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Research Report

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

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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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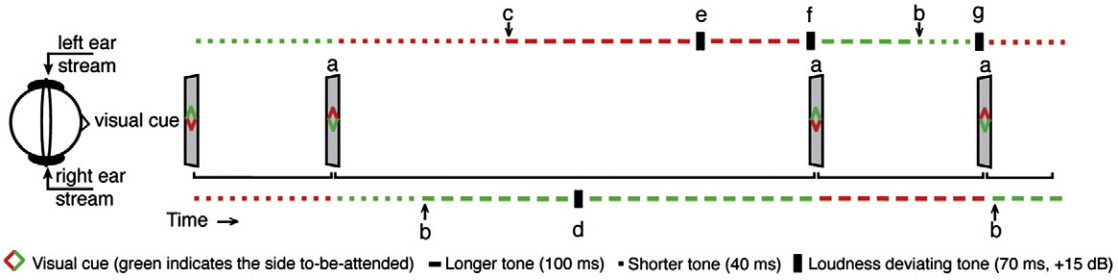

Fig. 1 – Participants selectively attended to tones at the left or right as indicated by a visual cue composed of green and red arrowheads and occasionally shifted their attention between the two tone streams when the cue color changed (a, cue-guided attention shift, CAS). Performance was measured as 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