

# Inhibition of Visual Discrimination During a Memory-Guided Saccade Task

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**Ostendorf, Florian, Carsten Finke, and Christoph J. Ploner.** Inhibition of visual discrimination during a memory-guided saccade task. *J Neurophysiol* 92: 660–664, 2004. First published February 18, 2004; 10.1152/jn.01045.2003. Voluntary behavior critically depends on attentional selection and short-term maintenance of perceptual information. Recent research suggests a tight coupling of both cognitive functions with visual processing being selectively enhanced by working memory representations. Here, we combined a memory-guided saccade paradigm (6-s delay) with a visual discrimination task, performed either 1,500, 2,500, or 3,500 ms after presentation of the memory cue. Contrary to what can be expected from previous studies, our results show that memory of spatial cues can transiently delay speeded discrimination of stimuli presented at remembered locations. This effect was not observed in a control experiment without memory requirements. Furthermore, delayed discrimination was dependent on the strength of actual memory representations as reflected by accuracy of memory-guided saccades. We propose an active inhibitory mechanism that counteracts facilitating effects of spatial working memory, promoting flexible orienting to novel information during maintenance of spatial memoranda for intended actions. Inhibitory delay-period activity in prefrontal cortex is a likely source for this mechanism which may be mediated by prefronto-tectal projections.

## INTRODUCTION

Only a small fraction of the visual information available on our retinae can be processed simultaneously to guide voluntary behavior. Depending on the behavioral context, selection of visual information is achieved by reflexive orienting and by directing attention voluntarily to relevant locations in the visual field (Müller and Rabitt 1989; Posner 1980). In the latter case, sustained facilitation of visual processing at attended locations may occur (Müller and Rabitt 1989; Posner 1980). Once selected, visual information is actively maintained in working memory to guide intended actions (Baddeley 1986; Goldman-Rakic 1996). A growing body of evidence indicates a mutual dependency of spatial attention and spatial working memory. While covertly directed attention seems to gate access of visual information to working memory (Di Pellegrino and Wise 1993; Rainer et al. 1998), psychophysical experiments (Awh et al. 1998) and electrophysiological data (Awh et al. 2000; Bisley and Goldberg 2003; Supèr et al. 2001) indicate spatially selective facilitation of visual processing by working memory representations. A current hypothesis proposes that rehearsal in spatial working memory depends on sustained attention to remembered locations (Awh and Jonides 2001; Awh et al. 1998). However, recent single-neuron recordings from neurons in parietal cortex of nonhuman primates suggest that this dependency is not obligate: distracters flashed during the delay

of memory-guided saccade tasks evoked larger responses at nonmemorized positions (Powell and Goldberg 2000; Steinmetz et al. 1994) and caused a transient attention shift to their position as measured in a subsequent discrimination task (Bisley and Goldberg 2003). Moreover, distracters in these tasks had no detrimental effect on working memory, since accuracy of memory-guided saccades was unaffected (Powell and Goldberg 2000).

In this study, we have investigated the relationship between spatial working memory and spatial attention on a behavioral level. We asked whether, when, and how visual processing is modulated during the memory phase of a modified oculomotor delayed-response task. At variable interstimulus intervals (ISIs) after the memory cue, a target letter was presented either in the same or opposite visual hemifield. Successful discrimination of this stimulus has previously been shown to depend on focal attention (Braun and Julesz 1998). We analyzed reaction times (RTs) to the discrimination target as a function of ISI and position of preceding memory cue. We expected attentional effects of spatial working memory to be reflected in the time needed for discrimination of the target letter. Contrary to what can be predicted from previous studies, we show that speeded discrimination can selectively be inhibited at the location of a preceding memory cue, provided that the cue position is accurately maintained in spatial working memory. These results point toward a flexible association of spatial working memory and spatially directed attention. Net facilitating or inhibitory effects of spatial working memory may critically depend on the behavioral context.

## METHODS

### *Subjects*

Twenty naïve, right-handed subjects were tested. Ten each were tested in a memory and control experiment [4 vs. 5 males; mean age, 24.4 (range, 21–27 yr) vs. 24.6 yr (range, 21–31 yr)]. Informed consent was obtained from all subjects before participation in the study which was approved by the local ethics committee and conducted in conformity with the Declaration of Helsinki.

### *Eye movement recording*

Eye movements were recorded by horizontal infrared oculography of the right eye (Eyetracker, AMTech, Weinheim, Germany). Data were sampled at a frequency of 200 Hz. The subjects' head was fixed to the recording system by means of a chinrest and a bite-bar. Calibration trials were performed regularly during recording sessions.

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### Stimulus presentation

Subjects sat 50 cm away from a 22" monitor with a 110-Hz refresh rate. Stimuli were green (luminance, 30 Cd/m<sup>2</sup>), seen against a homogenous gray background (luminance, 3 Cd/m<sup>2</sup>). Experiments were run in an otherwise darkened room. While fixating on a central fixation cross (0.5°), subjects were presented a peripheral cue (0.4°) for 500 ms at either 6, 9, or 12° horizontally to the left or right. In the memory experiment, subjects were instructed to remember the cue position for a delay of 6 s (Fig. 1). The subsequent offset of the fixation cross served as signal to execute a memory-guided saccade to the remembered cue position. No feedback about targeting error was given. At variable ISIs of 1,500, 2,500, or 3,500 ms after the first cue, a rotated "T" or "L" (0.76°) was presented in the same or opposite visual hemifield at 9°. Subjects performed a speeded discrimination of this stimulus by pushing a button with their right (T) or left (L) index finger. Discrimination stimuli were presented maximally for 1 s, with presentation being terminated by the response. In the control experiment, a trial ended after presentation of the discrimination target. All other stimulus parameters and ISIs were identical to the memory experiment. Subjects in the control experiment were instructed to respond to the discrimination letter that would appear at variable intervals after a first cue. No further instructions were given. The experiment consisted of a total of 432 trials in pseudorandom order, split into three sessions of six blocks each. Trials were presented equally across blocks, with every trial type occurring in every 1.5 blocks, i.e., within a sequence of 36 trials. Sessions were recorded on consecutive days. Prior to the first session, subjects received training in the discrimination task and one test block in the final experimental condition. Subjects tested in the memory experiment received additional training in the memory-guided saccade task prior to the first test block.

### Data analysis

Saccades were analyzed off-line, using EYEMAP-Software (AMTech). Saccade onset was defined using a velocity criterion (35°/s). The first saccade after fixation offset entered analysis. Saccade accuracy was described as median amplitude error in degree with negative values assigned to hypometric saccades. Trials in which eye movements occurred during stimulus presentation or delay period were excluded from analysis (memory experiment: 10.0 ± 1.8%; control experiment: 13.3 ± 1.8%). After eliminating false responses (memory: 5.1 ± 1.2%; control: 5.4 ± 1.2%) and responses longer than 1,000 ms (memory: 0.92 ± 0.31%; control: 0.41 ± 0.31%), RTs to discrimination stimuli were analyzed as a function of ISI and position of preceding memory cues. Medians were used to describe individual RTs. For the group analyses of each dependent variable,

repeated measures ANOVAs, including the factors ISI (1,500, 2,500, and 3,500 ms), hemifield (discrimination stimulus same vs. opposite to memory cue position), and position (12, 9, and 6°) were used. With respect to analysis of discrimination RTs and accuracy, repeated measures ANOVAs with an additional between-subject factor task (memory vs. control) were used. Post hoc comparisons were performed with paired *t*-tests.

### RESULTS

ISI, hemifield, position, and the between-subject factor task significantly interacted with each other to influence RTs to the discrimination stimulus (4-way:  $F_{(4,72)} = 3.6$ ,  $P = 0.01$ ). In the following, for the sake of clarity, results for the memory and control experiments are described separately.

As is evident from the results of the memory experiment (Fig. 2A), overall RTs decreased progressively with increasing ISI, presumably because of the rising probability of a discrimination to be performed (Niemi and Näätänen 1981). Respective mean RTs were 578 ± 23 (1,500-ms ISI), 540 ± 20 (2,500-ms ISI), and 522 ± 17 ms (3,500-ms ISI). In addition, we observed a significant co-variation of RTs with the position of the preceding memory cue. However, contrary to our expectations, RTs to discrimination stimuli were on average longer when the memory cue was presented on the same side of fixation (1,500-ms ISI: 589 ± 24 vs. 565 ± 22 ms, paired *t*-test,  $P < 0.001$ ; 2,500-ms ISI: 548 ± 21 vs. 532 ± 20 ms,  $P < 0.007$ ; 3,500-ms ISI: 529 ± 17 vs. 515 ± 17 ms,  $P < 0.003$ ). With the 1,500-ms ISI, we observed a peak in RTs to discrimination stimuli presented at the position of the memory cue [605 ± 24 ms at 9° vs. 582 ± 25 ms at 12° (paired *t*-test,  $P < 0.02$ ) and vs. 579 ± 26 ms at 6° ( $P < 0.03$ )]. This finding is unlikely to be due to a trade-off between discrimination speed and accuracy: discrimination accuracy was high in all trial types (mean accuracy memory experiment: 94.9 ± 1.24%; control experiment: 94.6 ± 1.24%), and a four-way ANOVA revealed no significant effect of ISI ( $F_{(2,36)} = 0.08$ ,  $P = 0.93$ ), hemifield ( $F_{(1,18)} = 0.00$ ,  $P = 0.99$ ), or memory cue position ( $F_{(2,36)} = 1.47$ ,  $P = 0.24$ ), and no significant interactions between these factors and the between-subject factor task (all  $P > 0.13$ ). We also assessed the effects of the different experimental factors on accuracy of memory-guided saccades. Statistical analysis revealed a significant effect of stimulus position ( $F_{(2,18)} = 9.8$ ,  $P < 0.001$ ). Neither the presentation side of the discrimination stimulus (hemifield:  $F_{(1,9)} = 2.9$ ,

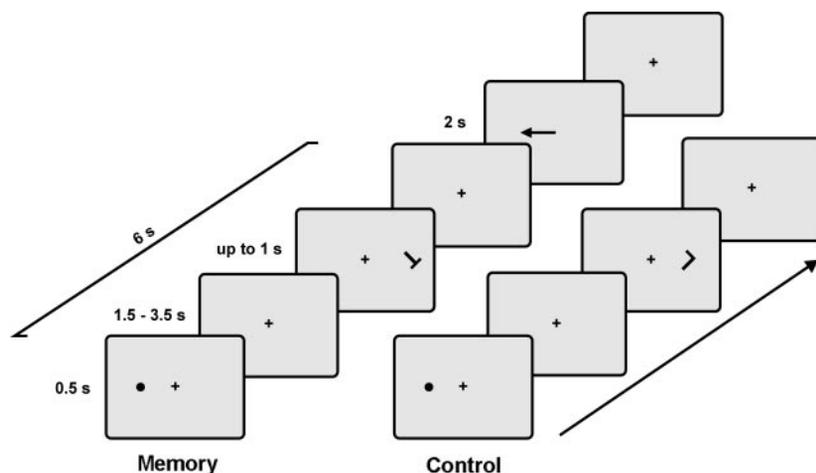


FIG. 1. Schematic of tasks. While fixating on a central fixation cross, subjects were presented a peripheral cue for 500 ms at either 6, 9, or 12° to the left or right. In the memory experiment, subjects were required to remember position of cue and to perform an eye movement toward the remembered cue position after a delay period of 6 s. In the control experiment, no instructions were associated with cue: 1,500, 2,500, or 3,500 ms after the 1st cue, a rotated "T" or "L" was presented at 9° in the same or opposite visual hemifield. Subjects performed a speeded discrimination of this target.

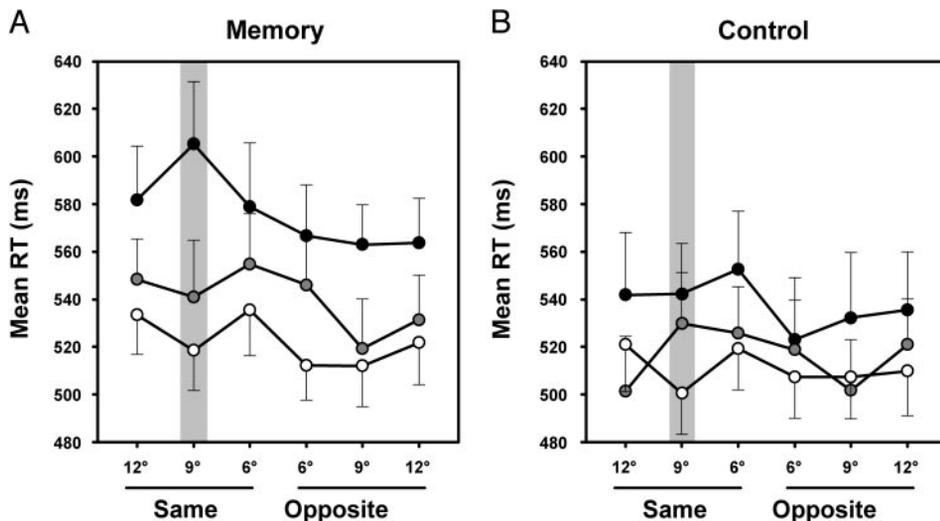


FIG. 2. Mean reaction times (RTs) ± SE for letter discrimination, averaged across subjects for memory (A) and control (B) experiments as a function of 1st cue position in degree. “Same” and “opposite” refers to presentation side of 1st cue with respect to discrimination stimulus. Gray shaded area indicates position of discrimination stimulus. Circle colors correspond to different interstimulus intervals [ISIs; 1,500 (black), 2,500 (gray), and 3,500 ms (white), respectively].

$P = 0.12$ ) nor the ISI ( $F_{(2,18)} = 2.8, P = 0.09$ ) significantly affected accuracy of memory-guided saccades (Table 1). No significant interactions between these parameters were obtained (all  $P > 0.05$ ). Hence, although an overall impairment of memory performance by the dual demands of the task cannot be ruled out, memory of the saccade target was not systematically distorted by the intervening discrimination.

We wondered if the observed modulation of discrimination RTs might simply be a passive consequence of the physical displays used, since initial facilitation of visual processing in and near the location of a nonpredictive peripheral event is followed by an inhibitory aftereffect termed inhibition of return (IOR) (Klein 2000; Posner and Cohen 1984). Thus a possible facilitating effect of spatial memory on RTs might have been masked by superposed IOR as an automatic consequence of the sudden appearance of a peripheral stimulus (Berlucchi et al. 2000; Müller and Rabitt 1989). To deal with this account, we ran a second experiment on another 10 subjects. While employing identical visual displays, we instructed the subjects just to respond to the discrimination letter that would appear at variable intervals after a nonpredictive first cue. In this experiment, RT differences between ISIs were generally smaller [Fig. 2B,  $538 \pm 23$  ms (1,500-ms ISI),  $517 \pm 20$  ms (2,500-ms ISI), and  $511 \pm 17$  ms (3,500 ms ISI)], suggesting that RT differences in the memory experiment might partially be explained by the demands of the concurrent memory task (Jolicœur and Dell’Acqua 1998). At the 1,500-ms ISI, no peak for RTs to discrimination stimuli presented at the position of the memory cue was observed [ $542 \pm 24$  ms at  $9^\circ$  vs.  $542 \pm 25$  ms at  $12^\circ$  (paired  $t$ -test,  $P = 0.98$ ) and vs.  $553 \pm 26$  ms at  $6^\circ$  ( $P = 0.42$ )], although a nonselective RT difference between hemifields was evident ( $546 \pm 24$  vs.  $530 \pm 22$  ms, paired

$t$ -test,  $P < 0.004$ ). This hemifield difference was absent at 2,500- and 3,500-ms ISI (2,500-ms ISI:  $520 \pm 21$  vs.  $513 \pm 19$  ms,  $P = 0.36$ ; 3,500-ms ISI:  $514 \pm 17$  vs.  $508 \pm 17$  ms,  $P = 0.18$ ). We infer that beyond a mere passive aftereffect, an additional inhibition was present in the memory experiment.

Since the behavioral significance of the cue preceding the discrimination target was different in both tasks, inhibitory modulation may not necessarily have depended on the mnemonic component of the memory task. To settle this issue, we split trials of the memory experiment intra-individually into an accurate and inaccurate half depending on absolute error of memory-guided saccades (Fig. 3, A and B). Average amplitude error was  $-0.53 \pm 0.17^\circ$  in accurate trials and  $-2.05 \pm 0.28^\circ$  in inaccurate trials. This approach was chosen to account for interindividual variability of saccade accuracy. Group RTs for trials with 1,500-ms ISIs and coinciding positions of memory cue and discrimination target were significantly longer in accurate than in inaccurate trials (mean RT,  $614 \pm 29$  vs.  $574 \pm 20$  ms, paired  $t$ -test,  $P < 0.03$ ). This difference could point to pronounced inhibition at accurately memorized positions or to a general trade-off between tasks, with response speed in the discrimination task killed for accuracy in the memory task. We therefore computed an index of inhibition separately for accurate and inaccurate trials. It was computed as the individual average of median RTs for trials where memory cue and discrimination stimulus differed in position (i.e.,  $12$  and  $6^\circ$  in the same hemifield and  $12, 9,$  and  $6^\circ$  in the opposite hemifield), subtracted from median RT for the  $9^\circ$  position in the same hemifield. As shown in Fig. 3C, inhibition at the 1,500-ms ISI clearly depended on saccade accuracy. Accuracy of memory-guided saccades is correlated with neuronal activity in prefrontal cortex and provides reliable informa-

TABLE 1. Median targeting error of memory-guided saccades, expressed in degree

ISI (ms)	Same Hemifield			Opposite Hemifield		
	$12^\circ$	$9^\circ$	$6^\circ$	$6^\circ$	$9^\circ$	$12^\circ$
1,500	$-0.71 \pm 0.36$	$-1.12 \pm 0.28$	$-1.37 \pm 0.23$	$-1.49 \pm 0.19$	$-1.47 \pm 0.26$	$-0.49 \pm 0.29$
2,500	$-0.42 \pm 0.38$	$-1.21 \pm 0.27$	$-1.73 \pm 0.20$	$-1.61 \pm 0.25$	$-1.48 \pm 0.31$	$-0.68 \pm 0.29$
3,500	$-0.23 \pm 0.34$	$-1.09 \pm 0.29$	$-1.42 \pm 0.23$	$-1.57 \pm 0.20$	$-1.65 \pm 0.31$	$-0.22 \pm 0.35$

Values are mean ± SE.

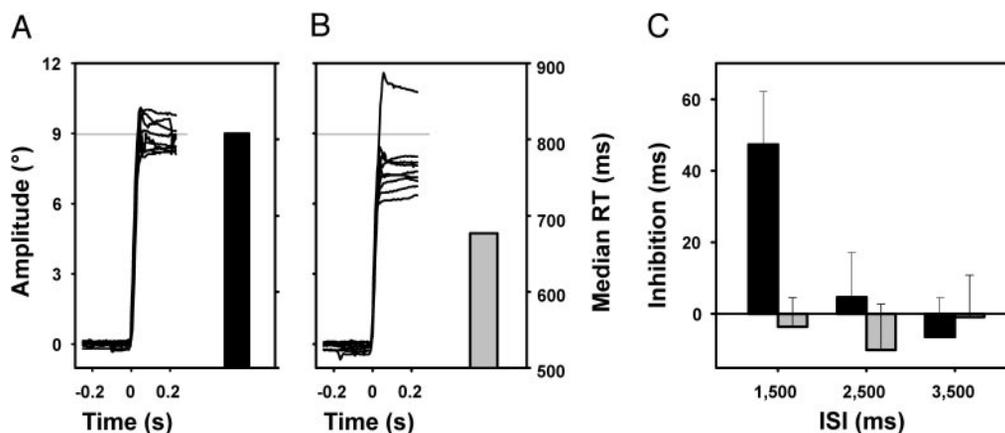


FIG. 3. Accurate (A) and inaccurate (B) memory-guided saccades of 1 representative subject, aligned on saccade onset. Trials with 1,500-ms ISIs and same position of memory cue and discrimination target (represented by gray reference line) are shown. Bars represent corresponding median RTs in the discrimination task. C: spatially selective inhibition expressed as inhibition index (see RESULTS for definition). Averaged individual indices with SE for trials with accurate (black) and inaccurate (gray) memory-guided saccades at different ISIs. Significant inhibition was observed for accurate trials at 1,500-ms ISIs (1-sample *t*-test,  $P = 0.01$ ). Other index values were not significantly different from 0.

tion about the actual strength of spatial working memory representations (Compte et al. 2000; Funahashi et al. 1989). Thus this result demonstrates that actual working memory representations indeed imposed an inhibitory impact on visual processing with efficient maintenance leading to inhibition at remembered positions.

#### DISCUSSION

The spatially selective inhibition observed in this study closely matches the spatial distribution of IOR obtained in a cue-saccade paradigm (Dorris et al. 1999). We therefore speculate that the presentation of the memory cue led to an inhibition of discrimination performance similarly to IOR. Consistent with this hypothesis, IOR has not only been found in detection tasks, but also in visual discrimination tasks (Lupianez et al. 1997; Pratt et al. 1997), suggesting that IOR may result from inhibitory modulation of visual processing (Handy et al. 1999; McDonald et al. 1999). IOR has been demonstrated in tasks involving reflexive orienting to peripheral events (Klein 2000; Posner and Cohen 1984) and in tasks requiring execution or preparation and subsequent cancellation of a saccade (Posner and Cohen 1984; Rafal et al. 1989). In contrast, the spatially selective inhibition presented here apparently constitutes an active mechanism that accompanies efficient maintenance of spatial representations in working memory. This effect has not been reported so far and appears to contradict previous findings, since modulation of visual processing at remembered locations has previously been shown to be mainly facilitating (Awh and Jonides 2001; Awh et al. 1998, 2000; Supèr et al. 2001; Bisley and Goldberg 2003). What causes this discrepancy? Net facilitation or IOR following a peripheral stimulus is thought to result from superposed facilitating and inhibitory effects of attentional orienting, which follow different time courses after stimulus appearance (Berlucchi et al. 2000; Müller and Rabitt 1989). It appears therefore possible that distinct rehearsal mechanisms in spatial working memory (Awh and Jonides 2001; Awh et al. 1998) lead to differential modulation of these facilitating and inhibitory effects depending on ISI and current behavioral demands. Direct

support for this hypothesis will require additional experiments, e.g., recording of visual evoked potentials, in humans performing the paradigms used here.

In a previous study, facilitating effects of spatial working memory have been reported with a delayed matching-to-sample procedure (Awh and Jonides 2001; Awh et al. 1998). However, apart from sensory registration of a peripheral cue and active short-term maintenance of its position, memory-guided saccade tasks rely on additional cognitive operations, such as preparation and execution of an internally triggered saccade and suppression of a saccade toward the remembered cue position during the memory delay (Funahashi et al. 1989). We therefore hypothesize that, compared with delayed matching-to-sample tasks, the particular behavioral demands of our oculomotor spatial working memory task require pronounced inhibitory activity in neuronal substrates of spatial working memory. Indeed, during the delay of a memory-guided saccade task, there is both spatially selective excitatory and inhibitory neural activity in dorsolateral prefrontal cortex (Funahashi et al. 1989, 1993). Activity of these neuronal populations shows distinct time courses, with excitatory activity increasing and inhibitory activity decreasing as the memory delay proceeds (Funahashi et al. 1989). A central operation attributed to these latter neurons is the suppression of saccadic eye movements during the memory delay (Funahashi et al. 1989, 1993; Pierrot-Deseilligny et al. 2003) via prefronto-tectal projections to the superior colliculus (Gaymard et al. 2003), a midbrain structure critically involved in control of saccadic eye movements and shifts of attention (Kustov and Robinson 1996). We speculate that the function of these neurons is not restricted to suppression of inappropriate saccades but extends to covert attention shifts as well, with behavioral net inhibitory or facilitating top-down effects being critically dependent on the necessity of overt orienting in a particular behavioral context. Hence, active inhibition may be more marked shortly after presentation of the peripheral target and thus determine the behavioral outcome. With increasing memory delay, facilitating effects may become more important and attention may finally be allocated to the target location shortly before attention is shifted overtly, i.e., before a memory-guided saccade is executed, as has been

shown previously in single-unit recordings in nonhuman primates (Bisley and Goldberg 2003). The latter is consistent with psychophysical studies, showing that attention is allocated to the target location of an impending saccade (Deubel and Schneider 1996; Kowler et al. 1995).

Of course, our findings do not allow for conclusions on the generality of the observed inhibition. Hence, the exact spatial distribution of memory-dependent inhibition deserves further investigation with paradigms employing discrimination stimuli across the entire visual field. Nevertheless, our observations show that visual processing is modulated much more flexibly by spatial working memory than assumed previously (Awh and Jonides 2001; Awh et al. 1998). This is in line with recent single-unit studies, indicating a flexible association between active maintenance of sensory information for a coming action and covert shifts of attention (Bisley and Goldberg 2003; Powell and Goldberg 2000). In analogy to previous accounts of IOR (Klein 2000; Posner and Cohen 1984), we propose that the memory-dependent inhibitory mechanism observed in our experiments may encourage attentional orienting to new locations in conditions that require both orienting to novel information and maintenance of spatial memoranda for intended actions. Our findings therefore complement previous single-neuron studies by suggesting that the neuronal circuitry controlling IOR not only involves parietal cortex and superior colliculus (Dorris et al. 2002; Klein 2000), but also a significant contribution of intentional states mediated by prefrontal cortex (Funahashi et al. 1989; Goldman-Rakic 1996). Behavioral deficits seen in patients with prefrontal pathology, e.g., in schizophrenia or Huntington's disease, may, at least partially, result from defective inhibitory top-down modulation of perceptual processing.

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#### GRANTS

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