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Research article

Human sensory cortex structure and top-down controlling brain network determine individual differences in perceptual alternations

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HIGHLIGHTS

- GM volumen and density (GMV/GMD) of the left FFA were significantly positively correlated with the alterations in individual variability.
- Top-down modulations from high-level brain regions, such as the SPL and PCC to the left FFA, were positive.

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ABSTRACT

Bistable perception is a type of subjective perception that spontaneously alternates between two perceptual interpretations of an ambiguous sensory input. Past functional magnetic resonance imaging (fMRI) studies have examined the activation patterns underlying bistable perception, yet the variability between individuals in the alternations is not well understood. Therefore, voxel-based morphometry (VBM) was introduced in this study to correlate the GM of the sensory cortex with the alternations of Rubin face-vase illusion in a large group of young adults. We found that the GM volume and density (GMV/GMD) of the left fusiform face area (FFA) were significantly positively correlated with the alternations. Next, Granger causality analysis (GCA) was introduced to investigate the top-down modulation from high-level areas to the sensory cortex using resting-state fMRI data. Correlations between the perceptual alternations and Granger causalities showed that the top-down modulations from high-level brain regions, such as the superior parietal lobule (SPL) to the left FFA, were positive. Together, these findings indicated that the anatomical structure of the face-selective area may determine individual alternations of the Rubin face-vase illusion. This process may be controlled by a high-level cortex associated with attentional modulation, such as the SPL or Posterior Cingulate Cortex (PCC).

1. Introduction

In daily life, the subjective perceptual interpretations of sensory information are presumed to be processed by the human visual system [33]. Visual perception is a process involving the organization, identification, and interpretation of sensory information [28]. The human brain seeks to interpret what is occurring by relying on the current patterns of sensory input during the perceptual process, and must cope with the fact that any two-dimensional retinal images could be the projection of object configurations in the three-dimensional world [1]. There are occasions when human visual perceptions alternate between different interpretations of a stimulus [1]. That is, subjective perceptions may alternate spontaneously while sensory inputs are held constant [1]. Therefore, visual perception represents a process of disambiguation, which makes us perceive a stable world. and we are not completely aware of this process until it rises to our consciousness [30]. The different types of interpretations of sensory inputs are called multistable perception. For example, the Rubin face-vase illusion containing two possible interpretations (face vs. vase) is referred to as bistable perception [36]. Rubin face-vase illusion thus offers us a feasible way to investigate alternations in perceptual awareness [29,30].

Researches on bistable perception over the past few decades has significantly advanced our understandings [7,23,29,30,38]. On the one hand, some studies found that the sensory cortex contributed

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to multistable perception, which may underpin the spontaneous alternations in perception [1,47]. For example, the BOLD signals of the FFA were found to be greater when perceiving the face of the Rubin face-vase illusion [1]. In addition, functional MRI activities in the primary visual cortex were correlated with the fluctuating perceptions [21,24].

On the other hand, some studies indicated that top-down modulation from high-level regions such as the frontal/parietal areas determined the perceptual alternations [6,10,23,35,37,38]. For example, a fMRI study showed that activation in the bilateral inferior frontal cortex was greater when viewing an ambiguous motion stimulus than viewing an unambiguous stimulus [44]. Another transcranial magnetic stimulation (TMS) study found that transient disruption in the human SPL decelerated the alternations [25]. Moreover, neuropsychological studies showed that patients with frontal cortex lesions exhibited greater difficulty shifting from one perception to another than the patients with more posterior lesions and the controlled subjects [37].

In addition to the findings of sensory cortex and higher-order frontal/parietal regions, brain-imaging studies provided evidence for the involvement of both low-level and high-level regions in bistable perception [36,44,49,51]. For example, a fMRI study showed that the right inferior frontal cortex peaked earlier than extrastriate cortex during spontaneous perceptual alternations [44]. Therefore, both the primary visual cortex and higher frontal areas influenced the perceptual alternations in bistable perception. In addition, studies revealed that a progressively larger fraction of neurons showed percept-modulated firing rate changes at different levels of the visual hierarchy, from ~20% neurons reflected the in V1 to ~90% in the inferior temporal, which showed that both the primary visual cortex and temporal cortex reflected the perceived visual stimuli [27,30]. Additionally, studies have found that the neural circuits of frontal and extrastriate regions were related to alternations in perceptual stability [30,32].

Although people may see a similar ambiguous image, their perceptual alternations often vary due to the individual variability [3,5,46]. Many studies investigated the neural mechanisms underlying bistable perception, but there are little studies on the individual variability of the Rubin face-vase illusion [3,39].

The Rubin face-vase illusion provides a well-controlled experimental material to investigate the neural mechanisms of bistable perception [1,20,49]. Subjective perceptions alternate between two interpretations in a spontaneous manner [49]. The current study focused on the relationship between the individual differences in the alternations and potential neural mechanisms (structural basis and resting-state functional connectivity).

Functional MRI studies showed that enhanced activation in face-selective areas such as the FFA was observed in the face perceptual state but not in the other perceptual state [1,20]. Based on these studies, we mainly focused on the region of interest (ROI), such as the FFA, to conduct the investigation [26]. In addition, other important face-selective areas, such as the occipital face area (OFA) and the superior temporal sulcus (STS) [22], were included in our analysis [34].

Furthermore, Granger causality analysis was applied to the resting-state fMRI data to examine whether there were relationships between the perceptual alternations and the top-down modulation. The GCA of the multivariate autoregressive models was introduced to examine the resting-state time series [19], a method that is used to investigate whether one time series from the fMRI could correctly predict another time series based on multiple linear regression. GCA has been proven to be an effective generic statistical tool for analyzing the direct functional interactions for fMRI data [30,31].

According to previous studies [1,49], we hypothesized that both the sensory cortex and frontal/parietal regions could determine the individual alternations of the Rubin face-vase illusion. To some extent, this study may be the first to investigate the individual differences on the structural basis and the effective connectivity of Rubin face-vase illusion.

2. Materials and methods

2.1. Participants

Sixty-two (39 females) healthy graduate students from Southwest University participated in our experiment. They were paid to participate in this study. The age range was 18–24 (mean age = 20 years; SD = ±1.59 years). All subjects were right-handed and had normal or corrected-to-normal vision. The participants were screened to confirm their healthy development using a self-report questionnaire before the scan. Participants who had a history of psychiatric or neurological disorders were excluded. The Brain Imaging Center Institutional Review Board of Southwest China University approved this study.

2.2. Behavioral stimuli & performance

In this study, the behavioral design was only implemented outside of the scanner, and the experiment included the Rubin face-vase illusion (Fig. 1). The stimulus extended to $8.39^\circ \times 11.24^\circ$ of the visual angle and was presented at the center of a 17-inch screen with a spatial resolution of 1024×768 and a refresh rate of 60 Hz. Participants viewed the stimuli from a distance of 57 cm. Their head position was stabilized using a chin rest and a headrest.

Firstly, participants were instructed to complete a training trial. The experimental trial began with a fixation cross presented in the center of the screen. And then the Rubin face-vase figure lasted 6 min in each trial. Each participant completed 2 trials with a 3-min break between two trials. Participants pressed the 'Z' button when they perceived the face by using the left index finger. The button remained pressed until the perception changed from the face to the vase. Subsequently, the 'M' button was pressed using the right index finger while the vase was being perceived.

We calculated the alternations for each subject. For example, if a subject pressed the buttons 180 times in the 6 min' trial, the alternation rate should be 0.5 alternations/s (Hz).

2.3. The acquisition of the MRI data

For each participant, the high-resolution T1-weighted structural images were acquired by introducing a magnetization-prepared rapid gradient echo (MPRAGE) sequence (TR = 2000 ms; TE = 2.25 ms; TI = 900 ms; Slices = 176; Slice thickness = 1.0 mm; Flip angle = 9°; Resolution matrix = 256×256; Voxel size = $1 \times 1 \times 1\ mm^3$).

For the resting-state fMRI scans, the participants were instructed to keep their heads still, eyes closed and to not fall asleep for the duration of the scan, which would last 8 min. The images were acquired on a 3.0-T Siemens Trio MRI scanner (Siemens Medical, Erlangen, Germany). The covered whole brain was imaged using a T2-weighted gradient-echo planar imaging (EPI) device with the following primary parameters: repetition time (RT) = 2000 ms, echo time (TE) = 30 ms, slices = 30, flip angle = 90°, slice thickness = 3 mm, field of view (FOV) = 220 mm × 220 mm, slice gap = 1 mm, matrix = 64×64.

2.4. Voxel-based morphometry analysis

The MR images were processed using the SPM8 program (Wellcome Department of Cognitive Neurology, London, UK; www.fil.ion.ucl.ac.uk/spm) implemented in Matlab 7.8 (MathWorks Inc.,