Research Article

Visual Short-Term Memory Load Suppresses Temporo-Parietal Junction Activity and Induces Inattentional Blindness

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ABSTRACT—*The right temporo-parietal junction (TPJ) is critical for stimulus-driven attention and visual awareness. Here we show that as the visual short-term memory (VSTM) load of a task increases, activity in this region is increasingly suppressed. Correspondingly, increasing VSTM load impairs the ability of subjects to consciously detect the presence of a novel, unexpected object in the visual field. These results not only demonstrate that VSTM load suppresses TPJ activity and induces inattentional blindness, but also offer a plausible neural mechanism for this perceptual deficit: suppression of the stimulus-driven attentional network.*

Theories of visual attention distinguish between two forms of attentional control (Egeth & Yantis, 1997): goal-driven, in which attention is voluntarily deployed to serve a particular goal, and stimulus-driven, in which attention is reflexively summoned by salient or unexpected changes in the environment. These two attentional processes are also neurally dissociable (Corbetta & Shulman, 2002). The dorsal aspect of the parietal lobe, particularly the intraparietal sulcus (IPS), has been associated with goal-driven behavior: This brain region is recruited in studies of task-driven attention (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Nobre, Gitelman, Dias, & Mesulam, 2000; Shulman et al., 2003), and its activity strongly correlates with attentional or working memory task demands (Cohen et al., 1997; Culham, Cavanagh, & Kanwisher, 2001; Linden et al.,

2003; Todd & Marois, 2004). In contrast, the inferior portion of the parietal lobe and adjacent superior temporal cortex, which together make up the temporo-parietal junction (TPJ), have predominantly been associated with stimulus-driven attention. This brain region is involved in the identification and evaluation of, and reorienting of attention toward, salient or unexpected sensory events (Arrington, Carr, Mayer, & Rao, 2000; Corbetta et al., 2000; Downar, Crawley, Mikulis, & Davis, 2000, 2002; Marois, Leung, & Gore, 2000; Serences et al., 2005). Lesions of the TPJ, particularly in the right hemisphere, can lead to deficits in the conscious perception of sensory stimuli presented in the contralateral hemifield (Friedrich, Egly, Rafal, & Beck, 1998). On the basis of these and other findings, the TPJ has been proposed to act as a "circuit breaker" that interrupts ongoing processes for the analysis of potentially behaviorally relevant visual events (Corbetta & Shulman, 2002).

Interestingly, while the IPS is activated during attention-demanding visual search tasks, the TPJ is suppressed (Marois, Yi, & Chun, 2004; Shulman et al., 2003; Zacks, Gilliam, & Ojemann, 2003) relative to baseline conditions (see also Gusnard & Raichle, 2001; Shulman et al., 1997). These results suggest that TPJ activity may be inhibited during goal-driven behavior, perhaps to prevent interference from task-irrelevant sources during the execution of attention-demanding processes. This hypothesis leads to two predictions: First, as demands of a goal-oriented task increase, TPJ activity should be increasingly suppressed. Second, given the involvement of the TPJ in stimulus-driven attention, tasks that suppress TPJ activity should also impair the ability to detect task-irrelevant sensory events. Here we present functional magnetic resonance imaging (fMRI) and behavioral findings supporting both of these predictions.

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EXPERIMENT 1: VISUAL SHORT-TERM MEMORY LOAD SUPPRESSES TPJ ACTIVITY

As an initial test of the prediction that TPJ activity is inversely correlated with task demands, we determined the effect of manipulating the load of a visual short-term memory (VSTM) task on TPJ activity. Holding a number of objects in VSTM is evidently a goal-driven endeavor, and the demands of the task can be easily manipulated by increasing the number of items that must be held in VSTM (Cowan, 2001; Luck & Vogel, 1997; Pashler, 1988). Thus, although one visual object can be maintained in VSTM almost effortlessly, holding four items requires considerably more effort, as evidenced by a drop in performance as VSTM load increases from one to four (e.g., Todd & Marois, 2004; Vogel, Woodman, & Luck, 2001). Furthermore, VSTM load is correlated with activity in the IPS (Leung, Gore, & Goldman-Rakic, 2002; Linden et al., 2003; Todd & Marois, 2004), a region that is sensitive to attentional task demands (Culham et al., 2001). Thus, manipulation of VSTM load is well suited to assess whether the TPJ is sensitive to the demands of a goal-oriented task.

In a recent event-related fMRI experiment on VSTM load, we observed that activity in the IPS and intraoccipital sulcus (IOS) varied proportionally with the number of objects stored in VSTM (Todd & Marois, 2004). Here, we reanalyzed the data from that experiment to determine if TPJ activity is increasingly suppressed as VSTM load increases.

Method
Seventeen right-handed young adults (9 females) from the Vanderbilt University community participated for financial compensation. All had normal or corrected-to-normal vision.

The experimental methods have been published in detail elsewhere (Todd & Marois, 2004). Briefly, participants were presented with a sample display containing one, two, three, four, six, or eight colored discs for 150 ms and, following a 1,200-ms retention period, determined whether a single disc presented in a 1,750-ms-long probe display matched the location and color of one of the discs in the sample display (Fig. 1a). In order to minimize verbal encoding, we required participants to concurrently perform a verbal working memory/articulatory-suppression task. For each trial, two digits (250 ms/digit, followed by 250 ms of silence and a 250-ms auditory mask) to be rehearsed were presented through headphones 1,700 ms before the visual sample display. After subjects responded to the visual probe, they indicated by button press whether two visually presented digits were identical to the rehearsed digits. Each fMRI run included seven iterations of each of the seven trial types (six set sizes and a nonevent trial with no visual or auditory stimuli presented), with the order of the trial types counterbalanced within runs.

The fMRI data were analyzed with BrainVoyager 4.9.1 (Brain Innovation, Maastricht, The Netherlands), as described before (Todd & Marois, 2004), except that voxels whose activity in-versely correlated with VSTM load were isolated using a voxel-based multiple regression analysis with linear-weighted set-size coefficients (similar results were obtained with quadratic-weighted coefficients). The overall model fit was assessed with an F statistic using a random-effects model, and voxels were considered significantly activated if p was less than .05, corrected. For each region of interest (ROI), we first averaged the signal across all voxels and then extracted the time courses from the trials of each of the six set-size conditions. The average time course was then calculated across trials of each condition, and the percentage signal change was computed using the time series of the nonevent trials as baseline, standardized to the mean of the volume directly preceding and the volume containing the presentation of the sample array (time = 0 s and 2 s in Fig. 1c).

Results and Discussion
Figure 1b shows the statistical parametric map (SPM) for voxels whose activity varied inversely with VSTM load. The SPM revealed a single region in the right TPJ, with Talairach coordinates of the center of mass at $x = +59$, $y = -47$, and $z = +24$. Reducing the threshold 10-fold revealed additional activation in the left TPJ ($x = -55$, $y = -50$, $z = +24$). Time-course analysis of right TPJ activation confirmed that the peak response amplitude decreased with increased VSTM load (Fig. 1c), $F(5, 75) = 2.28$, $p = .05$, $\eta_p^2 = .13$, although there was insufficient statistical power to determine whether the hemodynamic response function was better described as linear or quadratic (Rosnow & Rosenthal, 1996; Todd & Marois, 2004).

By revealing that activity of the right TPJ is inversely correlated with VSTM load, these results support the prediction that TPJ activity is increasingly suppressed with increased task demands.

EXPERIMENT 2: TPJ ACTIVITY IS SUPPRESSED DURING VSTM MAINTENANCE

VSTM or visual working memory tasks are traditionally decomposed into encoding, maintenance, and retrieval phases (Cohen et al., 1997). Because of the short retention interval (1,200 ms), the first experiment could not determine which VSTM phases were associated with TPJ suppression. In Experiment 2, we used a retention interval (9,200 ms) long enough to dissociate activity related to each of the three VSTM phases (Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Zarahn, Aguirre, & D'Esposito, 1997).

Method
Fourteen young adults (8 females; 12 right-handed) with normal or corrected-to-normal visual acuity participated for financial compensation.

The experimental paradigm was similar to that of Experiment 1 except for the following modifications: The retention interval was extended from 1,200 to 9,200 ms (trial duration: 18 s; seven

trials/fMRI run); only two set sizes (1 and 3) were used, to compensate for the lower number of trials; and there were no nonevent trials. Colored discs were presented 1.5 s prior to the standarized volume (time = 0 s).

The right TPJ ROI isolated in Experiment 1 was analyzed as described earlier, except that the percentage signal change of each time course was standardized to the first image acquired after stimulus presentation (baseline), as the signal from the previous image still included the falling phase of the response to the previous trial (Todd & Marois, 2004). Volumes acquired 3.5 through 5.5 s, 9.5 through 11.5 s, and 15.5 through 17.5 s after stimulus presentation were selected for analysis of the blood-oxygenation-level-dependent (BOLD) response at encoding, maintenance, and retrieval, respectively. Early encoding and late response periods were selected to minimize contamination from the VSTM maintenance period.

Results and Discussion

The number of objects stored in VSTM, as determined by Cowan's K formula (Cowan, 2001; Todd & Marois, 2004), was
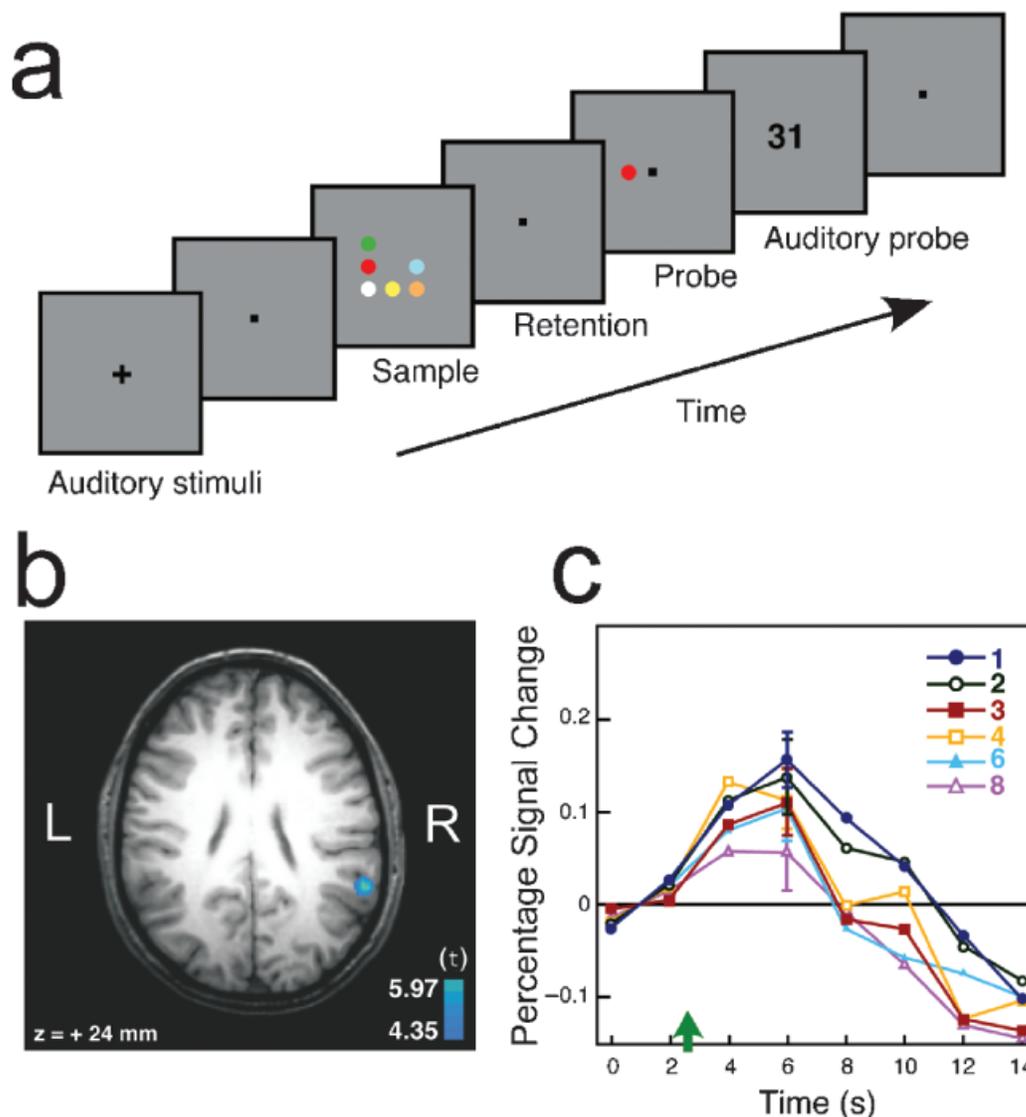
Fig. 1. Illustration of the stimulus sequence (Todd & Marois, 2004) and results from Experiment 1. The stimulus sequence is illustrated in (a). While subjects performed a verbal working memory/articulatory-suppression task, a sample display containing one to eight colored discs was presented briefly. Following a 1,200-ms retention interval, subjects decided whether a single disc presented in a probe display matched one of the sample discs in location and color. The statistical parametric map of an axial slice of the brain (b) shows activation inversely proportional to visual short-term memory load in the supramarginal gyrus of the right temporo-parietal junction, group-composite $t(16) = 4.35$, $p < .05$, corrected. The color scale depicts the range of t values of significantly activated voxels. L = left; R = right. The graph in (c) shows the time course of percentage signal change in this region as a function of set size. The green arrow marks when the visual sample array was presented. Error bars represent standard error of the mean.
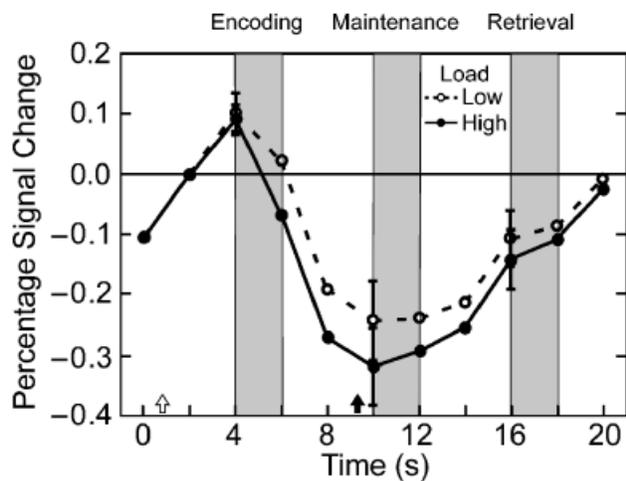
Fig. 2. Time course of activation in the right temporo-parietal junction during the encoding, maintenance, and retrieval phases of visual short-term memory (Experiment 2). Set size was 1 in the low-load condition and 3 in the high-load condition. The white and black arrows correspond to presentation of the sample and probe displays, respectively. Gray vertical bars indicate the volumes used for statistical analyses.

greater at set size 3 than set size 1 (2.00 vs. 0.88), one-tailed t-test, $t(13) = 6.24$, $p < .0001$. Accuracy was also lower at the larger set size (83.45% vs. 94.16%), $t(13) = 4.50$, $p = .0003$. Not only was right TPJ activity suppressed below baseline level during the maintenance phase of VSTM, but this suppression was greater for set size 3 than set size 1 (Fig. 2), $t(13) = 2.84$, $p = .007$. In contrast, there was no effect of VSTM load at encoding, $t(13) = 0.69$, $p = .25$, or retrieval, $t(13) = 1.37$, $p = .10$.

These results not only provide further evidence that right TPJ activity is suppressed by VSTM load, but also establish that this suppression is prominent during the maintenance phase of VSTM.

EXPERIMENT 3: TPJ ACTIVITY IS INVERSELY PROPORTIONAL TO VSTM DEMANDS

Although the first two experiments indicate that VSTM load affects TPJ activity, they could not establish whether this effect is related to general task effort or more specifically to VSTM task demands. Experiments 3 and 4 addressed this issue.

Experiment 3 specifically determined whether TPJ activity is inversely proportional to VSTM maintenance demands rather than to overall task difficulty. We have previously shown that the number of objects stored in VSTM increases markedly between set sizes 1 and 3, but not much between set sizes 3 and 6 (Todd & Marois, 2004). Thus, if the TPJ response is related to VSTM maintenance capacity, we would expect an activation difference between set sizes 1 and 3, but little or no difference between set sizes 3 and 6. By contrast, if the TPJ response is related to overall task effort, TPJ activity should be further suppressed between set sizes 3 and 6.

Method

Six adults (3 females; 6 right handed) with normal or corrected-to-normal visual acuity participated for financial compensation. The experimental paradigm was identical to that of Experiment 2, except that we used three set sizes: 1, 3, and 6.

Results and Discussion

The number of objects stored in VSTM was greater at set size 3 than set size 1 (1.99 vs. 0.90), one-tailed t-test, $t(5) = 6.05$, $p < .01$, but there was no difference between set sizes 3 and 6 (1.99 vs. 1.68), $t(5) = 0.76$, $p = .48$. Correspondingly, TPJ activity showed greater suppression at set size 3 than set size 1, $t(5) = 2.34$, $p < .05$, one-tailed (Fig. 3a), but no difference between set size 6 and set size 3, $t(5) = 0.79$, $p = .23$, one-tailed. These results suggest that TPJ activity suppression is proportional to the number of objects maintained in VSTM, rather than to the number of objects displayed. Because the TPJ is also suppressed during attention-demanding tasks (Marois et al., 2004; Shulman et al., 2003; Zacks et al., 2003), the VSTM load-related suppressive effects likely correspond to the attentional demands for VSTM maintenance.

EXPERIMENT 4: TPJ ACTIVITY IS NOT MODULATED BY PERCEPTUAL DIFFICULTY

Another approach for assessing whether modulation of TPJ activity by VSTM load can be accounted for by overall task effort is to determine whether the TPJ is similarly affected by any demanding tasks. Specifically, Experiment 4 tested whether the TPJ responds to a manipulation of perceptual difficulty. Subjects made a perceptual judgment about the color of a foveally presented object under varying levels of visual degradation.

Method

Twelve individuals (6 females; 11 right-handed) from the Vanderbilt University community participated for financial compensation. All had normal or corrected-to-normal vision.

A trial began with a fixation cross for 900 ms, followed by a 100-ms blank screen, and then by a single equiluminant red or green disc ($1.1°$ of visual angle) on which was overlaid a $3.3° \times 3.3°$ field of randomly colored noise that covered 20% of the pixels making up the disc (Fig. 3b). The 150-ms-long stimulus display was followed by a 250-ms blank screen and by a 2,600-ms fixation screen during which participants made a two-alternative forced-choice response regarding the disc's color. On any given trial, the disc contrast was set to one of three possible values. These contrast values were adjusted prior to each fMRI run to obtain three different performance levels (easy, moderate, hard), as evidenced by reaction time (RT) and accuracy. In each fast event-related fMRI run, there were four conditions (three difficulty manipulations and a nonevent condition), with 24 trials per condition. The order of conditions was counterbal-
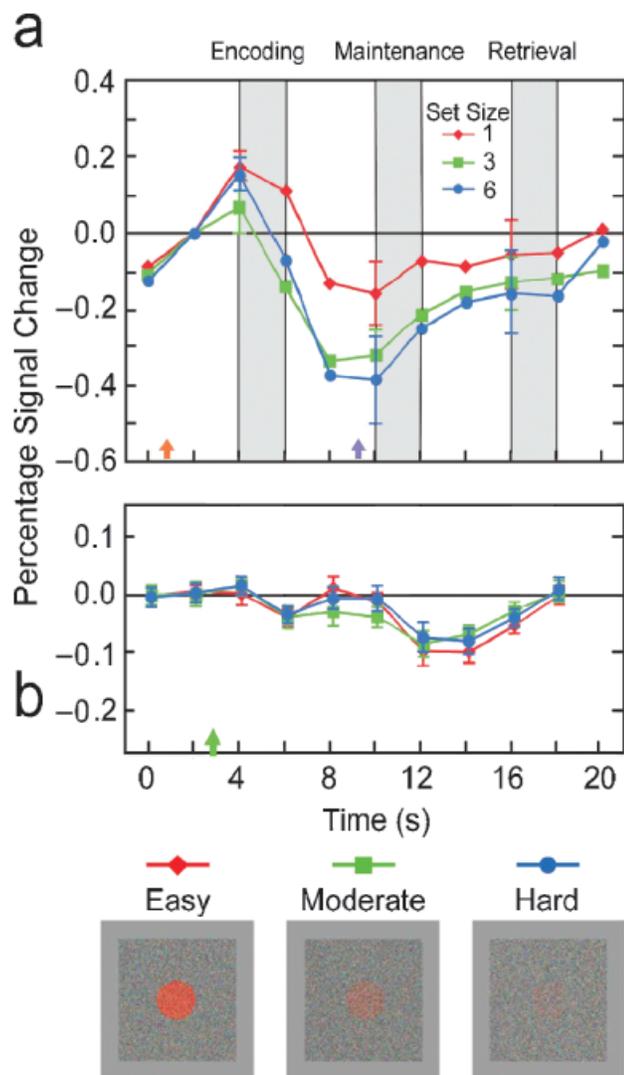
Fig. 3. Time course of activation in the right temporo-parietal junction in Experiments 3 and 4. In Experiment 3 (a), visual short-term memory load was manipulated by varying set size (1, 3, or 6 colored discs). The orange and purple arrows correspond to presentation of the sample and probe displays, respectively. Gray vertical bars indicate the volumes used for statistical analyses. In Experiment 4 (b), perceptual difficulty (target contrast) was manipulated (easy, moderate, or hard). The green arrow corresponds to the onset of the display. The examples at the bottom illustrate the three levels of target contrast used.

anced within each run, and each participant performed four to six functional runs. The fMRI parameters and TPJ ROI analysis were identical to those of Experiment 1.

Results and Discussion

Accuracy decreased (easy, 96.7%; moderate, 93.3%; hard, 79.5%) and RT increased (easy, 519 ms; moderate, 579 ms; hard, 684 ms) with decreased target contrast, $F(2, 22) = 26.37$, $p < .001$, $\eta_p^2 = .36$, and $F(2, 22) = 17.26$, $p < .001$, $\eta_p^2 = .09$, respectively. The 17% drop in accuracy between the easy

and hard conditions was larger than that between set sizes 1 and 3 in the VSTM tasks of Experiment 2 and our previous study (Todd & Marois, 2004). Yet there was no effect of perceptual difficulty on TPJ activity either 5 s or 7 s after stimulus presentation, when the BOLD response would be expected to reach its peak of activation, $F(2, 11) = 2.70$, $\eta_p^2 = .045$, and $F(2, 11) = 2.30$, $\eta_p^2 = .05$, $ps > .05$ (Fig. 3b). The finding that TPJ activity is not affected by perceptual difficulty provides converging evidence that the VSTM-related suppression of TPJ activity is not due to general task effort.

EXPERIMENT 5: VSTM LOAD INDUCES INATTENTIONAL BLINDNESS

Given the purported role of the TPJ in stimulus-driven attention (Corbetta et al., 2000; Corbetta & Shulman, 2002; Downar et al., 2000, 2002; Marois et al., 2000), the finding that VSTM load suppresses TPJ activity indicates that it should also impair the detection of visual events. We tested this prediction with an inattentional blindness (IB) paradigm (Mack & Rock, 1998; Simons, 2000), which measures detection performance for an unexpected salient stimulus when attention is engaged in a primary task. By assessing the extent to which unexpected, task-irrelevant stimuli are consciously detected, such a paradigm provides a strong test of stimulus-driven attention (Simons, 2000). We therefore measured the effect of manipulating the load of a VSTM task on the detection of an unexpected stimulus presented during the maintenance phase of VSTM.

Method

Ninety-one young adults (41 males) with normal or corrected-to-normal visual acuity participated for financial compensation. Data from 15 of these 91 participants were discarded because they failed to detect the critical stimulus in the full-attention trial (described later in this section), leaving 76 participants for further analysis.

Participants performed a VSTM task as described in Experiment 2, except that the retention interval was 5 s and the set sizes were 1 and 4 (low and high VSTM loads, respectively). The 76 participants were split evenly into the high-load and low-load groups (between-subjects design). Participants were instructed to maintain fixation throughout each trial, and all colored discs were shown within 2° of fixation. After four practice trials, participants performed six experimental trials. The first three were like the practice trials. The next three consisted of the inattention, divided-attention, and full-attention trials, described next.

Inattention (Fourth) Trial

On the fourth trial, 2 s into the retention interval, the unexpected critical stimulus (a 1° white clover in Zapf Dingbats font) was presented for 60 ms, 9.9° from fixation in one of the four quadrants of the screen. Participants were not informed of the

presentation of this stimulus. After the end of the trial, participants were probed with three questions to determine whether they had detected the critical stimulus. The questions were self-paced and presented on the computer monitor. The first question assessed whether subjects had seen anything unusual during the trial; they responded "yes" or "no" by pressing the appropriate key on the keyboard. The second question asked participants to select which stimulus they might have seen among 12 possible objects and symbols selected from MacIntosh font databases (⬜ ✆ ✚ √ ♣ ♫ ⌛ ✌ ✈ ⊕ ▤ ✍). The third question asked participants to select the quadrant in which the critical stimulus may have appeared by pressing one of four keys, each of which corresponded to one of the quadrants. In keeping with previous studies (Most et al., 2001), participants were considered to have detected the critical stimulus successfully if they (a) reported seeing an unexpected stimulus and (b) correctly selected its quadrant location. The object-identity test was too difficult even under full-attention conditions (performance was at chance), owing to the brief peripheral presentation of the unexpected stimulus. Thus, performance with this question was not analyzed further.

Thirty-six of the participants (18 for each load condition) were probed with the three questions after the normal completion of the trial (i.e., following the VSTM and verbal working memory responses). In order to ascertain that poor detection performance reflected IB instead of memory loss (i.e., inattentional amnesia; Wolfe, 1999), we probed the other 40 participants (20 for each load condition) with the same questions immediately after presentation of the critical stimulus by interrupting the trial. Analysis of detection performance showed no effect of critical-probe delay (delayed probe: 61% detection, immediate probe: 70% detection, $p = .47$). These results suggest that deficits in detecting the critical stimulus reflected IB as opposed to inattentional amnesia, and justify the combination of the data from the two probe-delay groups for the main analysis.

Twelve participants from both load groups performed the experiment while being filmed on video camera so we could monitor for eye movements or blinks during the inattention trial. Neither eye movements nor blinks were detected for any of these participants during the presentation of the unexpected stimulus. Thus, performance differences between the VSTM-load groups are unlikely to have been due to eye movements or eye blinks.

Divided-Attention (Fifth) Trial
At the onset of the fifth trial, participants were visually instructed to do as well as they could on the memory task, but also to look for a stimulus appearing during the retention interval. The VSTM display and critical stimulus appeared as described for the inattention trial, followed by an additional 2,940-ms retention interval, and then by the VSTM and verbal working memory response screens. After both responses were recorded, participants were given the three questions regarding detection of the critical stimulus.

Full-Attention (Sixth) Trial
At the onset of the sixth trial, participants were visually instructed to ignore the memory task and instead to look for a stimulus appearing during the retention interval. The trial proceeded as described for the fifth trial except that only the three questions about the critical stimulus were presented 2,940 ms following the critical stimulus.
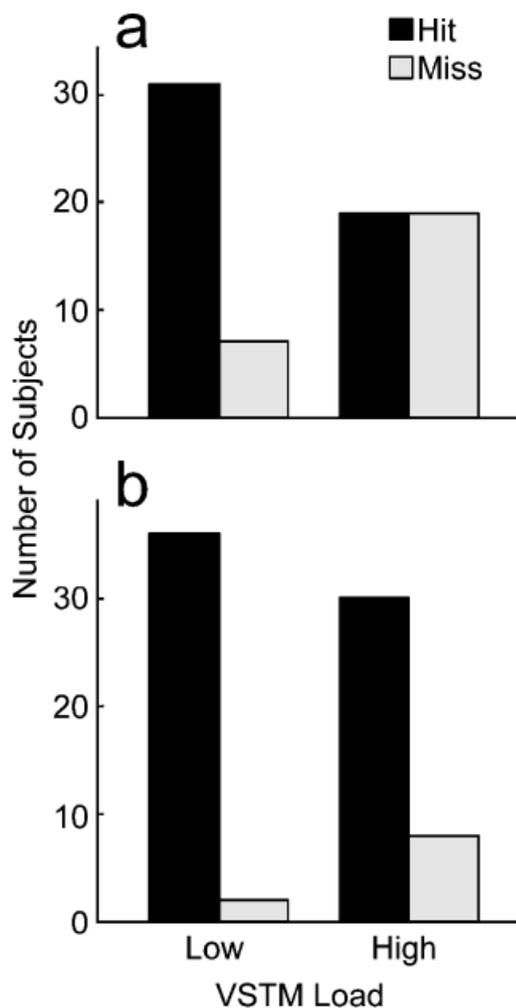
Results and Discussion
VSTM performance for the three experimental trials preceding the inattention trial confirmed that the number of objects stored in VSTM was greater in the high- than in the low-load condition (2.61 vs. 0.91), $t(33) = 5.67$, $p < .0001$. Correspondingly, fewer participants detected the presence and location of the unexpected stimulus (inattention trial) in the high- than in the low-load condition (Fig. 4a, Fisher's exact test, $p < .01$). All of these participants were able to detect and localize the stimulus in a subsequent trial when instructed to ignore the VSTM task (full-attention trial); this result confirms that the impairment was attention based. In addition, participants were impaired at detecting the critical stimulus under divided attention: Marginally fewer participants detected the critical stimulus under high load than under low load (Fig. 4b; Fisher's exact test, $p = .08$). However, the effect of load was smaller under divided attention than under inattention. The detection index (the difference between hits and misses for a given set size) was more affected by VSTM load under inattention (detection index = 24 for set size 1 and 0 for set size 4) than under divided attention (detection index = 34 for set size 1 and 22 for set size 4; Fisher's exact test, $p < .001$). This was the case despite the fact that subjects were still attending to the VSTM task in the divided-attention trial, as indicated by the VSTM performance difference between set sizes 1 (92%) and 4 (71%; Fisher's exact test, $p < .05$). This attenuation of the influence of VSTM load on detection of the critical stimulus under divided attention is consistent with previous IB studies showing that the effects of divided attention on critical-stimulus detection are moderate relative to the effects of inattention (Most et al., 2001).

Taken together, the results of this experiment demonstrate that VSTM load induces IB, supporting the prediction, derived from imaging data, that increased VSTM load should impair stimulus-driven attention.

GENERAL DISCUSSION

The TPJ is a key neural locus of the stimulus-driven attentional network (Corbetta & Shulman, 2002). It is involved in the identification and evaluation of, and reorienting of attention toward, salient visual stimuli (Corbetta et al., 2000; Downar et al., 2000, 2002; Marois et al., 2000). The TPJ is responsive to both task-relevant stimuli and unexpected sensory events (Corbetta & Shulman, 2002; Downar et al., 2002). This response

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Fig. 4. Results from the inattention (a) and divided-attention (b) trials in Experiment 5. The graphs show the number of subjects who detected the critical stimulus (hits vs. misses) as a function of visual short-term memory (VSTM) load (low: set size 1, high: set size 4).

demands of a VSTM task increase, TPJ activity is increasingly suppressed, thereby decreasing the likelihood that unexpected, task-irrelevant stimuli will reach awareness.

More broadly speaking, the TPJ has been proposed to act as a "circuit breaker" that interrupts ongoing processes for the analysis of potentially behaviorally relevant visual events (Corbetta & Shulman, 2002). Thus, suppression of TPJ activity may serve to diminish the ability of unexpected task-irrelevant stimuli from interfering with ongoing behavioral goals. Alternatively, TPJ suppression may reflect not a general protection of goal-driven behavior, but rather a specific interaction between preserving a VSTM image and processing new visual input. Distinguishing between these alternatives will require a systematic determination of the circumstances under which TPJ suppression occurs. It will be of particular interest to determine whether the TPJ is suppressed by tasks that involve other sensory modalities, such as audition, or that engage executive stages of processing (Baddeley, 1986).

It will also be important to determine whether the effect of VSTM load on IB generalizes to all forms of stimulus-driven attention. In particular, VSTM load could also affect the ability of task-irrelevant stimuli to distract attention in attentional-capture (AC) paradigms (Simons, 2000). However, AC tasks involve cognitive processes (e.g., top-down visual search, distractor filtering) that are not involved in our IB paradigm, and some of these processes may also affect, and be affected by, VSTM load and TPJ activity. For example, target search and detection can modulate TPJ activity (Serences et al., 2005; Shulman et al., 2003), and visual search is affected by visuo-spatial short-term memory (Oh & Kim, 2004; Woodman & Luck, 2004). These interactions make it difficult to predict and interpret the potential effects of VSTM load in AC paradigms.

Differences in task composition likely also explain why VSTM load impairs stimulus-driven attention whereas working memory load can increase interference by distractors (de Fockert, Rees, Frith, & Lavie, 2001; Lavie, Hirts, de Fockert, & Viding, 2004). Working memory includes not only VSTM stores, but also executive processes that operate on the contents of these stores (Baddeley, 1986). Tasks that increase executive load impair the top-down attentional mechanisms necessary for filtering out perceived distractors (de Fockert et al., 2001; Lavie et al., 2004). By contrast, here we have shown that increasing the load of VSTM storage impairs stimulus-driven attentional processing. Evidently, the extent to which task-irrelevant stimuli are processed by the brain depends either on the working memory stage at which load is imposed or on the type of attentional mechanism affected.

is maximal for the initial stimulus presentations (Yamaguchi, Hale, D'Esposito, & Knight, 2004) and occurs in the very same TPJ region affected by VSTM load (Marois, Todd, & Gilbert, 2005). Here we showed not only that holding in mind a representation of a visual scene suppresses TPJ activity, but also that the magnitude of this suppression depends on VSTM demands. This finding suggests that TPJ activity levels are tightly regulated during ongoing goal-driven behavior.

What might be the consequences of such task-related control of TPJ activity? Given the TPJ's role in stimulus-driven attention and its VSTM-induced suppression, VSTM load was predicted to impair the ability of unexpected stimuli to capture attention. The IB experiment strongly supported this assertion. These two findings—that VSTM load suppresses right TPJ activity and induces IB—conjure up a plausible neural mechanism of IB, namely, that it at least partly results from the failure of an unexpected stimulus to significantly activate the TPJ. According to this hypothesis, as

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