

Prefrontal cortex hemispheric specialization for categorical and coordinate visual spatial memory

Scott D. Slotnick^{a,*}, Lauren R. Moo^b

^a Department of Psychology, McGuinn Hall, Boston College, Chestnut Hill, MA 02467, USA

^b Neuropsychology Laboratory, Massachusetts General Hospital, Boston, MA 02114, USA

Available online 3 March 2006

Abstract

During visual spatial perception of multiple items, the left hemisphere has been shown to preferentially process categorical spatial relationships while the right hemisphere has been shown to preferentially process coordinate spatial relationships. We hypothesized that this hemispheric processing distinction would be reflected in the prefrontal cortex during categorical and coordinate visual spatial memory, and tested this hypothesis using functional magnetic resonance imaging (fMRI). During encoding, abstract shapes were presented in the left or right hemifield in addition to a dot at a variable distance from the shape (with some dots on the shape); participants were instructed to remember the position of each dot relative to the shape. During categorical memory retrieval, each shape was presented centrally and participants responded whether the previously corresponding dot was ‘on’ or ‘off’ of the shape. During coordinate memory retrieval, each shape was presented centrally and participants responded whether the previously corresponding dot was ‘near’ or ‘far’ from the shape (relative to a reference distance). Consistent with our hypothesis, a region in the left prefrontal cortex (BA10) was preferentially associated with categorical visual spatial memory and a region in the right prefrontal cortex (BA9/10) was preferentially associated with coordinate visual spatial memory. These results have direct implications for interpreting previous findings that the left prefrontal cortex is associated with source memory, as this cognitive process is categorical in nature, and the right prefrontal cortex is associated with item memory, as this process depends on the precise spatial relations among item features or components.

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Keywords: fMRI; Item memory; Lateralization; Perception; Source memory; Visual memory

1. Introduction

Visual spatial perception of an item (e.g., a face, an object, or an abstract shape) produces activity in both the ventral cortical processing stream – occipital and ventral temporal cortex – for item identification and the dorsal cortical processing stream – occipital and parietal cortex – for item spatial localization in non-human primates (Ungerleider & Mishkin, 1982; although there are between stream connections, see Felleman & Van Essen, 1991). In humans, neuroimaging evidence indicates that the ventral (‘what’) processing stream extends from occipital cortex to ventral temporal cortex and into ventral prefrontal cortex, while the dorsal (‘where’) processing stream extends from occipital cortex to parietal cortex (Haxby et al., 1991; Haxby et al., 1994; Köhler, Kapur, Moscovitch, Winocur, & Houle, 1995).

There has been a long-standing debate as to whether this dorsal–ventral visual spatial perceptual processing distinction also exists in the prefrontal cortex during working memory (given that this cognitive function has been associated with the prefrontal cortex; see Baddeley & Della Sala, 1996). There is now compelling evidence that the ventral prefrontal cortex is preferentially associated with item working memory and the dorsal prefrontal cortex is preferentially associated with spatial working memory (Belger et al., 1998; Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998; Courtney, Ungerleider, Keil, & Haxby, 1996; Haxby, Petit, Ungerleider, & Courtney, 2000; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000; Sala, Rämä, & Courtney, 2003). Although some researchers have failed to find differential item and spatial working memory effects in prefrontal cortex (D’Esposito et al., 1998; Owen et al., 1998; Postle, Berger, Taich, & D’Esposito, 2000; Postle & D’Esposito, 1999), such null results can occur due to a number of reasons (e.g., a lack of sensitivity or insufficient task demands). In illustration of this point, a reanalysis of Postle et al.’s (2000) functional magnetic resonance imaging (fMRI) data was con-

* Corresponding author. Tel.: +1 617 552 4188; fax: +1 617 552 0523.
E-mail address: sd.slotnick@bc.edu (S.D. Slotnick).
URL: <http://www2.bc.edu/~slotnics>.

ducted using event-related timecourse analysis, rather than the more typically used beta-weight analysis, and revealed spatial working memory specific activity in dorsal prefrontal cortex, supporting the dorsal–ventral prefrontal cortex working memory distinction (Slotnick, 2005). Thus, the significant findings affirm that the ventral and dorsal visual spatial perceptual processing streams extend into ventral and dorsal prefrontal cortex during item and spatial working memory.

In everyday life, visual spatial perception not only involves processing items in isolation, but is also engaged in processing the positions of items relative to one another. Kosslyn (1987) proposed that the left hemisphere is preferentially associated with between-item categorical processing (e.g., one item is ‘above’ or ‘below’ the other, a discrete judgment) and the right hemisphere is preferentially associated with between-item coordinate processing (e.g., one item is ‘near’ to or ‘far’ from the other, an analog judgment). These distinct types of processing can also refer to the relative positions of parts or features of a single item (for further elaboration, see Section 4). This left–right hemisphere categorical–coordinate visual spatial perceptual processing distinction has been convincingly supported in a number of subsequent behavioral studies (Banich & Federmeier, 1999; Bruyer, Scailquin, & Coibion, 1997; French & Painter, 1991; Hellige & Michimata, 1989; Koenig, Reiss, & Kosslyn, 1990; Kosslyn et al., 1989; Laeng & Peters, 1995; Laeng, Shah, & Kosslyn, 1999; Michimata, 1997; Niebauer & Christman, 1998; Okubo & Michimata, 2002; Sergent, 1991; Servos & Peters, 1990). Some investigators have taken failures to find such categorical and coordinate hemispheric laterality effects as contradictory evidence (Bruyer et al., 1997; Cowin & Hellige, 1994; Rybash & Hoyer, 1992; Sergent, 1991). However, direct support for Kosslyn’s hemispheric processing distinction has been confirmed with patients that had one hemisphere (usually followed by the other) temporarily deactivated by injection with sodium amobarbital – the left hemisphere was preferentially associated with categorical visual spatial processing and the right hemisphere was preferentially associated with coordinate visual spatial processing, but only under sufficiently demanding task conditions (which may provide some explanation of previous null findings; Slotnick, Moo, Tesoro, & Hart, 2001). Furthermore, evidence from patients with focal lesions (Laeng, 1994; Laeng, Carlesimo, Caltagirone, Capasso, & Miceli, 2002) and neuroimaging (Baciu et al., 1999) suggests that categorical and coordinate perceptual processing may be particularly reliant on the left and right parietal lobes, respectively, although there is neuroimaging evidence that this hemispheric distinction also occurs in the prefrontal cortex during perceptual processing (Kosslyn, Thompson, Gitelman, & Alpert, 1998) and spatial imagery (Trojano et al., 2002). The overall pattern of results can be taken as strong evidence that the left hemisphere is preferentially associated with categorical visual spatial perceptual processing and the right hemisphere is preferentially associated with coordinate visual spatial perceptual processing (see meta-analysis by Laeng, Chabris, & Kosslyn, 2003).

Similar to the ventral–dorsal prefrontal cortex distinction that has been associated with item and spatial working memory, we hypothesized that the left–right hemisphere prefrontal

cortex distinction would be manifested during categorical and coordinate visual spatial memory. In particular, we focused on the dorsolateral and anterior prefrontal cortex, as these regions have been associated with source memory and item memory (Cansino, Maquet, Dolan, & Rugg, 2002; Nyberg, McIntosh, Cabeza, Habib, & Houle, 1996; Rugg, Fletcher, Chua, & Dolan, 1999; Slotnick, Moo, Segal, & Hart, 2003). To anticipate the results, a region in left prefrontal cortex was associated with categorical visual spatial memory while a region in right prefrontal cortex was associated with coordinate visual spatial memory.

2. Methods

2.1. Participants

After providing informed consent, 11 right-handed participants took part in the imaging study, which had been approved by the Johns Hopkins University institutional review board. Due to excessive head movement in three participants (i.e. greater than 1 mm), eight participants were included in the analysis (age range 23–35 years, five females), which was sufficient to conduct the imaging analysis (Friston, Holmes, & Worsley, 1999). A follow-up behavioral study, approved by the Harvard University institutional review board, was also conducted with eight additional participants that had provided informed consent (age range 23–37 years, five females). All participants had normal or corrected-to-normal visual acuity.

2.2. Behavioral protocol

The behavioral protocol is illustrated in Fig. 1. In a blocked design, participants completed two categorical (A) and two coordinate memory (B) runs (in the order ABBA). Immediately before the MRI scanning session, participants were briefly trained to familiarize them with both tasks. During the encoding phase of both types of runs, following a 6 s instruction screen, six abstract shapes (spanning 5.7–7.1° of visual angle) were presented every 4 s with equal probability on the left or right half of the screen (with the nearest shape boundary ranging from 2.1° to 2.8° of visual angle, as measured horizontally, from the display center). In addition, each shape was paired with a dot 0.3° of visual angle in diameter that varied in distance from the shape from 0° to 1.1° or 1.7° to 3.3° of visual angle (where 0° distance indicates the dot was centered directly on the boundary that defined a shape, and the spatial gap in dot to shape distance was based on the coordinate retrieval reference distance of 1.4°, as will be discussed below). The encoding phase format and instructions were identical for both run types. Participants were instructed to remember the position of the dot relative to each shape by visually encoding the shape-dot pair precisely as it appeared on the display, rather than using verbal encoding strategies (all participants reported using visual encoding strategies, as instructed). We emphasize here that had participants used verbal encoding strategies, similar categorical and coordinate memory related activity would be predicted, while employment of visual encoding strategies would predict differential activity (as observed; see Section 3). Participants were not informed as to the type of subsequent retrieval run in an effort to enforce consistent encoding strategies. During the retrieval phase of both types of runs, following an 8 s instruction screen, the six shapes from the encoding phase (without the dots) were presented at the center of the screen every 6 s, each for a duration of 3 s. Central presentation precluded participants from remembering dot location based upon cues other than relative position to the associated shape (e.g., the use of the screen as a frame-of-reference; see Banich & Federmeier, 1999) that might have diminished or eliminated differential categorical and coordinate effects beyond the initial block (Koenig et al., 1990; Kosslyn et al., 1989; Laeng et al., 1999; Michimata, 1997). Shapes were never repeated. When presented with a shape, participants had been encouraged to retrieve a visual representation of the associated shape-dot pair (all participants reported doing so). It should again be noted that if participants simply retrieved verbal labels, similar categorical and coordinate memory related activity would be predicted; as differential activity was observed (see Section 3), this supported their use of visual spatial retrieval. During categorical memory runs, participants

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