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Functional interplay between stimulus-oriented and stimulus-independent attending during a prospective memory task

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ABSTRACT

Recent studies have suggested that medial (medBA10) and lateral (latBA10) portions of the Brodmann area 10 subserve respectively stimulus-oriented (SO) and stimulus-independent (SI) attending during prospective memory (PM) tasks. We investigated this dissociation by manipulating the saliency (SO) and the memory load (SI) of PM cues. Sixteen healthy subjects participated to a functional imaging protocol with a $2 \times 2 \times 2$ experimental design, including the factors: task (ongoing target vs. PM cue), Saliency (high vs. low; with targets/cues either embedded or standing out from distracters), and memory load (high vs. low; with 1 or 4 possible PM targets). We localized the medBA10 and latBA10 by means of a localizer task. In medBA10 we found a significant main effects of high Saliency and low memory load; whereas in the left latBA10, we found a significant task $\times$ load interaction, with maximal activation for PM cues presented in the high load condition. These results are in agreement with the gateway hypothesis: during a PM task medBA10 biases attention toward external salient stimuli, SO attending, while latBA10 biases attention toward internal mnemonic representations, SI attending. Additional whole-brain analyses highlighted activation of other areas besides BA10, consistent with recent proposals that emphasise the role of distributed networks during PM performance.

1. Introduction

Complex situations of everyday life require a continuous alternation between so-called stimulus-independent (SI) and stimulus-oriented (SO) attending (Burgess, Dumontheil, & Gilbert, 2007; Burgess, Simons, Dumontheil, & Gilbert, 2005). Attending refers to the allocation of processing resources for the access to central representations in order to execute cognitive tasks. In particular, SO attending enhances our ability to notice changes in the environment when our attention is oriented toward external stimuli experienced through the senses. SI attending is when attention is directed toward self-generated thoughts. The interplay between SO and SI attending is commonplace in multitasking situations, i.e. when a subject performs two or more dovetailed tasks but, due to cognitive constraints, only one task can be performed at any one time (Burgess, Veitch, de Lacy Costello, & Shallice, 2000). PM is a particular condition of multitasking that refers to cognitive processes that underlie the realization of intended actions in the future. In a typical experimental PM event-based paradigm, during an initial encoding phase, an action is linked to a cue that triggers the realization of the intended action (i.e. event-based PM task; Einstein & McDaniel, 1990). The delay between the encoding and the cue presentation should be quite long and filled with a continuous attention-demanding activity called the ongoing (ONG) task that is meant to prevent a continuous rehearsal of the intention (see Burgess, Scott, & Frith, 2003 for key features of a PM task). This particularly fits with ecological situations, whereas experimental paradigms usually require more multitasking abilities because delays are usually shorter and the frequency of PM cues higher. The PM task is formed by distinct components that seems to be mediated by different brain substrates (see West, 2011): the encoding of delayed intentions, the cue identification and the consequent intention retrieval (Einstein, Holland, McDaniel, & Guynn, 1992). These last two components rely on different processes (Cohen, West, & Craik, 2001): the cue identification is influenced by stimulus-driven processes such as saliency or distinctiveness; the intention retrieval is influenced by conceptually-driven processes (Cohen et al., 2001; Mäntylä, 1996), such as the strength of the association between the PM cue and the intention (Cohen et al., 2001; Cohen, Dixon, Lindsay, & Masson, 2003). Thus, it can be postulated that cue identification involves SO

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attending more than SI attending, whereas intention retrieval involves SI attending more than SO attending (Simons, Scholvinck, Gilbert, Frith, & Burgess, 2006). Indeed, during an event-based PM task, attention is continuously biased between SO attending for the cue detection and SI attending for the maintenance and the access to the characteristics of the intended actions.

SO and SI attending are thought to be neuro-anatomically as well as behaviourally segregated. Neuropsychological (Burgess, Alderman, Volle, Benoit, & Gilbert, 2009; Burgess et al., 2000; Shallice & Burgess, 1991), neuroimaging (Benoit, Gilbert, Frith, & Burgess, 2012; Burgess, Quayle, & Frith, 2001; Burgess et al., 2003; den Ouden, Frith, Frith, & Blakemore, 2005; Gilbert, Gollwitzer, Cohen, Burgess, & Oettingen, 2009; Gilbert, 2011; Hashimoto, Umeda, & Kojima, 2011; Haynes et al., 2007; Okuda et al., 1998, 2007; Poppenk, Moscovitch, McIntosh, Ozcelik, & Craik, 2010; Reynolds, West, & Braver, 2009; Simons et al., 2006) and TMS (Costa et al., 2011, 2013) studies reported a consistent relationship between brain activity in Brodmann area 10 (BA10) and PM task performance. In particular, a functional dissociation in BA10 has been proposed within the framework of the gateway hypothesis (Burgess et al., 2005, 2007). In this view, the lateral portion (latBA10) is mainly involved in SI attending, whereas, the medial BA10 (medBA10) mediates SO attending (Benoit et al., 2012; Simons et al., 2006). According with this view, BA10 acts as a gateway that biases attention between SO and SI attending.

Only two previous functional magnetic resonance imaging (fMRI) studies tested this hypothesis during a PM task (Benoit et al., 2012; Simons et al., 2006). Simons et al. (2006) increased SO attending by presenting PM cues perceptually embedded in the ONG task, and SI attending by increasing the number of actions constituting the delayed intention. During both PM conditions, they showed increased brain activity in latBA10 and decreased brain activity in medBA10 (in agreement with previous neuroimaging studies, cf. Burgess et al., 2003; Okuda et al., 2007). Consistent with the gateway hypothesis, this effect was larger when the intention retrieval demands (i.e. SI attending) were increased. Similarly, Benoit et al. (2012) explored the relationship between the hemodynamic changes in BA10 during PM performance and differences between SI and SO attending conditions. In an fMRI factorial design, they modulated SO-SI attending by asking subjects to execute a task based on visually presented vs. internally generated information (i.e. participants had to picture the visual stimulus in their mind). This was done during an ongoing task alone (ONG) or during a task that also required carrying out a delayed intention (i.e. the PM condition). This study showed that medBA10 was jointly associated with ONG task activity and SO attending. Conversely, left latBA10 showed an effect of PM task, an interaction between PM task and stimulus phase and an effect of switch between SO and SI. These findings are consistent with the proposal that the lateral portion of BA10 is recruited to bias attention toward internal representations.

Nonetheless, these previous studies did not directly address the relative contribution of SO and SI attending specifically on the PM cue identification, which is a central tenet of the gateway hypothesis. Here, to bias attention toward SI attending, we increased the prospective memory Load (i.e. the number of PM cues), whereas to bias attention toward SO attending, we increased the perceptual Saliency of PM cues. Accordingly, we were able to test the gateway hypothesis directly on mechanisms of PM cue identification.

We used an event based PM paradigm that orthogonally crossed three factors in a $2 \times 2 \times 2$ design: Task, Saliency and memory Load. Each trial of the ongoing task (ONG) consisted in the presentation of a single letter (first display), followed by a string of 4 letters (second display). The subject was asked to report whether the letter presented in the first display was then shown on the left or the right side of the string in the second display (see Fig. 1). While doing this, the participants also maintained the intention to press a different button, whenever the string in the second display included a specific, pre-defined letter: i.e. the PM cue. The SO attending manipulation consisted of incrementing of the saliency of the ONG targets or the PM cues. We presented PM cues that were either embedded (low saliency) or stood out (high saliency) from distracters. Salient stimuli are distinctive sensory inputs that attract exogenous attention (stimulus-driven attention) (see Corbetta, Patel, & Shulman, 2008). Accordingly, we increased the perceptual distinctiveness of the PM cue and ONG target (Cohen et al., 2003). The SI attending manipulation consisted in changing the number of possible PM cues that the subject had to maintain and respond to (i.e. 1 or 4, pre-defined letters). The high-load condition, with 4 possible PM cues, will bias attention toward internal representations.

Based on the results of previous studies (Benoit et al., 2012; Simons et al., 2006), we expected that medBA10 would show enhanced activity for salient stimuli (SO attending, high saliency), in particular when the salient stimuli were PM cues. We expected that latBA10 would activate upon presentation of the PM cues and, more so, when their number was increased (SI attending, high memory load). We used a functional localizer based on previous literature (Burgess et al., 2003) to independently identify medBA10 and latBA10. In these two regions of interest we tested the main effects of SO and SI attending and their interactions with the PM task. In addition, because recent evidence indicated that medBA10 and latBA10 co-activate with distinct sets of other brain regions (see Gilbert, Gonen-Yaacovi, Benoit, Volle, & Burgess, 2010), here we also tested the effect of SI and SO at the whole-brain level. In particular, together with latBA10, we expected possible influence of SI in the anterior cingulate, insula and fronto-parietal cortex; whereas, together with medBA10, we expected SO to affect also activity in the posterior cingulate and temporal lobe (cf. Gilbert et al., 2010).

2. Material and methods

2.1. Participants

Sixteen right-handed (Edinburgh Inventory; Oldfield, 1971) volunteers (nine females and seven males, aged 18–44 years) with no history of neurological, psychiatric, or visual symptoms participated in the fMRI study. None of the participants was taking vasoactive or psychotropic medication. Written informed consent was obtained from each participant, and the experiment protocol was developed in accordance with the Declaration of Helsinki and was approved by the independent Ethics Committee of the Fondazione Santa Lucia (Scientific Institute for Research, Hospitalisation and Health Care).

2.2. Materials

The ongoing task stimuli and the prospective memory cues consisted of the sixteen uppercase consonants of the Italian alphabet (B C D F G H L M N P Q R S T V Z) written in white on a dark background. The localizer task also included four geometrical shapes: a circle, a square, a triangle and a rhombus. A script using Cogent software (Cogent 2000, Functional Imaging Laboratory, Wellcome Department of Imaging Neuroscience, UCL, London) on MATLAB environment (v 7.1, The MathWorks, Natick, MA, USA) controlled the stimuli presentation and the recording of responses. Participants laid into the scanner in a dimly-lit environment and viewed the stimuli presented by a DLP projector (60 Hz refresh rate) on a screen behind the head coil via a mirror system. Participants responded by pressing three buttons on a response pad using the right hand. Stimuli (letters and shapes) and the central fixation cross were approximately $1^{\circ} \times 1^{\circ}$ visual angle.

2.3. Task design

In the main experiment, we used a modified version of Cohen and collaborators' paradigm (Cohen et al., 2003) in order to minimize the access to internal representation and thus the SI attending. In the original visual search task, subjects were asked to identify the serial position of a target letter in a serially presented six letters string. Subjects could make their response after all letters were presented.