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ATTENTIONAL CONTROL UNDERLIES THE PERCEPTUAL LOAD EFFECT: EVIDENCE FROM VOXEL-WISE DEGREE CENTRALITY AND RESTING-STATE FUNCTIONAL CONNECTIVITY

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Abstract—The fact that interference from peripheral distracting information can be reduced in high perceptual load tasks has been widely demonstrated in previous research. The modulation from the perceptual load is known as perceptual load effect (PLE). Previous functional magnetic resonance imaging (fMRI) studies on perceptual load have reported the brain areas implicated in attentional control. To date, the contribution of attentional control to PLE and the relationship between the organization of functional connectivity and PLE are still poorly understood. In the present study, we used resting-state fMRI to explore the association between the voxel-wise degree centrality (DC) and PLE in an individual differences design and further investigated the potential resting-state functional connectivity (RSFC) contributing to individual's PLE. DC-PLE correlation analysis revealed that PLE was positively associated with the right middle temporal visual area (MT)—one of dorsal attention network (DAN) nodes. Furthermore, the right MT functionally connected to the conventional DAN and the RSFCs between right MT and DAN nodes were also positively associated with individual difference in PLE. The results suggest an important role of attentional control in perceptual load tasks and provide novel insights into the understanding of the neural correlates underlying PLE. © 2017 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: perceptual load effect (PLE), voxel-wise degree centrality, functional connectivity, attentional control.

INTRODUCTION

Selective attention is the ability to allocate limited resources to valuable information while filtering out large amounts of task-irrelevant ones. A key question is how and when the irrelevant information is filtered out (Murphy et al., 2016). Early versus late selection views differ on this issue, creating a debate between proponents of each view for a long time, and one issue of the discussions is the locus of selective attention. The perceptual load theory provides a solution to this long-standing debate. Perceptual load theory posits that the extent to which distraction information can be critically perceived depends on the information load required by the current task (Lavie and Tsai, 1994; Lavie, 1995). According to this theory, perception is a system with limited capacity and can automatically process all stimuli until available resources are diminished. In the low perceptual load task, task-irrelevant distractors can be processed as it falls within the capacity limit (Lavie, 2005, 2010). In the high perceptual load task, all available resources are used by relevant stimuli, and there are no additional resources for processing task-irrelevant information (Lavie, 2005, 2010). The reduced interference effect from peripheral irrelevant stimuli in high perceptual load tasks reflects the modulation of perceptual load on irrelevant information perception. This modulation from the perceptual load can play a major role in perceptual load effect (PLE). In our previous study, we operationally defined PLE as the decreased interference effect from peripheral distractors when task load varied from low to high (Liu et al., 2015).

Behavioral studies with human subjects provided considerable evidences about the reduced interference effect induced by perceptual load (Lavie and Tsai, 1994; Lavie and Cox, 1997; Rees et al., 1997). Previous functional magnetic resonance imaging (fMRI) studies reported that the activation of brain regions processing distractors decreased when perceptual load level was high, but simultaneously the activation of brain regions underlying attentional control increased (Yi et al., 2004; Schwartz et al., 2005; Wei et al., 2013). The findings may imply the involvement of attentional control in PLE performance. However, studies paid little attention to the

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Abbreviations: ANOVA, analysis of variance; DAN, dorsal attention network; DC, degree centrality; DPABI, Data Processing & Analysis for Brain Imaging; FDR, false discovery rate; FEF, frontal eye field; fMRI, functional magnetic resonance imaging; IPS, intraparietal sulcus; MT, middle temporal visual area; PLE, perceptual load effect; ROI, regions of interest; RSFC, resting-state functional connectivity; RT, reaction times; SPL, superior parietal lobule.

role of attentional control in perceptual load task. Previous studies about selective attention highlighted the important role of attentional control during tasks performance (Bavelier et al., 2012), which was mainly reflected in the increased attentional control when the task became more difficult (Kahneman, 1973). This evidence suggested that the selective attention in high perceptual load tasks could elicit stronger attentional control compared with low-load tasks. Accordingly, other than the reduced processing resources allocated to peripheral distractors, attentional control may also be associated with a reduced interference in high perceptual load tasks.

In studying the relationship between attentional control and perceptual load, Torralbo and Beck (2008) have proposed that the neglect of distracting information resulted from the need to actively resolve competitive interactions in visual cortex, accompanied by a greater need for top-down biasing to identify the target. Studies from fMRI and single-cell recordings revealed that when stimuli were simultaneously presented in the same visual field, their representations in the object recognition pathway interacted in a mutually competitive manner (Moran and Desimone, 1985; Connor et al., 1997; Kastner et al., 1998; Beck and Kastner, 2005). In a high-load situation, the greater competition impairs the representation of the target and a strong top-down bias is required to identify the target. Because of this strong top-down bias, interference from distractors is reduced (Scalf et al., 2013). Thus, they stated that top-down bias in selective attention was at the heart of the neural mechanisms underlying PLE (Torralbo and Beck, 2008; Scalf et al., 2013).

Based on the results from these studies, we hypothesize that the reduction of distraction effect in high perceptual load depends on available perceptual capacity as well as on attentional control. In the present study, we conducted a data-driven analysis and characterized neural correlates of PLE with network properties of the resting brain using the voxel-wise degree centrality (DC) measures of resting-state fMRI data and resting-state functional connectivity (RSFC). Voxel-wise DC is a graph theory-based measurement at the voxel level, and it represents the number of direct connections for a given voxel with the rest of the whole-brain voxel (Buckner et al., 2009; Lohmann et al., 2010; Zuo et al., 2012). The index of voxel-wise DC emphasizes the impact and significance of a network at voxel level and reflects the ability of brain network hubs in the network information communication. Previous research has confirmed that voxel-wise DC has a high sensitivity, specificity, and test–retest reliability (Zuo and Xing, 2014) and it is increasingly used in exploring the neural correlates of psychiatric disorders (Di Martino et al., 2013; Li et al., 2016) and cognitive activity (Markett et al., 2017). The data we used in the present study partly come from our previous study (Liu et al., 2015). However, the present study focuses on the PLE-related voxel-wise DC, which can provide novel insights into the PLE in different ways. We hypothesize that PLE could be associated with DC in regions that supported attentional control because per-

ceptual load may affect task-irrelevant stimuli processing via attentional control.

EXPERIMENTAL PROCEDURES

Participants

Ninety-six students (30 males, 66 females, 18–25 years) with normal or corrected vision from Southwest University in China voluntarily participated in the current study. No participant declared any history of neurological or psychiatric illness. Two participant's data were excluded from further analysis because of low accuracy, and four participant's data that showed excessive head motion during data pre-processing were also excluded (> 2 mm or 2°). This study was approved by the Southwest University Human Ethics Committee for the Brain Mapping Research. The participants voluntarily participated in the study after being fully informed about the nature and procedure of the experiment. Before participating, each participant was advised of the importance of protecting his or her privacy. They received monetary compensation for participation in the study.

Stimuli and procedure

Fig. 1 depicts the sequence of events in a trial. Each trial started with the presentation of a black fixation cross in the center of a gray screen for 600 ms. Then, the search display was presented for 200 ms on the central of a gray background. The search display in each trial consisted of a letter circle, a peripheral salient distractor letter presented to the left or right side of the circle; the search target in letter circle was randomly displayed as either X or N (Lavie and Cox, 1997). Subjects were instructed to ignore the distractor during target search and to respond as quickly and accurately as possible by pressing “1” key on the keyboard for “X” and “2” key for “N” (or “1” key for “N”, “2” key for “X” for the other half participants). In the high-load condition, non-target letters H, M, K, Z, and W randomly displayed in the circle (Lavie and Cox, 1997), which also varied from trial to trial. In the low-load condition, only the target was presented with small black points placed at a non-target position. The peripheral distractor letter could be incongruent with the target response (the alternative target letter) or neutral (either “T” or “L”). After the search display, there was a blank gray screen for the response, which lasted for 1800 ms, followed by an additional 500–800-ms gray blank screen appeared as the inter-trial interval. Each participant completed four blocks of pseudo-random experiment trials, with data in the first block removed as practice trials. The remaining 288 trials in three experiment blocks were used for data analysis. With regard to data collection, we first collected the resting-state fMRI data before we started the behavior experiment. After the completion of resting-state fMRI scanning, the participants were instructed to complete the perceptual load tasks in a different room, including the practice block.

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