



The salience network dynamics in perceptual decision-making



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ABSTRACT

Recent neuroimaging studies have demonstrated that the network consisting of the right anterior insula (rAI), left anterior insula (lAI) and dorsal anterior cingulate cortex (dACC) is activated in sensory stimulus-guided behaviors. This network is often known as the salience network (SN). When and how a sensory signal enters and organizes within SN before reaching the central executive network including the prefrontal cortex is still a mystery. Previous electrophysiological studies focused on individual nodes of SN, either on dACC or rAI, have reports of conflicting findings of the earliest cortical activity within the network. Functional magnetic resonance imaging (fMRI) studies are not able to answer these questions in the time-scales of human sensory perception and decision-making. Here, using clear and noisy face-house image categorization tasks and human scalp electroencephalography (EEG) recordings combined with source reconstruction techniques, we study when and how oscillatory activity organizes SN during a perceptual decision. We uncovered that the beta-band (13–30 Hz) oscillations bound SN, became most active around 100 ms after the stimulus onset and the rAI acted as a main outflow hub within SN for easier decision making task. The SN activities (Granger causality measures) were negatively correlated with the decision response time (decision difficulty). These findings suggest that the SN activity precedes the executive control in mediating sensory and cognitive processing to arrive at visual perceptual decisions.

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1. Introduction

The salience network (SN), consisting of the right anterior insula (rAI), left anterior insula (lAI) and dorsal anterior cingulate cortex (dACC) (Ham et al., 2013; Seeley et al., 2007), responds to behaviorally salient events (Seeley et al., 2007). It plays a crucial role in integrating sensory stimuli to initiate cognitive control (Menon and Uddin, 2010), to implement and maintain task sets (Dosenbach et al., 2006), and to coordinate behavioral responses (Medford and Critchley, 2010). When and how a sensory signal enters and organizes within SN in a sensory-driven, goal-directed task is not understood. Such understanding can help predict impending perceptual decisions and task executions that involve the prefrontal cortex.

There are two main competing theories that explain the possible 'driving hub' of the SN. First theory proposes that the dACC monitors performance and signals the need for behavioral adaptation (Ridderinkhof et al., 2004). Activity in the dACC signals the need for enhanced cognitive control, and interactions between the dACC and the lateral prefrontal structures implement subsequent behavioral changes (Egner, 2009; Ridderinkhof et al., 2004). In contrast, the second theory suggests that

the rAI is a 'cortical outflow hub' of the SN and it coordinates a change in activity across multiple neurocognitive networks, such as the default mode network (DMN) and central executive network (CEN) (Chand and Dhamala, 2015; Bonnelle et al., 2012; Menon and Uddin, 2010; Sridharan et al., 2008). Diffusion tensor imaging (DTI) study has demonstrated that the structural integrity of the white matter connection between the rAI and the dACC predicts behavioral and physiological abnormalities after traumatic brain injury (Bonnelle et al., 2012). Previous investigations using blood oxygenation level-dependent (BOLD) changes in functional magnetic resonance imaging (fMRI) showed that the rAI, not the dACC, drives the SN (Ham et al., 2013; Sridharan et al., 2008) and further suggested that a change in the effective connectivity of the dACC was associated with behavioral adaptation (Ham et al., 2013). As BOLD hemodynamic responses are sluggish, it might in fact include processes that happen on longer time-scale (seconds) and, if so, the 'driving hub' of the SN might even change in millisecond time-scale of neuronal activities. The studies mentioned above (Debener et al., 2005; Egner, 2009; Ham et al., 2013; Sridharan et al., 2008) had reports of conflicting findings of the earliest cortical activity. Therefore, how a sensory signal enters SN and organizes within before reaching the prefrontal cortex for central executive processing in the time-scales of human sensory perception and cognition has remained as a mystery. We seek to resolve these conflicting reports considering both anterior insulae and dACC in millisecond time-scale. In particular, how the cortical areas of the SN interact, what the

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temporal flow of underlying overall activity in these cortical areas is, and what frequency band(s) of information flow binds the SN are largely unknown.

As the dACC, rAI and lAI are often co-activated, it had been hard to disentangle their causal features (Ham et al., 2013), specifically on longer time-scale measures such as from fMRI. In this study, we recorded human scalp electroencephalography (EEG), reconstructed source waveforms and investigated the causal relationships between the areas of the SN using spectral Granger causality (GC) (Dhamala et al., 2008a, 2008b). In this EEG experiment, we used the standard face-house image categorization tasks and studied the temporal evolution of activity in the salience nodes and the patterns of oscillatory network activity flow binding SN nodes in a network. Adding noise to clear images, three noise levels of stimuli were created to examine whether a difficult task (or difficult decision) modulates the network activity flow.

2. Materials and methods

2.1. Participants

Twenty-six neurologically healthy human volunteers (21 males, 5 females) of age ranged from twenty-two to thirty-eight years (mean: 26.3 years, standard deviation: 4.7 years) participated for this study. A written informed consent was collected from the participants prior to data collection. The experimental protocol was approved from Institutional Review Board of Georgia State University. Three participants were excluded from the final analyses because of behavior performance and/or unmanageable artifacts and noise present in their EEG data.

2.2. Stimuli

We used total twenty-eight images of faces and houses (14 images of each category). Face images were from the Ekman series (Ekman and Friesen, 1976). Fast Fourier transforms (FFT) of these images were computed, providing twenty-eight magnitude and twenty-eight phase matrices. The average magnitude matrix of this set was stored. Stimulus-images were produced from the inverse FFT (IFFT) of average magnitude matrix and individual phase matrices. The phase matrix used for the IFFT was a linear combination of the original phase matrix computed during the forward Fourier transforms and a random Gaussian noise matrix. The resulting images were equalized for luminance and contrast as in the prior studies (Heekeren et al., 2004, 2008; Rainer and Miller, 2000). Finally, the stimuli consisted of three different noise-levels: 0%, 40% and 55% (i.e., clear stimuli, 40% noisy stimuli, and 55% noisy stimuli). Those steps were performed using Matlab scripts. The E-Prime 2.0 software was used to display the stimuli and control the task sequences.

2.3. Experimental design

Prior to experimental task, the participants were briefly explained about the task paradigm. Participant sat in a dark room with the only source of light from the experimenter's computer screen. The same computer screen with the same display settings was used throughout the experiment. However, we did not explicitly calculate voltage/luminance functions for gamma correction as specified by the relations between RGB (red-blue-green) and luminance values, which are device dependent. The stimulus viewing distance was ~60 cm (chin rest). Fig. 1 shows a schematic of experimental paradigm used. Experiment consisted of 4 blocks with 168 trials in each block. The stimuli were randomized but balanced across blocks in presentation. The experiment consisted of total 672 trials with 224 trials for each noise level. On each trial, a small fixation cross ('+' in the middle of the screen) was presented for 500 ms. Then a stimulus was presented for 150 ms, followed by black screen with question mark ('?') for 1500 ms during which time participants were allowed to indicate their decision (either

face or house) by keyboard button press. The responses after that delay were considered incorrect.

2.4. Data acquisition and preprocessing

EEG data were acquired with a 64-channel EEG system from Brain Vision LLC (<http://www.brainvision.com>). Analog signal was digitized at 500 Hz. The impedances of each electrode were kept below 10 k Ω , and the participants were asked to minimize blinking, head movements, and swallowing. EEG data were band-pass filtered between 1 and 100 Hz, and notch filtered to remove 60 Hz AC-line noises. The eye blinkings were removed using independent component analysis (ICA)-based ocular correction. Data from bad electrodes were discarded and replaced, when appropriate, by spatial interpolation from the neighboring working electrodes. These preprocessing steps were done using Brain Vision Analyzer 2.0 (<http://www.brainproducts.com>).

2.5. Data analysis

The preprocessed EEG data were analyzed in the following main steps:

- (1) *Computation of ERPs*: Continuous EEG data were segmented into trials of 300 ms duration (post-stimulus: 0 to 300 ms) based on the stimulus onset times as a reference. The trials that had three standard deviations below or above the global mean across time in each subject were considered as outliers (Junghofer et al., 2000) and they were discarded from the subsequent analysis.
- (2) *LORETA EEG-sources and single-trials source waveforms reconstruction*: All correct trials (ERPs for correct percept) from all three conditions were grand averaged and imported to BESA software version 5.3.7 (www.besa.de) to reconstruct EEG sources. We used the low resolution electromagnetic tomography (LORETA) (Pascual-Marqui et al., 1999, 1994), which is also referred as Laplacian weighted minimum norm, to reconstruct the EEG sources. LORETA is an extensively used source localization technique in EEG studies for both cortical and deep brain structures (Clemens et al., 2010; Herrmann et al., 2005; Jones and Bhattacharya, 2012; Thatcher et al., 2014; Velikova et al., 2010), including insula and hippocampus (Jones and Bhattacharya, 2012; Thatcher et al., 2014; Velikova et al., 2010). Depth weighting strategy implemented in LORETA overcomes the problem of surface-restricted localization methods, such as minimum norm estimates (MNE) (Michel et al., 2004; Painold et al., 2011; Pascual-Marqui et al., 1999). LORETA computes inverse solution at 2394 voxels with spatial resolutions of 7 mm in the Talairach Atlas (Pascual-Marqui et al., 1999, 1994). It is based on the assumption that the smoothest of all possible neural activity distributions is the most plausible one. This assumption is also supported by electrophysiology, where neighboring neuronal populations show highly correlated activity while EEG-LORETA results are the activity rendered by neighboring voxels with maximally similar activity (Haalman and Vaadia, 1997; Herrmann et al., 2005; Michel et al., 2004). Since functionally very distinct areas can be anatomically very close (e.g., the medial parts of the two hemispheres), LORETA can produce the results that include the two hemispheres (Fig. S1: activity in V1). Therefore, the results should be interpreted with caution and simultaneous EEG-fMRI recordings could be a good choice in such case. Locations of sources can be constrained to the cortical surface and their orientations perpendicular to the local cortical surface based on neurophysiological information that the sources of EEG are postsynaptic currents in cortical pyramidal cell, and that the direction of these currents is perpendicular to the cortical surface (Dale and Sereno, 1993; Hamalainen et al., 1993).

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