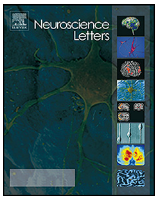
Neuroscience Letters xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Neuroscience Letters

journal homepage: www.elsevier.com/locate/neulet



Research article

The role of the frontopolar cortex in manipulation of integrated information in working memory

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HIGHLIGHTS

- Frontopolar cortex was involved in integrating representations in working memory.
- Task complexity did not affect the level of the frontopolar cortex activation.
- In contrast, dorsolateral prefrontal cortex was sensitive to the task complexity.

ARTICLE INFO

Article history:
Received 9 December 2014
Received in revised form 20 March 2015
Accepted 23 March 2015
Available online xxx

Keywords:
Functional MRI
Frontopolar cortex
Dorsolateral prefrontal cortex
Working memory
Manipulation
Integration

ABSTRACT

Cognitive operations often require integration of information. Previous studies have shown that, integration of information in working memory recruits frontopolar cortex (FPC). In this fMRI study, we sought to reveal neural mechanisms of FPC underlying the integration of information during arithmetic tasks. We compared a condition requiring manipulation of two features of an item held in working memory with manipulation of one feature. The results showed that, FPC was equally recruited in both conditions, while dorsolateral prefrontal cortex (DLPFC) tended to be more activated when manipulating two features. We suggest that, FPC plays an integrative role and is recruited by the production of representations in accordance with task constraints, whereas DLPFC appears to be sensitive to processing demands induced by the manipulation of information.

1. Introduction

Q4 Working memory (WM) plays a central role in complex cognitive activity, allowing us to temporarily maintain and manipulate task-related information. A number of studies have explained the neural mechanisms underlying the WM system [e.g., 6,11,13,18]. These studies, however, have dealt with tasks using relatively simple stimuli (i.e., single dimensional stimuli), such as objects or spatial locations. In contrast, a relatively small number of studies have focused on how the brain integrates two or more unrelated items held in WM [e.g., 2,8,9,14,20].

According to Baddeley's model [1], WM consists of the central executive, the visuospatial sketchpad, the phonological loop, and the episodic buffer. Baddeley [1] proposed that the episodic buffer works in conjunction with the visuospatial and phonological stores, binding visuospatial and phonological information together into episodic WM representations. The episodic WM store acts as a buffer through which these representations migrate to long term episodic memory. However, the underlying neural mechanisms and substrates involved in binding the visuospatial and phonological information to each other are integrated into single memory chunks are still unclear.

In this context, previous neuroimaging studies have sought to reveal the neural mechanisms of integration of information held in WM. Specifically, Prabhakaran et al. [20] demonstrated that holding integrated information during a WM task recruits frontopolar cortex (FPC). In their study, participants were asked to maintain four letters and four spatial locations indicated by parentheses. In one condition, each of the four letters appeared within one of the parentheses, such that each of them was bound into a single item. In another condition, the letters were situated centrally and the four locations were spread around the screen. Comparison of

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http://dx.doi.org/10.1016/j.neulet.2015.03.044
0304-3940/© 2015 Published by Elsevier Ireland Ltd.

Please cite this article in press as: C. Kim, et al., The role of the frontopolar cortex in manipulation of integrated information in working memory, Neurosci. Lett. (2015), http://dx.doi.org/10.1016/j.neulet.2015.03.044

the two conditions showed that, FPC was activated when identity and location were integrated, but not when they were encoded separately. Subsequently, they suggested that, maintenance of integrated information recruits FPC.

De Pisapia et al. [9] found FPC involvement in integration using different tasks. In their mental arithmetic tasks requiring participants to integrate a preloaded digit (e.g., “6”) into an ongoing calculation when cued (e.g., “+_”), they observed FPC activation during integration. In a follow-up study, De Pisapia and Braver replicated this [8]. However, the tasks used in these studies did not include the maintenance of multimodally-integrated information as in Prabhakaran et al. [20], but rather it required the integration process, which is an actively operative component. In line with these studies, Ramnani and Owen [21] reviewed different perspectives on FPC function including episodic memory retrieval [22], prospective memory [3], cognitive branching [16] and relational integration [14,17] and subsequently suggested that the role of FPC is to integrate the products of two or more cognitive operations.

However, in the previous studies, FPC activation during WM tasks might have resulted from the complexity of executing the task since manipulation required participants to change two features of two items in WM. In a study that employed the Tower of London task to measure planning ability, e.g., van den Heuvel et al. [24] found that FPC activity positively correlates with the number of moves required to transform the current state to the goal state. In other studies using Raven’s Progressive Matrices, FPC was recruited in a high complexity condition to a greater degree than it was in a low complexity condition [4,17], suggesting that it responded to the demand to integrate the multiple relations.

However, the nature of FPC involvement observed in previous studies is still unclear. It is not possible to differentiate, based on their findings, whether FPC is involved in manipulation of items held in WM or integration of them. The purpose of this study was to examine the neural mechanisms underlying integration-related processing. We tested whether FPC activation, which responds during manipulation of integrated information held in WM, is consistent with the hypothesis that FPC plays a role in production of integrated representations but not in executing manipulations of them. We designed a task consisting of a complex manipulation condition (CM) requiring participants to manipulate two features of an integrated item, a simple manipulation condition (SM) requiring them to manipulate only one feature of an item, and a control condition without integrated information (see Fig. 1). We expected different activation patterns between FPC and DLPFC. Specifically, both CM and SM would recruit FPC with the same intensity but with a temporal disparity, because there is a single integrated representation to be formed within the episodic buffer in both conditions but there are different numbers of features to be integrated into the representation. For DLPFC, in contrast, we expected that activity would be greater in CM than in SM since the cognitive demands of manipulating information are greater in CM.

2. Methods

2.1. Participants

Twelve healthy right-handed, native English speakers (four males) with an age range of 19–31 ($M = 22.9$, SD = 3.9) participated in this study. Informed consent forms approved by the University of New Mexico Institutional Review Board were obtained from all participants.

2.2. Stimuli and procedure

Three different conditions were employed: the control condition, SM and CM (Fig. 1). All trials began with two single digit numbers (the sample stimulus). A cue was then presented, followed by a probe stimulus. All stimuli were presented on a black screen. In the control condition, participants were asked to remember two numbers presented on the left and the right on a screen (e.g., “3” on the left and “6” on the right). Then, an additive or a subtractive operator with a single digit was presented randomly on either the left or right side and participants internally calculated the resulting arithmetic problem (e.g., “+2” on the right; compute “6 + 2”). This was followed by a probe containing a number presented on the left or right. Participants were asked to indicate whether the number matched the result of the calculation (e.g., “9” on the right; match result?) or the same as the unused sample number (e.g., “3” on the left; match the left sample number?). Numbers in samples and cues ranged from 2 to 9, and in probes were less than 16.

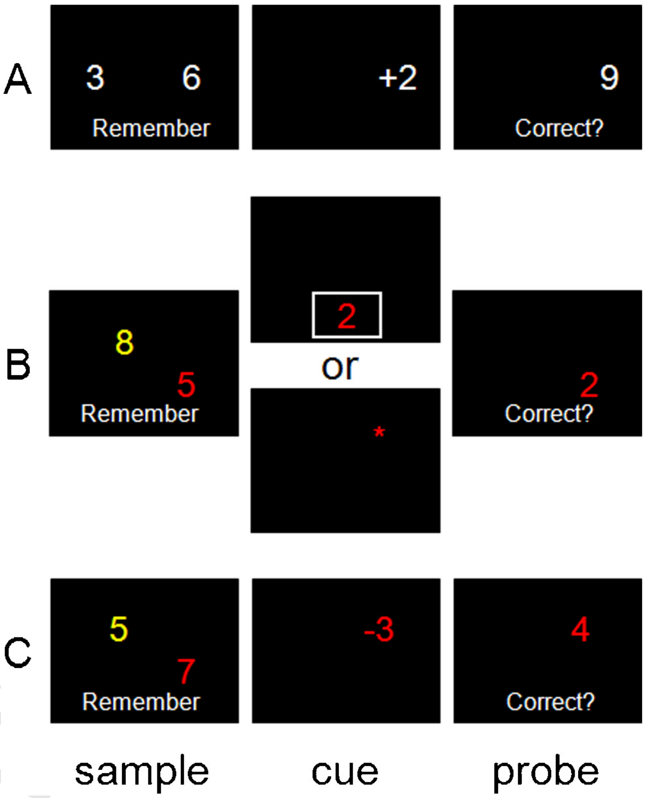

Fig. 1. Stimuli of each condition. (A) Control condition, “6” should be added by “2”, resulting in “8”, and, thus, the correct answer is “incorrect”; (B) Simple manipulation condition (SM). The cue is printed in red. Thus, “5” in the sample should be changed to “2” or moved to the location cued by the asterisk; (C) Complex manipulation condition (CM). Since the cue is printed in red, “7” in the sample should be subtracted by “3”, resulting in “4”, and moved to the location where the cue is presented. Thus, the correct answer is “correct”. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.) Q7

In the SM and CM, participants were asked to remember two numbers presented in different colors (red, green, blue, yellow, and magenta) and positions (two locations among 20 potential predefined positions). The cue indicated one of the sample stimuli to be manipulated using a colored asterisk or number (SM) or a colored operator with number (CM). In the SM, participants saw a cue (asterisk or number) whose color matched one of the numbers in the sample. Note that the number cue for the SM was presented in a white rectangle in order to present the cue without spatial information. Then, they were required to change the position of the matching sample number presented in the preceding sample phase to the position of the asterisk, or the identity of the matching sample number to the identity indicated by the number. For the CM, participants were asked to both calculate the arithmetic

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