BRAIN RESEARCH 1134 (2007) 187–198

Available online at www.sciencedirect.com

SciVerse ScienceDirect

www.elsevier.com/locate/brainres

BRAIN RESEARCH

Research Report

The neural circuitry underlying the executive control of auditory spatial attention

C.-T. Wu[a,b], D.H. Weissman[d], K.C. Roberts[a], M.G. Woldorff[a,b,c,*]

[a]Center for Cognitive Neuroscience, Duke University, Durham, NC 27708, USA
[b]Department of Psychology and Neurosciences, Duke University, Durham, NC 27708, USA
[c]Department of Psychiatry, Duke University, Durham, NC 27708, USA
[d]Department of Psychology, University of Michigan at Ann Arbor, MI 48109, USA

ARTICLE INFO

Article history:
Accepted 21 November 2006
Available online 3 January 2007

Keywords:
fMRI
Supramodal
Top-down control
Fronto-parietal network

ABSTRACT

Although a fronto-parietal network has consistently been implicated in the control of visual spatial attention, the network that guides spatial attention in the auditory domain is not yet clearly understood. To investigate this issue, we measured brain activity using functional magnetic resonance imaging while participants performed a cued auditory spatial attention task. We found that cued orienting of auditory spatial attention activated a medial–superior distributed fronto-parietal network. In addition, we found cue-triggered increases of activity in the auditory sensory cortex prior to the occurrence of an auditory target, suggesting that auditory attentional control operates in part by biasing processing in sensory cortex in favor of expected target stimuli. Finally, an exploratory cross-study comparison further indicated several common frontal and parietal regions as being involved in the control of both visual and auditory spatial attention. Thus, the present findings not only reveal the network of brain areas underlying endogenous spatial orienting in the auditory modality, but also suggest that the control of spatial attention in different sensory modalities is enabled in part by some common, supramodal neural mechanisms.

1. Introduction

Spatial attention enables individuals to enhance the processing of stimuli that occur at behaviorally relevant locations in the environment (Hillyard and Anllo-Vento, 1998; Kanwisher and Wojciulik, 2000). Although numerous studies have indicated that the control of spatial attention is enabled by a network of frontal and parietal brain areas (Corbetta and Shulman, 2002; Hopfinger et al., 2000; Mesulam, 1999; Woldorff et al., 2004), almost all of these studies have been conducted entirely within the visual modality. Thus, it has not yet been firmly established whether similar brain areas enable spatial attention in other sensory modalities, such as in audition.

Previous work suggests that spatial attention may be supported by a combination of supramodal and modality-specific brain mechanisms. With regards to supramodal mechanisms, previous studies have shown that attending to a specific location in space in one sensory modality can influence the processing of stimuli in a different sensory modality at or near that location (Macaluso et al., 2000; Talsma and Kok, 2002). Furthermore, patients with parietal-lobe damage often exhibit neglect in both the visual and the

* *Corresponding author*. Center for Cognitive Neuroscience, Duke University, Box 90999, Durham, NC 27708-0999, USA. Fax: +1 919 681 0815.
E-mail address: woldorff@duke.edu (M.G. Woldorff).

0006-8993/$ – see front matter
doi:10.1016/j.brainres.2006.11.088

auditory modalities (Bellmann et al., 2001; Bisiach et al., 1984; Pavani et al., 2003). On the other hand, the existence of modality-specific mechanisms is suggested by behavioral studies indicating greater interference between two tasks when those tasks are presented in the same versus different sensory modalities (Arnell and Larson, 2002; Duncan et al., 1997; Soto-Faraco and Spence, 2002). Despite these suggestive findings, however, lesion and behavioral studies lack the anatomical precision necessary to reveal the precise neural mechanism underlying the control of auditory spatial attention.

A few recent neuroimaging studies have investigated the brain regions that control auditory spatial attention, and the results suggest that these regions are anatomically similar to those that control visual spatial attention (Mayer et al., 2006; Shomstein and Yantis, 2006; Tzourio et al., 1997). However, these prior studies had several significant limitations. In one study (Tzourio et al., 1997), the use of a block-design did not allow brain regions involved in orienting auditory spatial attention to be distinguished from regions that detect and process auditory targets. In a second study (Mayer et al., 2006), the use of monaurally presented tones as cues did not permit a dissociation between endogenous and exogenous aspects of attentional orienting and, furthermore, may have confounded these attentional effects with lateralized activations resulting from the monaural presentation. Finally, a third recent study reported that the posterior parietal cortex contributes to shifting versus maintaining both spatial and non-spatial auditory attention (Shomstein and Yantis, 2006); however, that study may not have revealed the entire network that underlies top-down orienting of auditory spatial attention since only switch-specific processes were isolated. Thus, the neural mechanisms that enable top-down orienting of auditory spatial attention – and the degree to which these mechanisms are similar to those used to orient spatial attention in other sensory modalities – remain unclear.

To identify the brain regions that enable top-down orienting of auditory spatial attention, we asked participants to perform a cued auditory spatial attention task while we recorded their brain activity using event-related fMRI. In this task, participants were cued to attend to either the left or the right auditory space in order to detect a faint target sound that appeared in some of the trials. There were mainly two types of cues: Attend-cues (human voice saying "Left" or "Right"), which instructed subjects to orient their attention to the left or right auditory space for a possible target, and "Interpret-cues" (human voice saying "Past"), a control trial type which instructed subjects to not orient their attention to either side. There were also trials in which no cues were presented, which served as No-stim trials. These No-stim trial types were included to facilitate the extraction of the event-related fMRI responses and the removal of overlapping responses from adjacent trials in the sequence (see Section 4.5.1). Lastly, subjects were instructed to delay their behavioral responses until after a "respond signal," rather than making their responses immediately after detecting the target.

The inclusion of the Interpret-cues, which needed to be fully processed and identified but instructed subjects to not orient attention, provided a control condition that allowed us to isolate and identify the brain areas selectively involved in cue-triggered, voluntary orienting of auditory spatial attention while controlling for the basic sensory and semantic processing of the cue stimuli. Moreover, since the paradigm was directly analogous to the one we used previously to investigate visual spatial attention (Woldorff et al., 2004), we were able to perform an exploratory cross-study comparison to identify supramodal brain areas that enable the control of spatial attention in both the auditory and the visual modalities.

2. Results

2.1. Behavior

Because subjects were instructed to delay their responses until after a "respond signal", the reaction time could not serve as a meaningful measure of task performance. However, percent hit rate was analyzed, using a one sample paired *t*-test across participants. The average accuracy for left and right targets, respectively, was 82% and 72%. These values did not differ significantly from one another [$t(12)=1.93$, $p=.08$].

2.2. fMRI

2.2.1. Cue-related activity

Fig. 1 presents the brain activation maps for the main contrasts, including those related to cue interpretation (Interpret-cue-only trials minus No-stim trials), attentional orienting (Attend-cue-only trials minus Interpret-cue-only trials), and target-related processing (Attend-cue-plus-target trials minus Attend-cue-only trials). As illustrated in Figs. 1a and 1b, both Interpret-cue-only trials and Attend-cue-only trials activated frontal and parietal areas as well as the right and left auditory cortices; however, Attend-cues also appeared to activate additional areas that were not activated by the Interpret-cues.

Both Attend-cues and Interpret-cues were expected to elicit cue interpretation processes, but Attend-cue-only trials also required the deployment of auditory spatial attention. We therefore directly contrasted these two trial types to identify which brain regions were selectively involved in orienting spatial attention within the auditory modality. As revealed in Fig. 1c, spatial attentional orienting in the auditory modality (i.e., Attend-cue-only versus Interpret-cue-only trials) bilaterally activated superior, medial, middle and inferior frontal gyri, anterior cingulate cortex (ACC), middle cingulate cortex (MCC), precuneus/superior parietal lobe (SPL), bilateral anterior insula and bilateral putamen/caudate nuclei. The location of the middle frontal gyrus activations (Fig. 1c, $Z=44$ mm) was close to the locations of human FEF reported in previous studies (Koyama et al., 2004; Paus, 1996).

Table 1 lists the Talairach coordinates (center of mass) for the regions defined by the contrast of Attend-cue-only trials versus Interpret-cue-only trials. The time courses for the Attend-cue-only and Interpret-cue-only trials in these regions are plotted in Fig. 2. Generally, the distribution of the cue-related fronto-parietal activation for auditory spatial attentional orienting was somewhat more superior and medial than that observed in our analogous study in the visual