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The effects of changes in object location on object identity detection: A simultaneous EEG-fMRI study

Ping Yang[a], Chenggui Fan[a], Min Wang[a], Noa Fogelson[b], Ling Li[a,*]

[a] Key Laboratory for NeuroInformation of Ministry of Education, High-Field Magnetic Resonance Brain Imaging Key Laboratory of Sichuan Province, Center for Information in Medicine, School of Life Science and Technology, University of Electronic Science and Technology of China, Chengdu 610054, China

[b] EEG and Cognition Laboratory, University of A Coruña, Spain

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ABSTRACT

Object identity and location are bound together to form a unique integration that is maintained and processed in visual working memory (VWM). Changes in task-irrelevant object location have been shown to impair the retrieval of memorial representations and the detection of object identity changes. However, the neural correlates of this cognitive process remain largely unknown. In the present study, we aim to investigate the underlying brain activation during object color change detection and the modulatory effects of changes in object location and VWM load. To this end we used simultaneous electroencephalography (EEG) and functional magnetic resonance imaging (fMRI) recordings, which can reveal the neural activity with both high temporal and high spatial resolution. Subjects responded faster and with greater accuracy in the repeated compared to the changed object location condition, when a higher VWM load was utilized. These results support the spatial congruency advantage theory and suggest that it is more pronounced with higher VWM load. Furthermore, the spatial congruency effect was associated with larger posterior N1 activity, greater activation of the right inferior frontal gyrus (IFG) and less suppression of the right supramarginal gyrus (SMG), when object location was repeated compared to when it was changed. The ERP-fMRI integrative analysis demonstrated that the object location discrimination-related N1 component is generated in the right SMG.

Introduction

Visual working memory (VWM) is a limited-capacity cognitive system for temporarily maintaining and manipulating external information (e.g. object information used in an object VWM task) to support human cognition and behavior (Baddeley, 2003). In an object VWM task, object location plays a crucial role throughout the encoding, maintenance and retrieval phases of VWM, since it indicates the spatial coordinates of the object (for memory or retrieval) and the focus of attention allocation (Pertzov and Husain, 2014). A number of studies have reported that the change of task-irrelevant object location in a test array, relative to a memory array, impairs the detection of changes during the identification of a task-relevant object (Hollingworth, 2007; Hollingworth and Rasmussen, 2010; Jiang et al., 2000; Jiang and Makovski, 1992; Olson and Marshuetz, 2005; Tsal and Lamy, 2000). This suggests that the object location, even when it is task-irrelevant, is stored automatically and has a role in VWM change detection processes. This is consistent with object-location binding theory, proposed by Kahneman et al. (1992), which asserts that object features are bound to their location to form an object file that is maintained and processed in VWM. Others have suggested that multiple cognitive processes are involved in the detection of object identity change, so that subjects may first establish the spatial correspondences between an initial memory array and a current test array, by comparing the spatial configuration of the displays, and then retrieve the object identity from the corresponding location (Hyun et al., 2009). Thus, when one object changes its location in the test array, the spatial index of that changing object needs to be updated to form a new correspondence between the memory and the test array, a procedure which is known as resolving the "correspondence problem" (Hollingworth and Rasmussen, 2010; Levillain and Flombaum, 2012). Conversely, when the memory array and the test array share the same location, subjects respond faster and more accurately, a process known as the "spatial congruency advantage" (Boduroglu et al., 2009; Hollingworth, 2007; Hollingworth and Rasmussen, 2010). In addition, VWM and attention resources have severe capacity limitations, so that the spatial correspondence problem is enhanced and further impairs the subsequent color and shape change detection with increasing VWM load (Jiang et al., 2000). However, it remains unclear whether the spatial correspondence problem exists when a low VWM (perceptual) load is utilized.

* Corresponding author.
E-mail address: liling@uestc.edu.cn (L. Li).

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Several behavioral studies have investigated the effects of object location changes on object identity change detection (Hollingworth, 2007; Hollingworth and Rasmussen, 2010; Jiang et al., 2000; Olson and Marshuetz, 2005; Tsal and Lamy, 2000). However, none of these investigated the underlying neural correlates of this cognitive process. Thus, in the present study, we combined event-related potentials (ERPs) that have a high temporal resolution, with functional magnetic resonance imaging (fMRI) that has a high spatial resolution, in order to investigate the underlying brain activation during object color change detection and how this is modulated by the manipulation of object location repeat/change conditions. In addition, we examined the effect of VWM load during the object color change detection period. The attention and VWM systems seem to recruit common neural mechanisms (Ikkai and Curtis, 2011; Leung et al., 2007) and can hold a limited number of objects (Vogel and Machizawa, 2004), thus, creating a competition for common resources (Fu et al., 2008; Lavie et al., 2004; Yang et al., 2015). Consequently, we hypothesized that changes in object location would induce an impairment in the detection of object color changes, and that increasing VWM load would further exacerbate this. On the other hand we hypothesized that when low VWM load is utilized, the interference of the location change would decline. We employed a change detection paradigm, in which subjects were asked to maintain two or four objects for 6 s and then to indicate whether the test array matches or mismatches the memory array of object colors, regardless of the location of the object. The location repeat condition refers to the condition in which the test array shares the same spatial location as the memory array, whereas in the location change condition the original location of the objects is changed in the test array.

We focused on the brain regions that are known to be involved in spatial attention and the processing of object location. The supramarginal gyrus/ inferior parietal lobule (SMG/IPL) (BA 40) has been proposed to subserve bottom-up attentional processes during perception (Corbetta and Shulman, 2002) and memory (Cabeza et al., 2011; Schenkluhn et al., 2008) of multiple objects. Activity in this region has also been shown to be associated with the retrieval of memorial representations (Cabeza et al., 2012, 2011), especially during the retrieval of object locations versus object identities (Moscovitch et al., 1995; Passaro et al., 2013). In addition, SMG lesions result in deficits of spatial VWM (Malhotra et al., 2005; Pisella et al., 2004) and in deficits of binding object identity to location (Robertson, 2003). TMS studies showed that stimulation of the SMG selectively facilitated or impaired spatial attention rather than feature-based attention (Heuer et al., 2016; Schenkluhn et al., 2008). Thus, we hypothesized that when the object location is changed in the test array, more spatial attention is recruited compared with the repeat location condition, thus leading to an increase in SMG/IPL activation. With regards to the prefrontal cortex (PFC), there is ample evidence to suggest that the DLPFC is responsible for monitoring and integrating diverse information, whereas the VLPFC is responsible for maintaining and retrieving memorial representations (Grubert and Eimer, 2015; Prabhakaran et al., 2000). The inferior frontal gyrus (IFG) has been shown to be sensitive to the retrieval of the spatial location of a stimulus (Kochan et al., 2011) and findings show that this region is more responsive to stimuli that match compared to those that do not match a sample stimuli (Leung et al., 2005; Mandzia et al., 2004). Thus, we predicted that the IFG would be more active in the location repeat compared to the location change condition.

ERPs are suited to investigate the time course and the electrophysiological correlates associated with the modulatory effect of task-irrelevant spatial location changes on the detection of object color changes. The posterior N1 component, which peaks 150–200 ms after the onset of the VWM test array, is proposed to reflect sensory perceptual processing and attentional allocation (Daffner et al., 2013; Kumar et al., 2009), as well as discriminative processes between the test array and the memorial representations (Hopf et al., 2002; Vogel and Luck, 2000). In a set of simple and choice reaction time tasks, Vogel and Luck (2000) found that N1 was sensitive to visual discrimination demands for both object color and form, and that the N1 amplitude was independent of the number of objects in the reaction stimulus array. Other studies, using the delayed match-to-sample paradigm, have shown that the N1 is greater following probes that matched the memory set compared to those that did not match (Frings and Groh-Bordin, 2007; Henson et al., 2004; Ji et al., 1998; Soldan et al., 2006). Thus, we predicted that the *location repeat* condition would elicit greater N1 activity compared to the *location change* condition. Furthermore, the N2-posterior-contralateral (N2pc), which is based on a "contralateral – ipsilateral" difference at PO7/PO8 electrode sites, 200–300 ms after the test array onset (Eimer and Mazza, 2005; Kumar et al., 2009; Li et al., 2013; Mccollough et al., 2007) was also evaluated in the present study. N2pc is proposed to reflect spatial attentional allocation, showing greater activity at contralateral compared to ipsilateral posterior sites with respect to the hemi-field of the stimulus (Eimer, 1996). We predicted that the high VWM load condition would attract more spatial attentional allocation, resulting in a greater N2pc compared to that in the low VWM load condition (Drew and Vogel, 2008; Störmer et al., 2013).

The subsequent P300 ERP component, a positive wave observed at central-parietal electrode sites, approximately 300–600 ms after the test array onset, is thought to reflect the demands of 'central resources' (Bledowski et al., 2006; Kok, 2001; Morgan et al., 2008). Several studies have reported that the P300 amplitude decreases with increasing VWM load during the retrieval period, suggesting that high VWM load requires more processing resources (e.g. information retrieval, comparison between probe perception and memorial representations), and thus less 'central resources' remain (e.g. Bledowski et al., 2006; Pinal et al., 2014). Accordingly, we hypothesized that in the current study the P300 amplitude would also decrease with increasing VWM load.

For the purpose of integrating the ERP components with the fMRI activations, (1) we conducted a source localization analysis to identify the brain regions generating the ERP components, and expected the sources of the ERP components to overlap with the regions from the fMRI activation maps; (2) we used the task-related fMRI clusters as source regions to obtain the source waveforms and the corresponding scalp voltage projection, in order to investigate the contribution of these regions to the ERP components (Bledowski et al., 2006; Cottereau et al., 2014; Youssofzadeh et al., 2015).

Materials and methods

Subjects

Eighteen right-handed subjects (9 females), age 19–27 (mean age = 21.9 years, standard deviation = 2 years), participated in the present study for monetary compensation. Subjects were recruited at the University of Electronic Science and Technology of China. All the subjects had no history of neurological problems and had normal color vision. An informed consent was signed by each subject before the experiment. The study was approved by the local committee for the Protection of Human Subjects for the University of Electronic Science and Technology of China. The methods were carried out in accordance with the approved guidelines and all experiments conformed to the declaration of Helsinki.

Stimuli

The stimuli were presented using the E-prime software (Psychology Software Tools Inc., Pittsburgh, USA; http: //www.pstnet.com/eprime.cfm), and were projected via a LCD projector onto a flat panel screen placed in the front of the MR scanner. Subjects viewed the screen through a mirror attached to the head coil with a distance of approximately 57 cm. The screen size was 28° × 22° within the field