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Engagement of the prefrontal cortex in representational momentum: an fMRI study

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Behavioral studies have identified a robust phenomenon that an observer's memory of the final position of a moving target is shifted a little further in its motion direction, which is usually called representational momentum (RM). However, the neural substrates underlying RM are poorly understood. The current study measured hemodynamic responses in association with RM using functional magnetic resonance imaging (fMRI). Two experiments using block and event-related designs, respectively, were conducted in which subjects compared the orientation of a probe rectangle with the remembered orientation of the final inducing figures in a set of rotating rectangles. Both experiments showed that, relative to the control task in which behavioral data did not show RM effects, RM task induced stronger activation in the prefrontal cortex. However, no activation was found in MT/MST complex in association with RM. The fMRI results suggest that RM may not simply reflect implicit motion perception and high level cognitive mechanisms underpinned by the prefrontal cortex may be involved in the RM effect.

Keywords: Representational momentum; Implied motion perception; fMRI; Prefrontal cortex; MT/MST

Introduction

When an observer is required to remember the final position of a moving target that vanishes without warning, the observer's memory is often displaced a little further in the direction of the target's motion. Freyd and Finke (1984) referred to this memory displacement as *representational momentum* (RM) for its similarity to physical momentum, that is, the observer's mental representation of a target's motion cannot be halted immediately because of the analogous momentum within the representational system. The analogy between the dynamics and kinematics of the memory of the final position of a target in the representational system and that of a physical object suggests a spatiotemporal coherence between the represented physical world and the representing mental world (Freyd, 1987, 1993) or an incorporation of environmental invariant physical principles to mental representational system (Hubbard, 1995a,b, 1996, 1998a,b, 1999).

Although the RM effect has been demonstrated in previous behavioral studies, the underlying neural mechanisms are still unclear. Recent functional magnetic resonance imaging (fMRI) studies (Kourtzi and Kanwisher, 2000; Senior et al., 2000) have tried to identify the neural substrates related to RM effect using "frozen-motion" pictures, which are motion-snapshots of objects or creatures captured in the middle of motion and thus contain implicit motion information (Freyd, 1983). The fMRI studies showed that the medial temporal/medial superior temporal cortex (MT/MST complex), which is generally believed to underpin actual or illusory motion perception in the dorsal visual pathway (Barton, 1998; David and Senior, 2000; Greenlee, 2000; Van Essen and DeYoe, 1995), is more activated by "frozen-motion" pictures than by pictures without implicit motion. Therefore, it is proposed that the RM effect can be attributed to the inferring motion perception that is modulated by the high-level semantic knowledge and is supported by the MT/MST complex (Senior et al., 2000).

The paradigms used in the aforementioned fMRI studies emphasized the effect of implicit motion (i.e., "motion" in a single frozen-action photograph) process in the RM effect since the results were obtained by comparing neural activities induced by images with or without implicit motion information. However, several studies have shown that the implicit motion is not necessary for the generation of the RM effect. For example, it is observed that the RM effect occurs when using shapes that changed in width (Kelly and Freyd, 1987) or a pitch of sound that changed in auditory frequency (Freyd et al., 1990).[1] The

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[1] It should be noted that not all consistent changes in different types of inducing stimuli result in RM. For example, Brehaut and Tipper (1996) found a backward displacement in memory for changes of luminance, and they argued from this that in order for RM to be exhibited, the changes are limited to be correlated to the motion in the real world.

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findings of the RM effect induced by the stimuli without implicit motion as that in frozen-action photographs suggest that MT/MST complex is not necessarily engaged in the generation of the RM effect when the contribution of implicit motion perception is diminished.

The current study examined the neural substrates of the RM whether other brain areas are activated by the RM effect under

P values smaller than an uncorrected P value of 0.005 for the group analysis.

Results

Behavioral results

The behavioral performances were analyzed by calculating the percentage of reports that the orientation of the probe rectangle was the same as that of the third inducing figure. Table 1 summarizes the mean percentage of same responses as a function of the actual orientation of the probes relative to the third inducing figure in the RM tasks and the control tasks in Experiments 1 and 2. For each subject and each task, the magnitudes of the RM effect (in degrees) were determined by calculating the weighted mean estimates of the memory shift (i.e., the sum of the products of the proportion of same responses and the distance of the probe from true-same, in degrees, divided by the sum of the proportions of same responses). A shift of zero would be expected if there was no memory distortion. When the inducing figures did not imply rotation in a consistent direction in the control tasks, no significant difference was found between the weighted mean estimates of the memory shift and zero in both experiments (averaged $M = 0.07$ for Experiment 1 and averaged $M = 0.15$ for Experiment 2, both $P > 0.1$). Thus, no RM effect was observed in the control conditions. However, when the inducing rectangles implied a consistent rotation in RM tasks, RM effects were observed in both experiments, that is, the weighted mean estimates of the memory shift were significant higher than zero (averaged $M = 0.55$ for Experiment 1, $P < 0.05$; and averaged $M = 1.47$ for Experiment 2, $P < 0.02$). Moreover, the difference between the weighted mean estimates of the memory shift for the RM tasks in the two experiments was marginally significant ($P = 0.078$).

fMRI results

One contrast of the RM task vs. the control task was conducted for both experiments. The activations confirmed by the group random effect analysis in the two experiments were listed in Tables 2 and 3, respectively. In Experiment 1, the RM task induced stronger activations in the right frontopolar cortex (see Fig. 2a) and the right posterior precuneus/gyrus cinguli (PCu/GC) compared to the control task. In Experiment 2, relative to the control task, the RM task induced stronger activations in multi-prefrontal areas (see Fig. 2b), including the right frontopolar cortex, the right gyrus frontalis inferior/medialis (GFi/GFd), the right sulcus callosomarginalis (Scm), bilateral gyrus frontalis superior/medius (GFs/GFm), and the left posterior GC. However, no activation was found in the MT/MST complex in either experiment.

Table 1
Summary of the mean percentage of same responses for the backward probes, same probe, and forward probes for RM task and control task in Experiments 1 and 2

Experiment	Percentage of same responses				
	−6° probes	−3° probes	0° probes	3° probes	6° probes
Experiment 1					
RM task	42.7	61.7	83.5	76.5	54.2
Control task	36.3	59.3	88.3	63.1	35.6
Experiment 2					
RM task	35.4	52.4	73.7	82.5	48.8
Control task	28.7	45.9	78.4	50.3	29.4

Table 2
Brain areas associated with the RM effect in Experiment 1

Region	BA	*X*	*Y*	*Z*	Z value
Right hemisphere					
Frontopolar	BA10	2	54	16	3.35
PCu/GC	BA31/23	2	−38	46	3.21

Note. BA, Brodmann's area; PCu: Precuneus; GC: Gyrus cinguli; height threshold, uncorrected $P = 0.005$; cluster extent threshold, $k = 40$ voxels; Voxel size, $2 \times 2 \times 2$ mm^3.

Discussion

The current study used RM and control tasks[2] similar to those of Freyd and Finke (1984). Robust RM effects were observed in such a way that subjects were more likely to respond same if the probe was rotated slightly forward from the orientation of the final inducing rectangle than if the probe was rotated slightly backward from the orientation of the final inducing figure. However, when the three inducing rectangles were presented in an order that did not imply rotation in a coherent direction (i.e., the control condition), the RM effect was not observed.

Previous fMRI studies found activation in the MT/MST complex when using stimuli with implicit motion to produce the RM effect (Kourtzi and Kanwisher, 2000; Senior et al., 2000). Similar stimuli were used in a recent transcranial magnetic stimulation (TMS) study (Senior et al., 2002), which showed that disruption of the extrastriate cortical function in the MT/MST system impedes the RM effect. Thus, it has been proposed that the MT/MST complex is necessary for the RM effect. In the current experiments, however, although there was implied rotation in consecutive inducing figures, the implied rotation existed in both the RM and control conditions. Thus, the contribution of implied motion perception to the RM effect was reduced to minimum. Interestingly, we did not observe activations in the MT/MST complex in association with the RM effect when the implicit motion perception was weakened. By comparing Senior et al.'s (2000) work and the current study, it may be suggested that the MT/MST activation observed in the previous fMRI studies could reflect neural activities related to the implicit motion perception that is necessary for the RM effect produced by the "frozen-motion" photographs. When the RM effect is obtained by comparing the coherence of moving inducing figures in the RM and control conditions, however, the MT/MST complex may not be involved in producing the RM effect.

More interestingly, we found stronger activations in the prefrontal cortex in the RM compared to the control task. This was evident in both block design and event-related design experiments. It has been widely accepted that human prefrontal cortex plays an

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[2] By presenting only clockwise motion, we were unable to compare in the data between consistent/clockwise and inconsistent/counterclockwise conditions. However, other research has shown that RM occurs for both clockwise and counterclockwise motion and there is no difference between the clockwise and counterclockwise conditions (e.g., Kelly and Freyd, 1987).

Table 3
Brain areas associated with the RM effect in Experiment 2

Region	BA	*X*	*Y*	*Z*	Z value
Right hemisphere					
Frontopolar	BA10	24	52	−4	4.52
Scm	BA32	16	46	10	4.08
GFs	BA9/46	22	30	26	3.58
GFm	BA45/46	30	24	24	3.72
GFi	BA11	30	24	−16	3.45
GFd	BA8/9	2	26	40	3.34
		6	42	32	3.28
		6	36	42	3.06
Left hemisphere					
GFs	BA9/46	−10	38	36	3.85
		−18	38	34	3.09
GFm	BA8	−26	14	44	3.83
GC	BA23	−4	−30	24	3.29
		−8	−30	34	2.95

Note. BA, Brodmann's area; Scm: Sulcus callosomarginalis; GFs: Gyrus frontalis superior; GFm: Gyrus frontalis medius; GFi: Gyrus frontalis inferior; GFd: Gyrus frontalis medialis; GC: Gyrus cinguli; height threshold, uncorrected $P = 0.005$; cluster extent threshold, $k = 40$ voxels; Voxel size, $2 \times 2 \times 2$ mm^3.

important role in general intellectual ability and specific cognitive capabilities that require working memory, planning, and attention control (e.g., Winterer and Goldman, 2003; Wood and Grafman, 2003). Particularly, a "fronto-parietal cortical network" may be engaged in working memory processes that are suggested to be required for mental imagery and the RM effect (Amorim et al., 2000). In the paradigms used here, subjects had to maintain the orientation of the last inducing figure in working memory and compare it with the orientation of the probe figure. This was the same for the RM and control tasks. The RM phenomenon reflected per se the effect of the coherence of the inducing figures represented in working memory. One possible explanation of the prefrontal activation observed here is that the consecutiveness of the inducing figures in both time and space domain generated stronger representation of coherence of the inducing objects in working memory in the RM than the control conditions, which is congruent with the findings that representation of sequence of visual events induced activations in the prefrontal cortex (Huettel et al., 2002; Marshuetz et al., 2000). Alternatively, the prefrontal activations may reflect an automatic mental extrapolation (Finke and Freyd, 1989; Hubbard, 1999) or a mental anticipation (Verfaillie and d'Ydewalle, 1991) from the memory representation of the true position to the forward displacement according to the nonconscious knowledge of physical momentum principle internalized within the representational system (Hubbard, 1998a, 1999). The first account emphasizes the role of working memory in the RM effect whereas the second account proposes a mechanism relatively independent of working memory. These accounts can be tested in future studies.

The coordinates of the prefrontal activations were slightly different between the two experiments. However, if we use a higher *P* value of 0.01 to identify the prefrontal activations, the frontal activation in Experiment 2 overlapped that in Experiment 1. In addition, it appeared that the areas of activation in the prefrontal cortex were larger in the event-related than the block design experiments, consistent with the tendency of higher weighted mean estimates of the memory shift in the event-related design experiment. One possible account is that the prefrontal activations were related to the transient neural process underlying the order representation or the mental extrapolation within the memory representation, which was more salient in the event-related design relative to the block design conditions because the order of the three inducing rectangles with specific orientations did not change on successive trials in the latter condition and thus might give rise to habituation during the RM task. This is different from Kerzel's (2002) recent finding that the RM effect was decreased when the direction of rotation varied from trial to trial and the final position of the inducing rectangles was random. In the current study, Experiment 2 was different from Experiment 1 in stimulus inter-

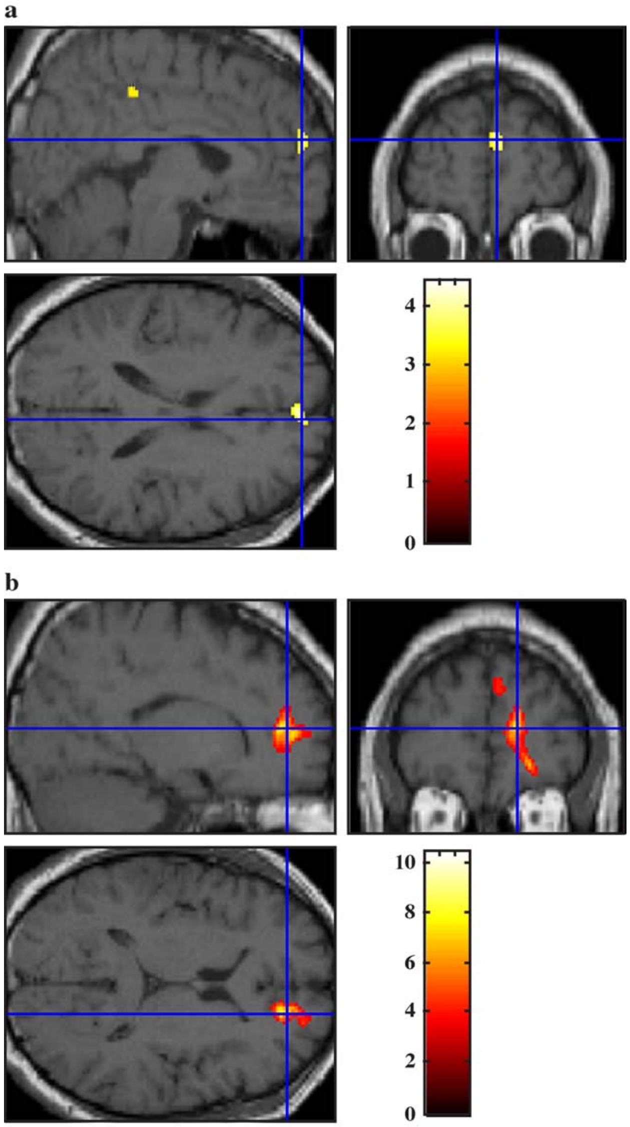

Fig. 2. Brain areas activated by the RM task compared to the control task in Experiments 1 and 2. The results of group analysis were superimposed on a normalized anatomical image of one representative subject. Threshold for activation of all clusters was uncorrected $P < 0.005$. (a) The activation in the prefrontal cortex in association with the RM effect in Experiment 1. (b) The activation in the prefrontal cortex in association with the RM effect in Experiment 2.

vals besides the sequence of RM and control tasks. Shorter stimulus intervals in the block design experiment might generate apparent counterclockwise rotation between the probe figure of the prior trial and the first inducing figure of the current trial and thus decreased the consecutiveness of the inducing stimuli in the current trial. This may result in decreased coherence representation or the mental extrapolation within memory representation and thus weakened the RM effect in the block design experiment.

In conclusion, the current study investigated the cortical mechanisms underlying the RM under the condition that the contribution of implicit and implied motion perception was minimized. We found the RM-related activations in the prefrontal cortex but not in the MT/MST complex. The findings suggest that high level cognitive mechanisms underpinned by the prefrontal cortex may be involved in the RM effect. The RM effect may be associated with the spatiotemporal order representation or the mental extrapolation in human working memory.

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