2005; Salmi et al., 2007a) and auditory attention (Mayer et al., 2006; Salmi et al., 2007a; Watkins et al., 2007), we observed activity also in the CG/midFG and posterior cerebellum. The CG/midFG is suggested to be involved in conflict processing, preparation of movements, and monitoring of performance (see, e.g., Isomura and Takada, 2004). In the present study, CG/midFG activity associated with target processing may have been involved in preparation of movements or monitoring of performance, or both. The posterior cerebellum, in turn, is suggested to be involved in voluntary shifting of attention (Allen et al., 1997; Le et al., 1998; Townsend et al., 1999; Salmi et al. 2007a). In accordance with this, the present results showed activity in the crus I/II of the cerebellum associated with CASs. The crus I/II was activated also in our other study on voluntary control of auditory attention (Salmi et al., 2007a). However, the present results also showed that posterior cerebellar activity following LDTs decreased as compared with sustained attention with no LDTs or duration changes (Fig. 3, bottom right). This might be caused, for example, by gating of signals from the parietal and frontal cortex to the ponto-cerebellar system (Schmahmann and Pandya, 1997), possibly due to LDT-induced processes interfering with processes involved in top-down controlled goal-directed behavior. The present results do not, however, allow conclusions on the exact role of decreased cerebellar activity associated with LDTs.

3.4. *Activity in the ventromedial prefrontal cortex*

LDTs in the to-be-ignored stream were associated with enhanced activity in the VMPFC when they were compared with LDTs in the to-be-attended stream. In parallel with this, RTs to the targets preceded by an LDT during sustained attention were longer when the LDT occurred in the to-be-ignored stream than when it occurred in the to-be-attended steam. As LDTs in the to-be-ignored stream were irrelevant distractors, this activity may be related to the suggested role of the VMPFC in inhibition of irrelevant stimuli (Rule et al., 2002). However, VMPFC activity was also observed when LDT in the to-be-ignored stream was followed by a CAS, that is, when the LDT served as an exogenous cue and facilitated the RT to a target in the same stream where the LDT had just occurred and where attention was shifted as guided by a CAS between the LDT and target. Rule et al. (2002), as well as others (Bechara et al., 2000; Rolls 2000), have suggested that the VMPFC is not only involved in inhibition of irrelevant stimuli, but also in the decision of when to release this inhibition in order to facilitate attention shifting. The present VMPFC activations may be related to such evaluation.

3.5. *Conclusions*

The present results suggest that bottom-up triggered and top-down controlled auditory attention shifting are associated with enhanced activity in brain areas belonging to the dorsal and ventral attention systems in vision (Corbetta and Shulman, 2002), and also in the CG/midFG, crus I/II of the posterior cerebellum, and VMPFC. Our findings suggest that different areas of the SPL might have different roles in auditory attention, since the IPS and superior parts of the SPL are activated specifically by top-down controlled attention shifting, while the ventromedial SPL is activated also by LDTs and to-be-ignored duration changes. Moreover, our results suggest that in audition, the so-called ventral attention system is not involved only in bottom-up processing of changes in the environment and attention shifts triggered by them, but also in top-down controlled attention shifts. Finally, the present results suggest that the VMPFC may have an important role in evaluating the significance of attention-catching events and in selection of the required behavioral response.

4. Experimental procedures

4.1. Participants

Twenty healthy right-handed participants (9 females; age 42–21 years, mean 27 years) with no hearing impairment, neurological or psychiatric history, or color blindness, and normal or corrected-to-normal vision participated in the experiment. Data from one participant were discarded due to an abnormality observed in structural MRI. All participants 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.

4.2. Stimuli and tasks

Iterated rippled noise tones (16 iterations, delay 4.1 ms, perceived pitch at 244 Hz) were presented monoaurally to the left and right ear canals via tubes penetrating earplugs (Etymotic Research, ER3, USA) applied for reducing acoustic scanner noise (approximately 102 dB SPL). Scanner noise was further attenuated by circumaural ear protectors and a viscoelastic mattress inside the headcoil. The effective intensity of most tones at the eardrum was about 70 dB SPL. These tones were of 40 or 100 ms in duration (including 5-ms rise and fall times). Most of these tones had the same duration as the previous tone but altogether 168 times (on average once in 13.7 s) during the experiment the tone duration changed from 40 to 100 ms or vice versa either in the to-be-attended or to-be-ignored location the minimum interval between subsequent duration changes being 2.8 s. In addition, occasionally ($p = 0.018$ of all tones), 70-ms tones with a 15 dB intensity increment (loudness deviating tones, LDTs, see Fig. 1) were presented among the other tones. Offset-to-onset interval of the tones varied randomly from 120 to 460 ms within each ear.

The participants were asked to focus on a black fixation cross (size 1.5°×1.5°) presented at the center of the screen on a gray background ($R = 190$, $G = 190$, $B = 190$) during the entire experiment. The fixation cross was surrounded by visual cue (size 1.5°×1.5°) that was composed of two arrowheads one pointing to the left and the other to the right and thus forming together a diamond shape (see Fig. 1). During the task blocks (duration of each block was 82 s) one of the arrowheads was green, indicating the direction where sounds were to be attended to, and the other was red, indicating the direction where the sounds were to be ignored. It was confirmed before the experiment that all participants could easily distinguish between the green and red colors of the visual cue. After each block there was a 6-s period during which no sounds were presented and the participants were required to focus on the fixation cross and to wait for the next task instruction. During these breaks both arrowheads in the visual cue were black.

When the cue changed (green and red switched their place) during task blocks, the participants were required to shift attention accordingly (cue-guided attention shifts, CAS; see Fig. 1). There were 168 CASs during the experiment. The minimum interval between CASs was 2.8 s, otherwise the cue changes occurred randomly. Half of the LDTs occurred either at the to-be-attended or to-be-ignored side 75 ms before the CAS and the rest of the LDTs appeared at least 2.8 s after a CAS, that is, they were presented during sustained attention. Presentation of LDTs and CASs was balanced between the left and right streams. Target duration changes (from 40 to 100 ms or vice versa) could happen during sustained attention to the left or right stream or when the attention was shifted (CAS) from one side where a row of long or short tones preceded the shift to the other side where a row of short or long tones, respectively, was going on. Thus, if attention was shifted as guided by the cue from one stream to the other stream and the duration of the tones was different in the two streams, the participant was instructed to regard this as a target event, as the duration of the attended tones changed (see the third b event in Fig. 1). The duration of the sounds never changed at the time of the CAS within either stream. Half of the LDTs in the to-be-attended or to-be-ignored stream during sustained attention to one ear, half of the pre-shift LDTs in the stream to be ignored and in the stream to be attended before the shift, and half of the CASs without LDTs were followed by a target to examine the effect of LDT and CAS on RTs to the targets and Miss%. Total number of targets in the experiment was 168. Responses were accepted as hits when they were given within 100–3000 ms from target onset.

In the first session, 14 blocks were presented, after which the participants were asked whether they wished to have a short break. During the break, the participants remained in the scanner and were not allowed to talk or move their head. When the participant was ready, the second session another 14 blocks was started.

4.3. Data acquisition and analysis

Functional brain imaging was carried out with a 3.0 T GE Signa Excite MRI scanner (GE Medical Systems, USA) using a quadrature 8-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 4 mm×4 mm, voxel matrix 64×64, TE 32 ms, TR 2000 ms, flip angle 90°). Functional images were acquired continuously during the experiment. Image acquisition was not time-locked to the beginning of the task blocks nor to the presentation of the different events during the tasks, that is, jittered acquisition was used (see, e.g., Price et al., 1999). A total of 1254 functional volumes were obtained. Thus, fMRI data acquisition lasted for 42 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 (in-plane resolution 1 mm×1 mm, matrix 256×256).

4.3.1. Voxel-vise analysis

First level data analysis was performed with fMRI Expert Analysis Tool software (version 5.43), part of the Functional Magnetic Resonance Imaging of the Brain Centre (FMRIB) software library (FSL, release 4.0, www.fmrib.ox.ac.uk/fsl; Smith et al., 2004). In order to allow for the initial stabilization of the fMRI signal, the first 6 volumes of the session were excluded from analysis (during this time no task was presented). The data were motion corrected and spatially smoothed with a Gaussian kernel of 7 mm (FWHM), and high-pass filtered (cutoff 150 s). Statistical analysis was performed using the FMRIB Improved Linear Model (FILM). Explanatory variables were derived from timing (onset of each event) of different events (LDTs in the to-be-attended and to-be-ignored stream, CAS, LDTs in the to-be-attended and to-be-attended stream with CAS, target duration change during sustained attention, to-be-ignored duration change during sustained attention) and rest periods. The hemodynamic response to CASs, LDTs, and duration changes during sustained attention was modeled using a double-gamma-function and its temporal derivative and rest periods were modeled using a gamma function. The high-pass filtering applied to the model was the same as that applied to the data. Sustained-attention periods when no targets or LDTs were presented served as a baseline in the model. Contrasts were specified to create Z-statistic images testing for the effects of sustained attention, attention shifting and duration changes. The exact comparisons are carefully reported in the Results section. The effects of target processing on LDT and CAS-related activity (see Fig. 3) was reduced by contrasting these events with same amount of targets that occurred independent of LDTs and CASs.

The two halves of the fMRI experiment were analyzed separately and then combined in a second level analysis (fixed effects). For group (third level) analysis, Z-statistic images of each participant were transformed into a standard space (MNI152; Montreal Neurological Institute). The group analysis was performed using FMRIB's Local Analysis of Mixed Effects (FLAME). Statistical inference was carried out using Gaussian random field theory and cluster-based thresholding, using a cluster-forming Z threshold (1.64–6.5 depending on the contrast) and a (corrected) cluster significance threshold ($P<0.01$–0.05).

4.3.2. *Region of interest analysis*

Several regions of interest (ROIs) were defined based on the group activation clusters to extract the activation time-series. Each group activation cluster (contrasts: LDTs vs sustained attention and CASs vs. sustained attention) was included as a ROI in the analysis but only statistically significant results are reported. For the ROI analysis, the data were first motion corrected and high-pass filtered (cutoff 60 s) using FSL. Then the ROI data were transferred to percent signal change values relative to the mean ROI signal across all volumes. After this the time points (volumes) were sorted in time relatively to the onset of the block, the ROI time-series was linearly interpolated, and temporally smoothed using a low-pass Butterworth filter. Finally, the baseline of the ROI time-series was set to the mean of time window of 5–0 s before block onset.

Acknowledgments

This research was supported by the Academy of Finland (grants #210587, 210186 and 209709), Nordic Council for the establishment of a Nordic Center of Excellence in Cognitive Control (NCOE grant #40043), Finnish Cultural Foundation, Finnish Graduate School of Psychology, and by the Funds of the University of Helsinki. We thank Ms. Marita Kattelus for her help in collecting the fMRI data and Dr. Alexander Degerman for his helpful comments in interpreting our results.

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