BRAIN RESEARCH 1583 (2014) 159–168

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Research Report

Functional connectivity of dorsal and ventral frontoparietal seed regions during auditory orienting

Stephanie Rossi[a], *Samantha Huang*[a], *Sharon C. Furtak*[a,b], *John W. Belliveau*[a,c], *Jyrki Ahveninen*[a,*]

[a]*Athinoula A. Martinos Center for Biomedical Imaging, Department of Radiology, Massachusetts General Hospital, Harvard Medical School, Charlestown, MA, USA*

[b]*Department of Psychology, California State University, Sacramento, CA, USA*

[c]*Harvard–MIT Division of Health Sciences and Technology, Cambridge, MA, USA*

ARTICLE INFO

Article history:
Accepted 4 August 2014
Available online 12 August 2014

Keywords:
Auditory attention
fMRI
Psychophysiological interaction
Auditory cortex
Voluntary orienting
Involuntary attention

ABSTRACT

Our ability to refocus auditory attention is vital for even the most routine day-to-day activities. Shifts in auditory attention can be initiated "voluntarily," or triggered "involuntarily" by unexpected novel sound events. Here we employed psychophysiological interaction (PPI) analyses of auditory functional MRI data, to compare functional connectivity patterns of distinct frontoparietal cortex regions during cued voluntary vs. novelty-driven involuntary auditory attention shifting. Overall, our frontoparietal seed regions exhibited significant PPI increases with auditory cortex (AC) areas during both cued and novelty-driven orienting. However, significant positive PPI patterns associated with voluntary auditory attention (cue > novel task regressor), but mostly absent in analyses emphasizing involuntary orienting (novel > cue task regressor), were observed with seeds within the frontal eye fields (FEF), superior parietal lobule (SPL), and right supramarginal gyri (SMG). In contrast, significant positive PPIs associated selectively with involuntary orienting were observed between ACs and seeds within the bilateral anterior interior frontal gyri (IFG), left posterior IFG, SMG, and posterior cingulate cortices (PCC). We also found indices of lateralization of different attention networks: PPI increases selective to voluntary attention occurred primarily within right-hemispheric regions, whereas those related to involuntary orienting were more frequent with left-hemisphere seeds. In conclusion, despite certain similarities in PPI patterns across conditions, the more dorsal aspects of right frontoparietal cortex demonstrated wider connectivity during cued/voluntary attention shifting, whereas certain left ventral frontoparietal seeds were more widely connected during novelty-triggered/involuntary orienting. Our findings provide partial support for distinct attention networks for voluntary and involuntary auditory attention.

*Correspondence to: MGH/MIT/HMS-Martinos Center, Building 149 13th Street, Charlestown, MA 02129, USA. Fax: +1 617 726 7422.
E-mail address: jyrki@nmr.mgh.harvard.edu (J. Ahveninen).

http://dx.doi.org/10.1016/j.brainres.2014.08.002
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1. Introduction

The ability to engage, disengage, and shift one's attention is vital for even the most routine activities in everyday auditory environments. Shifts in attention can be triggered by either top-down or bottom-up mechanisms (Corbetta and Shulman, 2002). Top-down (voluntary) attention shifting occurs in a goal-driven fashion, for example, when one switches between competing sound sources in a lively social situation. Bottom-up (involuntary) orienting, in turn, is driven by the salient properties of auditory stimuli, such as when attention is suddenly captured by an unexpected event occurring beyond the immediate perceptual field (e.g., a car backfiring) (Jääskeläinen et al., 2004; Näätänen, 1992; Schröger and Wolff, 1998). Neuronal networks governing these two distinct attentional control processes have been frequently studied utilizing various imaging techniques. While most of the existing studies are in the visuospatial domain (Corbetta and Shulman, 2002; Kim et al., 1999; Posner and Rothbart, 2007; Rosen et al., 1999; Serences and Yantis, 2007), a number of recent functional magnetic resonance imaging (fMRI) studies have sought distinct pathways for voluntary attention shifting vs. involuntary orienting using auditory stimuli (Huang et al., 2012; Mayer et al., 2006, 2009; Salmi et al., 2009; Wu et al., 2007). Although much headway has been made in the understanding of neural mechanisms associated with attention in humans (Huang et al., 2012; Kong et al., 2014; Mayer et al., 2006, 2009; Santangelo et al., 2009; Shomstein and Yantis, 2004, 2006; Wu et al., 2007), the picture of exact brain networks that govern auditory attentional control is still incomplete.

According to previous studies in the visual domain using fMRI (Corbetta and Shulman, 2002), activations associated with voluntary/endogenous attentional control processes could be located in more anterior/superior aspects of frontal and parietal cortices than those associated with involuntary/exogenous stimulus-driven orienting. The areas associated with voluntary attentional control include the frontal eye fields (FEF), superior parietal lobule (SPL), as well as regions anterior/superior to the intraparietal sulcus (IPS). In contrast the more inferior regions located near the border between the parietal and temporal cortices, such as the temporoparietal junction (TPJ), have been associated with involuntary orienting (Corbetta and Shulman, 2002). However, the evidence from fMRI studies in the auditory domain has not been fully consistent (Huang et al., 2012; Mayer et al., 2006, 2009; Salmi et al., 2009; Wu et al., 2007). For example, a recent study has suggested largely overlapping networks associated with both voluntary attention shifting and involuntary orienting (Salmi et al., 2009), while other studies have even suggested that the division of labor between dorsal and ventral auditory attention networks differs from that of visuospatial orienting (Mayer et al., 2009). The role of medial posterior parietal cortices (i.e., the precuneus, PC) in voluntary vs. involuntary attentional control is not fully clear either (Shomstein and Yantis, 2006; Shulman et al., 2009).

Thus far, the majority of studies on attentional processes in the visual and auditory modalities have concentrated on functional activations in various brain regions. While the value of studying brain function in terms of neural segregates is unquestionable, the emerging functional connectivity analyses have broadened the horizon of potentials to reveal functional "networks" rather than just uncovering the "key loci" associated with various aspects of brain functions. As attentional control likely involves dynamic processing, different brain regions may be recruited during the related processes. Therefore, investigating the functional networks associated with voluntary and involuntary attentional control processes should provide important insights into our understanding of the brain's attention systems. For example, a recent visual study using the resting state functional connectivity approach revealed three networks associated with attentional control processes (Shulman et al., 2009). These networks comprise a more ventral network including the inferior frontal gyrus (IFG) and TPJ, and a dorsal frontal parietal network including the IPS and FEF, as well as a basal ganglia–cortical network consisting of the basal ganglia, anterior cingulate cortex (ACC), dorsolateral prefrontal cortex (DLPFC), and anterior insula (AI). However, few studies have used analogous approaches to study the auditory attention systems. Therefore, to investigate functional connectivity patterns associated with cued (voluntary) and novelty-triggered (involuntary) attention shifting in the auditory domain, we reanalyzed our recently published fMRI data (Huang et al., 2012) by using psycho-physiological interaction (PPI) analysis, a method that characterizes the activity in one seed region of the brain by the interaction with another region's activity during a psychological condition. Our hypothesis was that dorsal aspects of frontal and parietal cortices (e.g., FEF, SPL) exhibit most significant PPI patterns with auditory cortices and other areas during voluntary attention, modeled as attention-cue related vs. novelty-related signal increase, and that more ventral areas (e.g., IFG) represent most extensive inter-regional connectivities during involuntary orienting (modeled as novelty- vs. cue-related signal increase).

2. Results

2.1. Overview

Behaviorally, the subjects discriminated the target at a mean $\pm$ standard deviation (SD) hit rate (HR) of $90\pm7.9\%$ and reaction time (RT) of 495 ± 48 ms. The mean $\pm$ SD false alarm rate was $1\pm1.5\%$. A separate behavioral control analysis ($N=10$, 4 females, age 22–43 years) demonstrated that spatial cueing significantly ($t(9)=-4.2$, $p<0.01$) speeded-up target discrimination, as compared to trials with the target occurring in the ear opposite of the cue (mean $\pm$ SD reaction times were 463 ± 68 to the validly cued and 555 ± 105 ms to the invalidly cued trials, respectively).

In the PPI analyses, the main "psychological" task regressors of interest were designed based on contrasts presumed to reflect cued attention shifting and novelty triggered reorienting processes defined as "cue+standards vs. standards only" and "cue+novel+standards vs. cue+standards," respectively. The psychological (task condition) regressors modeled the differences of these cued voluntary and novelty-triggered involuntary orienting conditions (i.e., in separate analyses, cue–novel and novel–cue). The "physiological regressor" was derived from individual maxima of the relevant contrast