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Sensory-biased attention networks in human lateral frontal cortex revealed by intrinsic functional connectivity

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ABSTRACT

Human frontal cortex is commonly described as being insensitive to sensory modality, however several recent studies cast doubt on this view. Our laboratory previously reported two visual-biased attention regions interleaved with two auditory-biased attention regions, bilaterally, within lateral frontal cortex. These regions selectively formed functional networks with posterior visual-biased and auditory-biased attention regions. Here, we conducted a series of functional connectivity analyses to validate and expand this analysis to 469 subjects from the Human Connectome Project (HCP). Functional connectivity analyses replicated the original findings and revealed a novel hemispheric connectivity bias. We also subdivided lateral frontal cortex into 21 thin-slice ROIs and observed bilateral patterns of spatially alternating visual-biased and auditory-biased attention network connectivity. Finally, we performed a correlation difference analysis that revealed five additional bilateral lateral frontal regions differentially connected to either the visual-biased or auditory-biased attention networks. These findings leverage the HCP dataset to demonstrate that sensory-biased attention networks may have widespread influence in lateral frontal cortical organization.

1. Introduction

The degree to which human frontal cortex conducts sensory modality-specific processing remains a controversial issue in neuroscience. Non-human primate research suggests that several areas within dorsal and ventral subdivisions of lateral frontal cortex exhibit a preferred sensory modality (Barbas and Mesalum, 1981; Petrides and Pandya, 1999; Romanski 2007, 2012; Romanski and Goldman-Rakic, 2002; Yeterian et al., 2012). On the other hand, human-based functional MRI (fMRI) studies of visual and auditory sensory processing in lateral frontal cortex (LFC) typically report either a relative lack of sensitivity to sensory modality (Lewis et al., 2000; Johnson and Zatorre, 2006; Ivanoff et al., 2009; Karabanov et al., 2009; Tark and Curtis, 2009; Tombu et al., 2011; Braga et al., 2013) or a bias for a single sensory modality (Crottaz-Herbette et al., 2004; Jantzen et al., 2005; Rämä and Courtney, 2005; Salmi et al., 2007). However, consistent with non-human primate studies, two recent human fMRI studies (Michalka et al., 2015; Mayer et al., 2017) and one study combining functional and structural connectivity (Braga et al., 2017) found that distinct regions of LFC exhibit strong biases for vision or audition. Another study also reported sensitivity to sensory modality within LFC (Tamber-Rosenau et al., 2013).

Using a task-based fMRI paradigm that controlled for task difficulty and stimulus drive (see Supplemental Methods and Supplemental Fig. 1), our laboratory previously reported that the contrast of visual spatial attention to auditory spatial attention revealed two visual-biased regions interleaved with two auditory-biased regions in lateral frontal cortex (Michalka et al., 2015). These four regions are located along the precentral sulcus and inferior frontal sulcus (Fig. 1); from dorsal to ventral, these regions are: superior precentral sulcus (sPCS), transverse gyrus intersecting precentral sulcus (tgPCS), inferior precentral sulcus (iPCS), and caudal inferior frontal sulcus (cIFS). sPCS & iPCS are visual-biased and tgPCS & cIFS are auditory-biased. In posterior cortical regions, this contrast of sensory attention modalities also revealed visual-biased activation along the intraparietal sulcus and transverse occipital sulcus (IPS/TOS) and auditory-biased activation in superior temporal gyrus and sulcus (STG/S; Fig. 1). This study also demonstrated, using resting-state

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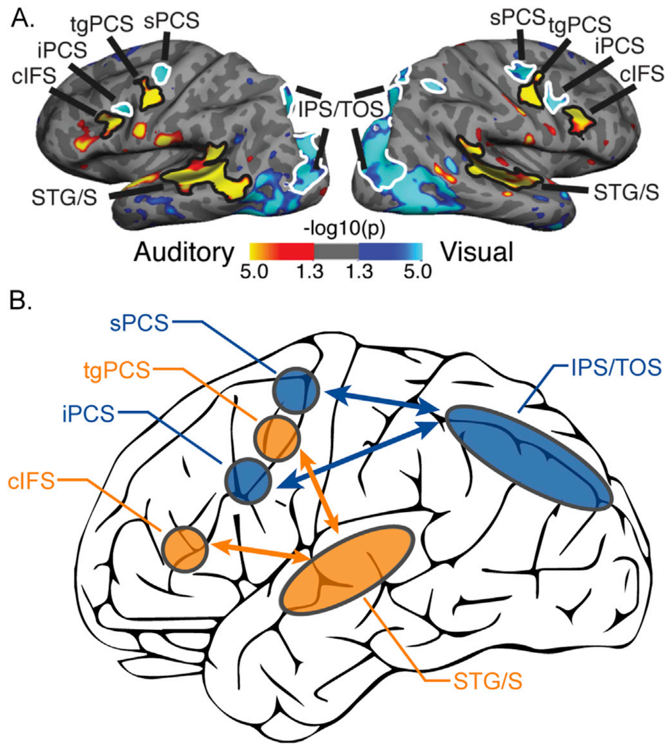

Fig. 1. Visual- vs. auditory-biased attention networks from Michalka et al. (2015). (A) Task-based fMRI contrast of visual- vs. auditory-spatial attention (VASA) from a representative individual. Bilaterally, 2 visual-biased attention regions, superior precentral sulcus (sPCS) and inferior precentral sulcus (iPCS), were observed to be interleaved with 2 auditory-biased attention regions, transverse gyrus intersecting the precentral sulcus (tgPCS) and caudal inferior frontal sulcus (cIFS). In posterior cortex, visual attention recruited intraparietal sulcus/transverse occipital gyrus (IPS/TOS), while auditory attention recruited superior temporal gyrus/sulcus (STG/S). (B) Summary of rsFC results from Michalka et al. (2015). sPCS, iPCS & IPS/TOS selectively form a visual-biased network, while tgPCS, cIFS & STG/S selectively form an auditory-biased network.

functional connectivity, that the frontal and posterior areas segregated into two sensory-biased networks: a visual-biased network, consisting of sPCS, iPCS & IPS/TOS and an auditory-biased network, consisting of tgPCS, cIFS & STG/S.

The Michalka et al. (2015) study successfully employed individual subject analysis to localize small, neighboring, functionally differentiated regions. Such regions can be challenging to identify with group averaging techniques. The individual-subject approach to cortical mapping has previously proven effective in human visual neuroscience, but commonly employs only small numbers of subjects (e.g. DeYeo et al., 1996; Tootell et al., 1997; Hansen et al., 2007; Swisher et al., 2007; Heinzle et al., 2011). Even though this approached revealed all eight bilateral ROIs in 90% of subjects, the study has been critiqued due to its small sample size ($N = 10$) (Mayer et al., 2017). The standard deviation of the location of these sensory-biased LFC regions was, on average, 87% of the radial width of the ROIs, thus the anatomical blurring inherent in group-average analyses could mask the existence of these areas even in larger N studies. In order to demonstrate the rigor and generality of these observations, and in light of recent publications detailing the challenges of reproducibility in neuroimaging (Poldrack et al., 2017), we seek to reproduce these laboratory-specific findings with a much larger sample size. Specifically, we define probabilistic ROIs based on task-based fMRI in a small number ($N = 9$) of individual subjects and apply these ROIs to examine resting-state functional connectivity patterns in a large ($N = 469$) publically available dataset from the Human Connectome Project (HCP; Smith et al., 2013; Van Essen et al., 2013). Resting-state functional connectivity (rsFC) can be a powerful technique for identifying functional brain networks (e.g., Biswal et al., 1995; Power et al., 2014; Yeo et al., 2011; Glasser et al., 2016), and here we use this approach to examine sensory-biased attention networks in lateral frontal cortex.

Our analyses reproduce our previous finding of a bilateral pattern of four interleaved lateral frontal lobe regions in a large dataset. The large N of the study afforded the power to make new observations; we identify five additional bilateral regions in LFC that exhibit selective functional connectivity to visual or auditory sensory-biased attention networks. The identification of these regions suggests that the influence of sensory modality may extend more anteriorly across LFC and provides candidate ROIs to be examined in future task-based studies.

2. Materials and methods

2.1. Subject datasets

Two separate datasets were used for this work: 1) visual vs. auditory spatial attention (VASA) task fMRI (t-fMRI) data (see Supplemental Materials) and resting state fMRI (rs-fMRI) from 9 healthy individuals previously published in Michalka et al. (2015), hereafter referred to as VASA9, and 2) rs-fMRI data from 469 subjects of the publically available HCP dataset (Van Essen et al., 2013; www.humanconnectome.org) and supported by the WU-Minn HCP Consortium, hereafter referred to as HCP469. The respective Institutional Review Boards of Boston University and Washington University approved all experimental procedures. All subjects provided written informed consent in accordance with the guidelines set by each institution. The VASA9 subjects consisted of healthy, right handed, native English speakers (mean age 27.6 ± 2.7, range 22–31, 5 females) recruited from the Boston University community. This dataset contained structural MRI, t-fMRI and rs-fMRI acquisitions. T-fMRI from the VASA9 dataset was used to create regions of interest (ROIs) from the observed lateral frontal, temporal and parietal sensory-biased attention regions. The HCP469 dataset was used for replication and extension of the Michalka et al. (2015) intrinsic functional connectivity results and novel large-scale characterization of lateral frontal sensory-biased attention networks. rs-fMRI and anatomical cortical surface reconstruction data from the 'S500' release dataset were used for this study. See Van Essen et al. (2013) for additional details on this dataset. Of the subjects available in this release, only subjects that possessed at least one pair of left-to-right and right-to-left phase encoded rs-fMRI acquisitions were included. Subjects that exceeded *a priori* motion thresholds of 1.5 mm total displacement or 0.5 mm mean framewise displacement (FD) were excluded from the study. Timepoints with FD over 0.5 mm were classified as spikes in movement and subjects with greater than 5% of timepoints categorized as spikes were excluded. Exclusion of subjects according to these criteria resulted in sample size of 469 subjects.

2.2. MRI acquisition

2.2.1. VASA9 dataset

The VASA9 dataset was acquired at the Center for Brain Science Neuroimaging Facility at Harvard University using a 3-Tesla Siemens Tim Trio MRI scanner (Siemens, Erlangen, Germany) equipped with a 32-channel phased array head coil. T-fMRI and rs-fMRI were acquired with a gradient echo echo-planar imaging sequence sensitive to blood oxygen level dependent contrast (repetition time (TR)/echo time (TE) = 2 600/30 ms, flip angle (FA) = 90°, 42 axial slices, 3 mm slice thickness, in-plane resolution 3.125×3.125 mm). Rs-fMRI acquisitions were 139 or 256 TRs long and subjects participated in one or two runs each and all available data were used. During rs-fMRI acquisitions, subjects were instructed keep their eyes open, maintain fixation on a centrally presented cross, allow their minds to wander and avoid mental activities such as counting. Details of the task paradigm are described below. In addition, high-resolution ($1.0 \times 1.0 \times 1.0$ mm) T1-weighted magnetization-prepared rapid gradient echo structural images were acquired for cortical surface reconstruction.