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.
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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.

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 effect using a classic paradigm studying the RM effect developed by Freyd and Finke (1984). As illustrated in Fig. 1, three inducing rectangles at different orientations are presented successively to produce a consistent clockwise or anticlockwise "implied rotation" or "implied motion" (i.e., "motion" arising from a sequence of static pictures). Subjects were asked to compare the orientation of a probe rectangle with the remembered orientation of the final inducing rectangle. It was found that subjects' memory for the orientation of the final rectangle tended to be displaced forward in the direction of the implied rotation (Freyd and Finke, 1984; Kelly and Freyd, 1987). In the control condition, the order of the presentation of the first two rectangles was reversed so that the coherent path of implied rotation was disrupted and no RM effect was found (Freyd and Finke, 1984). In such an experimental design, there is implied rotation in both the RM condition (implied rotation of rectangles with a coherent direction) and the control condition (implied rotation of rectangles with incoherent directions). The only difference between the two conditions is the direction of the implied rotation resulting from the order difference of presentation of the first two inducing figures. Therefore, by comparing hemodynamic responses in the RM and control conditions in the Freyd and Finke paradigm, it is possible to reveal

neural substrates underlying the RM effect beyond the contribution of implied motion supported by MT/MST complex because the difference of implied motion between the RM and control conditions was minimized.

Experiment 1 employed a conventional block design to reveal the neural substrates of the RM effect by comparing the fMRI signals in the RM condition relative to the control condition. In the block design, stimuli in the same condition are presented in separate epochs so as to generate functional activation images between alternated blocked conditions (Bandettini et al., 1993; Buckner et al., 1996). Studies using the block design usually obtain high a signal-to-noise radio. However, such blocked task paradigms do not allow separate trials within the task blocks to be distinguished. Thus, Experiment 1 could measure only the state-related activation in association with the RM effect but could not identify the transient activation related to memory encoding and maintaining of individual stimuli in the representation system (Donaldson et al., 2001; Otten et al., 2002). Therefore, in Experiment 2, we employed an event-related design to measure the item-related activities associated with the RM effect. In such a design, stimuli in the RM and control conditions were presented in a random order with long interstimulus intervals. This enabled us to directly examine the transient activity related to each of the task events that is not accessible to the conventional block design (Friston et al., 1998; Rosen et al., 1998). We were interested in whether the MT/MST complex is engaged in the RM effect under the condition that the effect of implicit and implied motion perception was minimized and
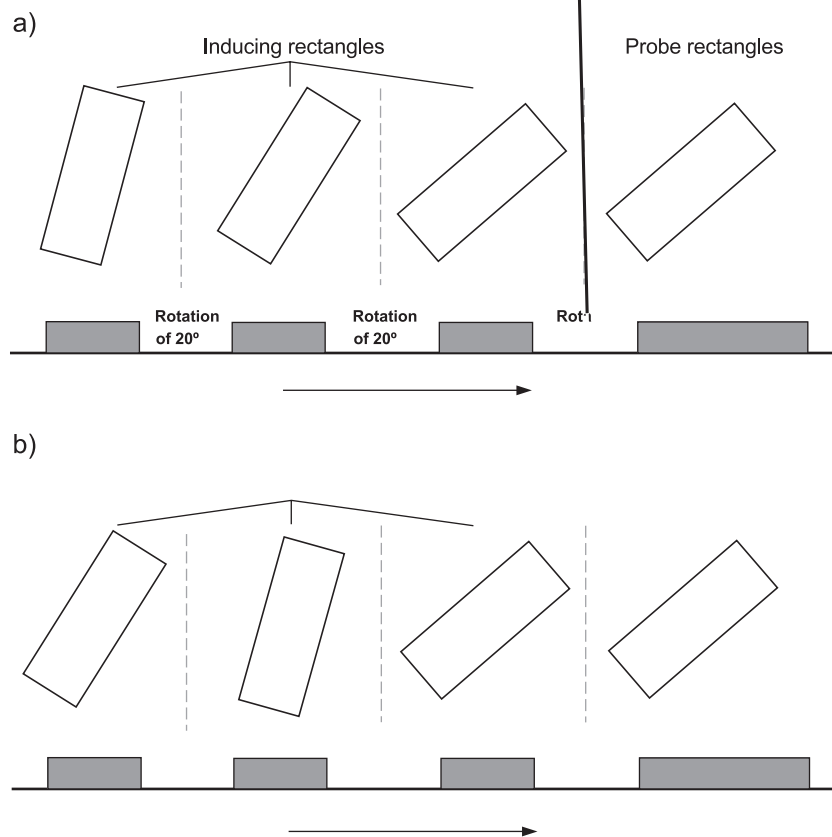
whether other brain areas are activated by the RM effect under this circumstance.

Material and Methods

Subjects

Nineteen subjects (8 women, 11 men, mean age 26 years, range from 21 to 38 years) participated in this study. Ten subjects participated in Experiment 1, six subjects participated in Experiment 2, and three subjects participated in both experiments. All subjects had normal or corrected-to-normal visual acuity and gave informed consents according to the guidelines of Department of Psychology, Peking University.

Stimuli and tasks

The stimuli and tasks were similar to those used in the previous work (Freyd and Finke, 1984; Kelly and Freyd, 1987). As illustrated in Fig. 1, three rectangles of identical dimensions with different orientations were used as the inducing figures. For the RM task, each inducing rectangle was oriented at $20°$ from the orientation of the previous inducing figure and presented in an order that these orientations could be thought of as sampled positions from an implied path of a clockwise rotation. First inducing rectangle was oriented at $15°$ from the vertical. After the third inducing rectangle was removed, a fourth rectangle, called the probe rectangle, was presented in the same orientation as the third one or slightly forward or backward relative to the implied rotation (i.e., the orientation difference between the third inducing rectangle and the probe rectangle could be $-6°$, $-3°$, $0°$, $3°$, $6°$). Each rectangle subtended at an angle of $6° \times 4°$. Subjects were asked to judge whether the orientation of the probe rectangle was the same as or different from that of the third inducing figure. A cross of $0.5° \times 0.5°$ was presented as the fixation during the intervals between two successive trials. The control condition was the same as the RM condition except that the first two inducing rectangles were presented in an opposite order so that no consistent rotation direction across the inducing figures within a given trial was implied. Each inducing rectangle was presented for 250 ms and the probe rectangle was presented for 800 ms. On each trial, the time interval between two successive figures was 250 ms. In Experiment 1, the stimulus interval between the onset of one trial's first inducing figure and the onset of next trial's first inducing figure was 3000 ms. Subjects performed 63 trials for the RM tasks and 63 trials for the control tasks during three fMRI runs for Experiment 1. In Experiment 2, the stimulus interval between the onset of one trial's first inducing figure and the onset of next trial's first inducing figure varied randomly among 7000, 7500, 8000, 8500, and 9000 ms (average was 8000 ms). Subjects performed 24 trials for the RM tasks and 24 trials for the control tasks during three fMRI runs for Experiment 2.

MRI scanning

fMRI data were collected in Beijing Chaoyang hospital between March and April, 2003. Subjects were scanned using a 1.5-T GE Signa scanner (Milwaukee, WI, USA) with a standard GE birdcage-type RF coil. Before scanning, subject practiced 10 trials for the RM task and 10 trials for the control task. Vacuum mattresses were used to position and fix subjects' heads to prevent head movements. The visual stimuli were projected on a translucent screen located at the front of the bore of the magnet. Subjects could see the stimulus displays through a mirror mounted on the head coil. They were instructed to lie as still as possible and to concentrate on viewing the stimuli during scan time. Subjects were asked to make the same or different judgments by pressing buttons beside the body with the left or right index fingers. The relation between hands and the same or different judgments was counter-balanced across subjects. Because of the technical limitation of connecting response buttons and a computer outside the scanner using optical fiber, behavioral data were not recorded during the scanning but collected when the subjects performing the same experiment outside the scanner after fMRI scanning.

The BOLD-contrast functional imaging used a single-shot, T2*-weighted EPI sequence [TR: 3000 ms, TE: 60 ms, FOV: 24×24 cm^2, Matrix: 64×64, Flip angle: $60°$] to acquire a set of 12 axial slices (6 mm thick/2 mm sp, from superior to inferior). Thus, the spatial resolution for functional images was $3.75 \times 3.75 \times 8$ mm^3. For each experiment, three runs (126 s per run) were performed on each subject for each task to acquire 126 (42×3) volumes. The first two volumes of each run were discarded to eliminate the effects of EPI onset. In Experiment 1, subjects were given the RM task and the control task in two successive 60 s of each run. The order of the RM task and the control task was counter-balanced across subjects. At least 2-min rest intervals were given between two runs. High-resolution anatomical images [T1-weighted, 66 axial slices, 2.0 mm thick/interleaved, FOV: 24×24 cm^2, Matrix: 256×256] were obtained to identify landmarks associated with the neural activity found in the functional images.

Analysis of fMRI data

SPM99 (Wellcome Department of Cognitive Neurology, UK) was used for imaging data processing and analysis. Slice-acquisition timing was first performed on the event-related fMRI data to correct the differences in acquisition time between slices during sequential imaging. For each subject, functional images were realigned to correct the head movement between scans. The anatomical image was coregistered with the mean images produced during the process of realignment. All images were normalized to a $2 \times 2 \times 2$ mm^3 Montreal Neurological Institute (MNI) template in Talairach space (Talairach and Tournoux, 1998) using bilinear interpolation. Functional images were spatially smoothed using a Gaussian filter with a full-width at half maximum (FWHM) parameter set to 8 mm. For block design in Experiment 1, data were modeled using a boxcar function. For event-related design in Experiment 2, data were modeled using a delta function with the default SPM basis function (hemodynamic response functions, HRF). One contrast of RM task vs. control task was defined in both experiments. Regions preferentially engaged by the RM effect were defined as areas more activated by the RM task than by the control task. Statistical effects were first assessed in individual subjects. Group analysis of random effects was then conducted across the group of subjects based on the statistical parameter maps from each individual subject to allow population inference. Areas of significant activation were identified at the cluster level for the

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

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.

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.

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	24320.2(give)f1was	

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-
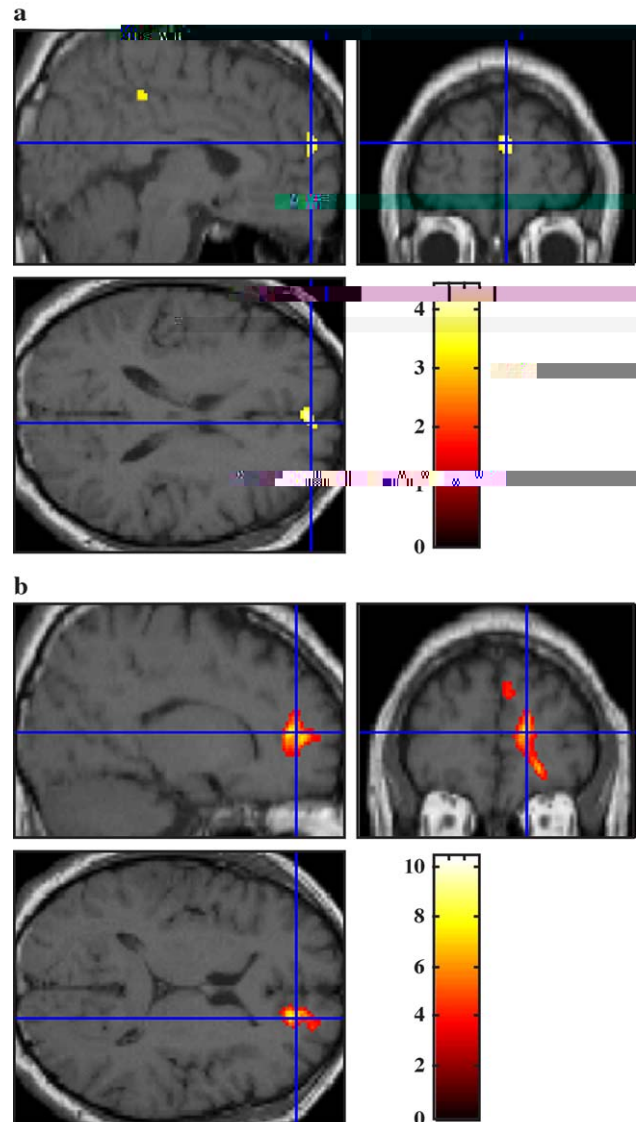

Fig. 2. Brain areas activated by the RM task compared to the control task in Experiments 1 and 2. The results of group analysis were superimposed on a normalized anatomical image of one representative subject. Threshold for activation of all clusters was uncorrected P < 0.005. (a) The activation in the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

Acknowledgments

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