Complementary Roles for Primate Frontal and Parietal Cortex in Guarding Working Memory from Distractor Stimuli

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SUMMARY

Prefrontal cortex (PFC) and posterior parietal cortex are important for maintaining behaviorally relevant information in working memory. Here, we challenge the commonly held view that suppression of distractors by PFC neurons is the main mechanism underlying the filtering of task-irrelevant information. We recorded single-unit activity from PFC and the ventral intraparietal area (VIP) of monkeys trained to resist distracting stimuli in a delayed-match-to-numerosity task. Surprisingly, PFC neurons preferentially encoded distractors during their presentation. Shortly after this interference, however, PFC neurons restored target information, which predicted correct behavioral decisions. In contrast, most VIP neurons only encoded target numerosities throughout the trial. Representation of target information in VIP was the earliest and most reliable neuronal correlate of behavior. Our data suggest that distracting stimuli can be bypassed by storing and retrieving target information, emphasizing active maintenance processes during working memory with complementary functions for frontal and parietal cortex in controlling memory content.

INTRODUCTION

Cognitive control involves the grouping of stimuli into meaningful categories, online storage in working memory, and selection of behaviorally relevant over irrelevant information (Baddeley, 2012). Because working memory has a limited capacity, relevant information needs to be protected against distracting representations (Luck and Vogel, 1997; Vogel et al., 2005). The prefrontal cortex (PFC) and posterior parietal cortex (PPC) are thought to be the major nodes that enable us to selectively attend to target stimuli while filtering distracting information.

A large body of experimental evidence suggests that PFC and PPC adopt specialized functions in working memory and selective attention. PPC neurons represent the most recent stimulus irrespective of its relevance to the current task (Constantinidis and Steinmetz, 1996), and thus fully encode distractors (Bisley and Goldberg, 2003, 2006; Suzuki and Gottlieb, 2013). In contrast, PFC has been associated with controlling lower-level visual areas and gating access to working memory (Anderson and Green, 2001; Feredoes et al., 2011; McNab and Klingberg, 2008). The ability to resist interfering stimuli is compromised in monkeys (Malmo, 1942; Suzuki and Gottlieb, 2013) and humans with lateral PFC lesions (Chao and Knight, 1995, 1998). Responses of single PFC neurons in the monkey are diminished for unattended targets (Everling et al., 2002). Compared to parietal cells, PFC neurons respond little to the presentation of distractors (di Pellegrino and Wise, 1993; Lennert and Martinez-Trujillo, 2011; Qi et al., 2010; Suzuki and Gottlieb, 2013). These studies collectively suggest that attentional filtering performance in primates relies on the ability of PFC neurons to suppress interfering stimuli.

Our current knowledge of the resistance to memory interference stems from experiments that measured neuronal responses to comparatively simple spatial stimuli placed in the visual periphery. Thus, there is currently insufficient data to determine whether prefrontal inhibition of distractors is a general principle of cognitive functioning or rather restricted to particular situations. Specifically, it is unknown whether prefrontal suppression of interfering stimuli is found when more complex features that typically drive PFC neurons, such as abstract cognitive categories, have to be filtered. To investigate the neuronal mechanisms of maintaining abstract category information in the light of interference, we trained two rhesus monkeys to memorize the number of visual items (numerosity) while resisting other distracting numerosities. We then simultaneously recorded single-unit activity from the PFC and the ventral intraparietal area (VIP) of the PPC, two key areas for numerosity processing that contain high proportions of quantity-selective neurons (Nieder and Miller, 2004; Nieder et al., 2002, 2006; Viswanathan and Nieder, 2013).

We considered two hypotheses. Task-irrelevant distractor numerosities could be processed primarily by parietal neurons, whereas prefrontal neurons might remain largely unaffected by interfering information. Alternatively, PFC target representations could break down in the face of strong distracting stimulation, possibly requiring this area to regenerate target information following the interference to solve the task. We found evidence for the latter. PFC readily represented the distractor but subsequently recovered target information, while,
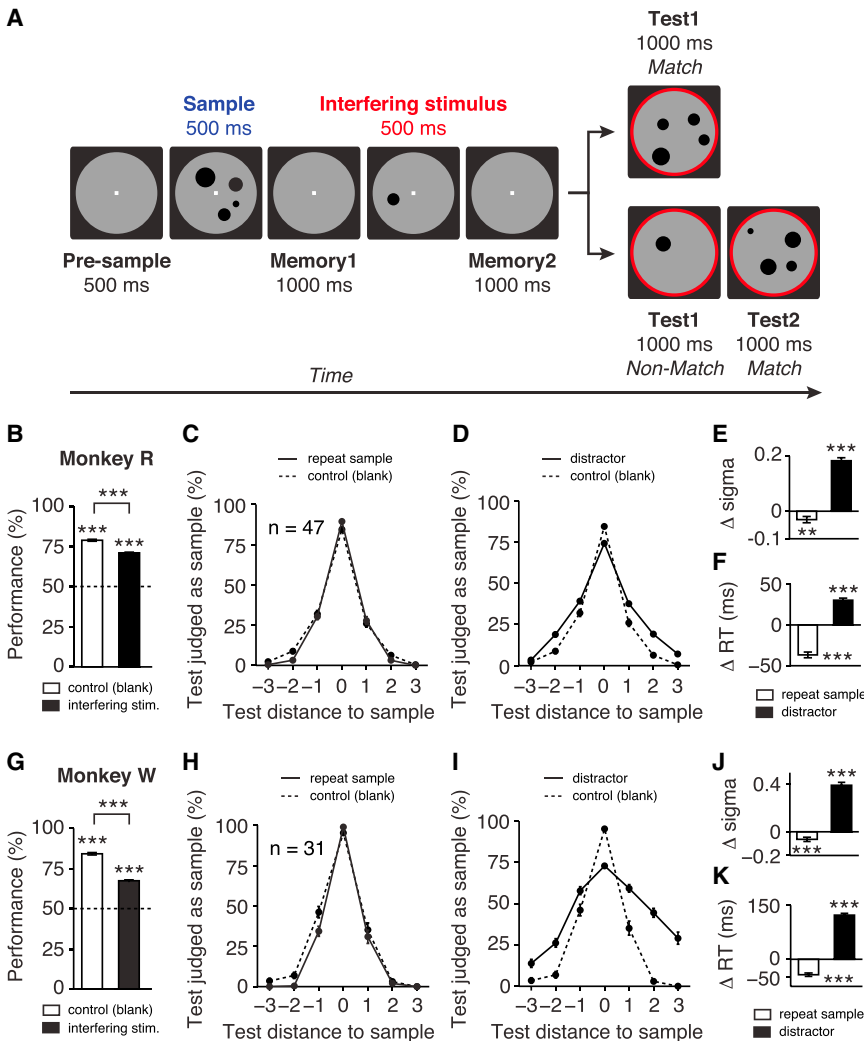
Figure 1. Task Protocol and Behavioral Performance

(A) Delayed-match-to-sample task. Monkeys had to release a bar if the sample and first test display contained the same number of items (match) and had to continue holding it if they did not (non-match). A task-irrelevant, interfering numerosity presented in the working memory period had to be resisted.

(B–F) Behavioral performance for monkey R (n = 47 sessions).

(B) Mean performance in trials without (control, blank) and with interfering stimuli. The dashed line denotes chance level.

(C) Performance curves for trials without interfering stimuli (control; dashed line) and for trials where the interfering numerosity was identical to, i.e., repeated the sample (solid line). The monkeys' performance for all sample test combinations is plotted against numerical distance between test and sample numerosity. The peak represents the percentage of correct match trials, and other data points mark the percentage of errors in nonmatch trials.

(D) Performance curves for trials without interfering stimuli (control; dashed line) and for trials where the interfering numerosity was not identical to the sample, i.e., a true distractor (solid line).

(E) Performance curve width was used as a measure of the precision of sample numerosity representation. Data are presented as the difference in width compared to the control condition for trials where the interfering numerosity repeated the sample (left bar) and for trials where the interfering numerosity represented a true distractor (right bar).

(F) Difference in RTs (correct match trials) compared to the control condition for trials where the interfering numerosity repeated the sample (left bar) and for trials with a true distractor (right bar).

(G–K) Same convention as in (B)–(F) for monkey W (n = 31 sessions). Error bars, SEM across sessions. **p < 0.01; ***p < 0.001.

surprisingly, target memories were maintained to a significantly greater extent in VIP neurons. Our results differ from previous studies by showing that neuronal suppression of interfering stimuli in PFC is not necessary to overcome distractors, and suggest different mechanisms by which the frontoparietal network controls working memory content to guide goal-directed behavior.

RESULTS

Behavioral Performance

Two monkeys performed a modified version of a delayed-match-to-numerosity task (Nieder et al., 2002) (sample numerosities 1–4), in which a task-irrelevant, interfering numerosity was embedded in the working memory period (Figure 1A). The 500-ms-duration interfering stimulus (ranging from 1 to 4 items) was presented during the memory interval on 80% of the trials (20% of the trials each with numerosity 1, 2, 3, and 4). In the remaining 20% of the trials, a blank gray background circle of

equal duration replaced the interfering numerosity, i.e., no task-irrelevant stimulus was shown (standard delayed-match-to-numerosity task). These trials served as control trials. Low-level visual features were controlled and could not systematically influence task performance (Nieder et al., 2002).

Both animals had previously received extensive training in the standard delayed-match-to-numerosity task (Nieder et al., 2006). Within 3 to 5 months of gradually introducing the interfering numerosity, performance also stabilized in these trials (see Experimental Procedures). As expected, performance in trials with interfering stimuli was lower compared to control trials (monkey R: 71% ± 0.5% versus 79% ± 0.6% [n = 47 sessions], p < 0.001, Wilcoxon signed-rank test, Figure 1B; monkey W: 67% ± 0.5% versus 84% ± 0.8% [n = 31 sessions], p < 0.001, Figure 1G). Importantly, both animals performed significantly above chance level in trials with interfering stimuli (p < 0.001, Wilcoxon signed-rank test, for monkey R, Figure 1B, and monkey W, Figure 1G). Successful filtering of the interfering stimulus was evident in match trials where the interfering