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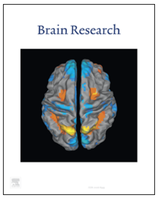

Research report

Working memory load influences perceptual ambiguity by competing for fronto-parietal attentional resources

Monika Intaitė*[1], João Valente Duarte[1], Miguel Castelo-Branco

Visual Neuroscience Laboratory – IBILI, Faculty of Medicine, University of Coimbra, Coimbra, Portugal

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ABSTRACT

A visual stimulus is defined as ambiguous when observers perceive it as having at least two distinct and spontaneously alternating interpretations. Neuroimaging studies suggest an involvement of a right fronto-parietal network regulating the balance between stable percepts and the triggering of alternative interpretations. As spontaneous perceptual reversals may occur even in the absence of attention to these stimuli, we investigated neural activity patterns in response to perceptual changes of ambiguous Necker cube under different amounts of working memory load using a dual-task design. We hypothesized that the same regions that process working memory load are involved in perceptual switching and confirmed the prediction that perceptual reversals led to fMRI responses that linearly depended on load. Accordingly, posterior Superior Parietal Lobule, anterior Prefrontal and Dorsolateral Prefrontal cortices exhibited differential BOLD signal changes in response to perceptual reversals under working memory load. Our results also suggest that the posterior Superior Parietal Lobule may be directly involved in the emergence of perceptual reversals, given that it specifically reflects both perceptual versus real changes and load levels. The anterior Prefrontal and Dorsolateral Prefrontal cortices, showing a significant interaction between reversal levels and load, might subserve a modulatory role in such reversals, in a mirror symmetric way: in the former activation is suppressed by the highest loads, and in the latter deactivation is reduced by highest loads, suggesting a more direct role of the aPFC in reversal generation.

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1. Introduction

The human visual system seems unfit to tolerate ambiguity. Vision is designed to guide behavior and a behaving organism cannot afford to be halted by indecision. However, some stimuli may be prone to perceptual changes that occur during visual processing. On such occasions, rather than choosing a single interpretation, perception interchanges between two (or more) valid alternatives. Ambiguous figures are a good example of such stimuli: they are physically constant, yet our brain perceives them as changing. The origin of perceptual reversals is still highly under debate regarding whether low or high level visual mechanisms play a major role in determining perceptual decisions (for a review see: Long and Toppino (2004)). Some studies suggest that bottom-up mechanisms are the most important for the perception of ambiguous figures (Toppino and Long, 1987): the neural channels determining one of the available percepts, satiate and thus perceptual interpretation changes to the alternative one. The cognitive theories suggest that perceptual decisions might be induced by feedback from higher to lower levels of processing, for example, by activation of a high-level "exploratory" mechanism that directs selective attention in a way that causes a recurrent "renewal" of the type of representation in low-level perceptual systems (e.g., Leopold and Logothetis, 1999). A growing number of studies (Hochberg and Peterson, 1987; Intaitė et al., 2013, 2014; Kornmeier and Bach, 2012; Kornmeier et al., 2009; Long et al., 1983; Long and Toppino, 2004) indicate that both perceptual processes play definable roles in the perception of ambiguity.

Selective attention orients the focus of conscious awareness toward relevant stimuli. Working memory (WM) maintains an active and brief representation of just obtained information to be used for subsequent processing or recall, while selective attention filters that information thus controlling what is encoded and maintained in WM. Studies using functional magnetic resonance imaging (fMRI) reveal an overlap between attention and WM networks over visual, parietal and frontal areas (Gazzaley and Nobre, 2012; Gazzaley et al., 2007; Mayer et al., 2007), supporting the view that these cognitive functions share neural resources and are both governed by the fronto-parietal attention network (Corbetta et al., 2002; Zanto et al., 2011).

The brain regions activated during perceptual changes seem as well to overlap with the fronto-parietal attention network (Knapen

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* Corresponding author.
E-mail address: mintaite@fmed.uc.pt (M. Intaitė).
[1] Both authors contributed equally to this work.

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et al., 2011; Lumer et al., 1998; Lumer and Rees, 1999; Sterzer and Kleinschmidt, 2007; Weilnhammer et al., 2013). Our study was motivated to help unravel the nature of such overlap. Prefrontal and dorsolateral prefrontal cortices (as parts of the fronto-parietal attention network) may control the updating of ambiguous stimulus representations in the extrastriate visual areas as suggested by transient signal increases in prefrontal cortex during perceptual reversals (Kleinschmidt et al., 1998; Lumer et al., 1998; Lumer and Rees, 1999). Sterzer and Rees (2008) reported activations in visual cortex alongside with activity in prefrontal and parietal regions for percept-specific signals in response to binocular rivalry stimuli and discussed comparable BOLD signal changes over visual and fronto-parietal regions in response to voluntary engagement of facial WM (Courtney et al., 1997; Haxby et al., 2000; Sala et al., 2003). The authors suggested that perceptual durations might be influenced by higher-order mechanisms that share a common anatomical substrate with WM. The Superior Parietal Lobule (SPL) might also be differentially involved in perception of reversals: stimulating the right anterior or right posterior SPL, respectively increases or decreases the number of perceived reversals (Baker et al., 2015; Kanai et al., 2011). Right SPL seems to be also activated when participants perform WM manipulation of stimulus content (Champod and Petrides, 2007). However, the exact role of fronto-parietal regions in shaping perceptual decisions remains to be clarified. Sterzer et al. (2009) hypothesize that fronto-parietal activations may participate in inferential processes that are helping to achieve perceptual stability and suggest that perceptual ambiguity might result from continuous reciprocations between low-level and high-level brain regions.

The aim of the present study was to investigate WM dependent brain mechanisms that induce perceptual bistability. We set to investigate how neural activity in response to perceptual decisions is modulated by concurrent recruitment of attentional resources in fronto-parietal regions that are hypothesized to subserve a dual role in such processes. More explicitly, the spatial locus of the possible effects related to concurrent processing was examined with fMRI. We chose a WM load (hereafter WML) task as a secondary task since it depletes the available attentional resources (Kumar et al., 2009; Singhal and Fowler, 2004). When WML, or a similar secondary task employing attentional resources (e.g., motion-detection, mental arithmetic), is used concurrently with the reversal task, the participants consequently perceive fewer reversals of a given ambiguous image (Intaitė et al., 2014; Paffen et al., 2006; Reisberg and O'Shaughnessy, 1984; Wallace and Priebe, 1985; Wallace, 1986; Zhang et al., 2011). In our study, participants were required to detect perceptual reversals of an ambiguous Necker cube while performing a concurrent task with four levels of WML. In order to manipulate the amount of available WM resources, the WML stimuli (letter strings) consisted of either no letters (sham-load), five, six or seven consonants (Fig. 1). The concurrent task involved memorization of the letter strings, which were followed by an ambiguous Necker cube presentation. Finally, to control for possible differences in perception of the perceptual versus real change of the Necker cube under WML and to verify that performing a WML task does not interfere with the capability to report perceptual reversals, we used an extra condition in which two unambiguous images, each representing one of the two different percepts of the Necker cube, were presented subsequently while the participants had to report the real changes while completing the WML task with six consonants. We theorized that if WM resources are actively involved in the construction of the available percepts of the ambiguous stimulus, a concurrent WML will decrease the reversal rates and modulate the efficiency of the neural processes involved in reversals. Due to enhanced usage of attentional resources, we hypothesized that BOLD signal changes in response to perceptual decisions under sham-load would be stronger than the signal variation obtained under WML conditions over anterior Prefrontal Cortex (aPFC), Dorsolateral Prefrontal Cortex (DLPFC) and SPL.

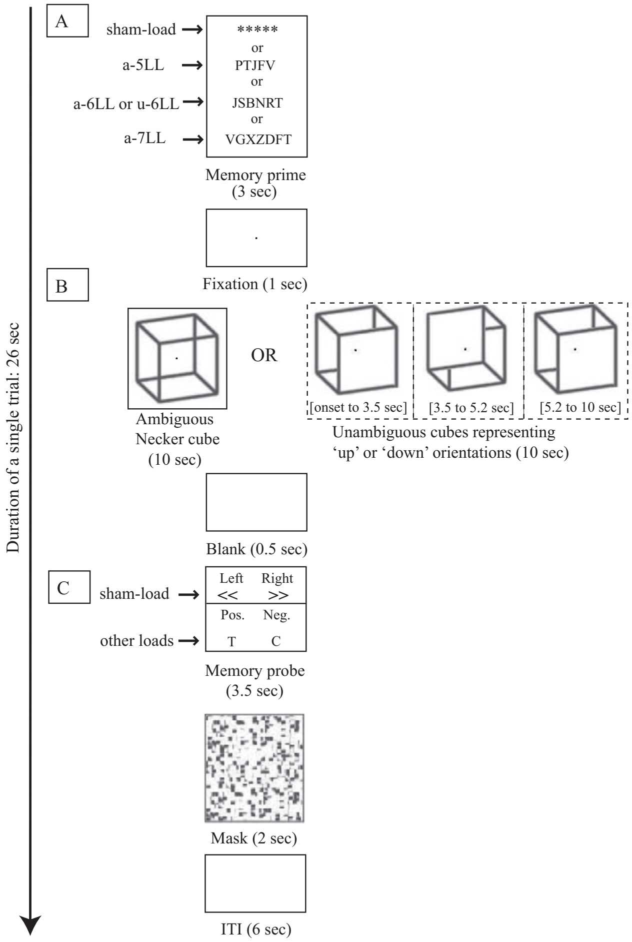

Fig. 1. Graphical representation of the stimuli and experimental protocol. (A) An illustration of the experimental trials in all conditions: schematic representation of the memory primes in the sham-load, ambiguous-five-letter-load (a-5LL), ambiguous-six-letter-load (a-6LL), unambiguous-six-letter-load (u-6LL), and ambiguous-seven-letter-load (a-7LL) conditions. (B) In each condition with perceptual changes, the memory prime is followed by a standard Necker cube. In the control condition (u-6LL) the prime is followed by a sequence of unambiguous cubes presented interchangeably during 10 s trials. (C) Schematic representation of the memory probes in all conditions.

2. Results

2.1. Working memory task performance

The memory probe response accuracy decreased with higher working memory load task, as expected ($F(3,39)=10.20$, *p-value* < 0.0001, $\eta p^2=0.44$) (Fig. 2A). The accuracy in the sham-load condition was higher than those acquired in response to all other conditions (all *p-values* < 0.01, Fisher's LSD corrected).

Probe response times increased with working memory load ($F(3,39)=56.42$, *p-value* < 0.0001, $\eta p^2=0.81$) (Fig. 2B). The increase was linear with augmentation in working memory load ($F(1,13)=149.47$, *p-value* < 0.0001, $\eta p^2=0.92$). The probe response times in the sham-load condition were shorter than those obtained in all other conditions (all *p-values* < 0.0001, Fisher's LSD corrected) and the probe response times to a-5LL were shorter than those in response to a-7LL (*p-value* < 0.05, Fisher's LSD corrected).

2.2. Reversal task performance

2.2.1. Pre-ranked reversal rate

The amount of perceived reversals decreased as working memory load increased ($F(3,39)=3.48$, *p-value* < 0.03, $\eta p^2=0.21$)

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