

The Spatially Asymmetric Cost of Memory Load on Visual Perception: Transient Stimulus-Centered Neglect

Davood G. Gozli, Kristin E. Wilson, and Susanne Ferber
University of Toronto

Recent evidence suggests that visual working memory (VWM) load reduces performance accuracy on a concurrent visual recognition task, particularly for objects presented in the left hemifield. It has also been shown that high VWM load causes suppression of activity in the right temporoparietal junction (TPJ). Given the resemblance of VWM load effects to symptoms of unilateral neglect (i.e., impaired perception on the left side and lesion to the right TPJ), we investigated whether VWM load effects are restricted to the left side of space or extend to object-centered reference frames. In other words, akin to object-centered neglect, can high VWM load cause a perceptual cost in attending to the left side of the stimulus? We addressed this question using an object recognition task (Experiment 1) and a visual search task (Experiment 2) showing that this transient left-neglect can indeed be modulated by an object-centered frame of reference. These findings suggest that load-induced impairments of visual attention are spatially asymmetric and can emerge within multiple spatial reference frames. Therefore, the attentional consequences of high VWM load on conscious perception may serve as a useful model of unilateral perceptual neglect.

Keywords: visual working memory, attention, neglect, hemispheric asymmetries, spatial reference frames

Visual attention arises from the interaction of multiple distinct neural networks (Corbetta & Shulman, 2002; Posner & Dehaene, 1994; Posner & Petersen, 1990). A classification proposed by Corbetta and Shulman (2002) distinguishes between a dorsal attentional network, including the intraparietal sulcus and the frontal eye field, and a ventral attentional network, including the ventral frontal cortex and the temporoparietal junction (TPJ). Although the exact functional distinction of the two networks is not fully understood, the dorsal network is thought to support goal-driven target selection (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000), target-response mapping (Rushworth, Paus, & Sipila, 2001), and maintenance of visual information in working memory (Todd & Marois, 2004; Sheremata, Bettencourt, & Somers, 2010). On the other hand, the ventral attentional network is thought to support detection of salience outside the current focus of attention (Corbetta et al., 2000). In this sense, the ventral attentional network, with the TPJ as its major hub, is thought to act as a “circuit breaker” to enable attentional disengagement from the ongoing task and allocation of attention to unexpected stimuli (Corbetta & Shulman, 2002).

Given that the TPJ subserves shifts of attention to unexpected and salient stimuli, reduced TPJ activity may shelter the current focus of attention from distraction by task-irrelevant information. In particular, when the observer’s goal involves maintaining information in a taxing visual working memory (VWM) task, it is useful to minimize attentional allocation to irrelevant external sources to avoid further demand on limited resources. Indeed, it has been found that a high VWM load is associated with suppressed TPJ activity (Emrich, Burianová, & Ferber, 2011; Todd, Fougne, & Marois, 2005) and that this decrease in TPJ activation is associated with impaired detection of an unexpected stimulus under high VWM load (Todd et al., 2005). These findings are consistent with the role of the TPJ in stimulus-driven attention, which can be inhibited with increased VWM load.

Interestingly, TPJ suppression seems to be more pronounced in the right hemisphere (Emrich et al., 2011; Todd et al., 2005), consistent with the right-hemisphere dominance of the ventral attentional network (Corbetta & Shulman, 2002, 2011), leading to a significantly larger cost of memory load on perception in the left hemifield (Emrich et al., 2011). Emrich et al. (2011) found that participants were less likely to recognize an object in the left visual field if it had been presented under high VWM load. The authors used the term *transient neglect* to describe this impairment, as it was largely confined to the left hemifield and was only present during the retention period of a high-load VWM task.

Visual perception under high VWM load thus seems to share some characteristics with the symptoms of spatial neglect, a neuropsychological disorder following lesions in and around the right TPJ (e.g., Karnath, Ferber, & Himmelbach, 2001). Patients with neglect have difficulty attending to information presented on the left side (Corbetta & Shulman, 2011; Kerkhoff, 2001; Vallar, 1998) and show severe deficits in VWM (Danckert & Ferber, 2006). That is, similar to neglect, the cost of VWM load in healthy

Davood G. Gozli, Kristin E. Wilson, and Susanne Ferber, Department of Psychology, University of Toronto, Toronto, Ontario, Canada.

This study was supported by a Discovery grant from the Natural Sciences and Engineering Research Council of Canada (NSERC), an Early Researcher Award, and a CIHR grant awarded to Susanne Ferber, as well as postgraduate NSERC scholarships awarded to Davood G. Gozli and Kristin E. Wilson.

Correspondence concerning this article should be addressed to Davood G. Gozli, Department of Psychology, University of Toronto, 100 Street George Street, Toronto, ON, Canada, M5S 3G3. E-mail: d.gharagozli@mail.utoronto.ca

adults is spatially asymmetric, with a larger cost in attending to the left hemifield. Given this apparent similarity, it is possible that visual perception under VWM load might provide a useful working model of neglect, representing an alternative to examining patients with brain lesions. To explore this assumption, the present study tests whether an important symptom of neglect, namely, neglect within a stimulus-centered frame of reference, can also be observed in healthy observers under high VWM load. This finding would provide strong support for the idea that visual perception under VWM load can indeed serve as a working model of neglect.

The purpose of the present study, therefore, is to test whether the load-induced transient neglect is limited to the left side of space in an egocentric (i.e., viewer-centered) reference frame or whether it can extend to an allocentric (i.e., stimulus-centered) reference frame. In other words, would transient neglect travel with mental rotations such that it would encompass the left side of an object, regardless of its orientation and position? Although the dominant behavioral symptom of neglect is a deficit in perceiving or exploring the left (i.e., contralesional) side of space within the egocentric frame of reference (Corbetta & Shulman, 2011; Danckert & Ferber, 2006), neglect has also been associated with a deficit in attending to the “left” portion within a stimulus-centered frame of reference (e.g., Behrmann & Moscovitch, 1994; Humphreys & Riddoch, 1994; Tipper & Behrmann, 1996; Walker, 1995). For instance, Driver and Halligan (1991) gave their neglect patient a same/different task with vertically aligned objects. Two objects were presented on each trial and their difference could be on the left or right side of the objects. By rotating both objects by 45°, an object-centered left-side difference could be placed within the egocentric right hemifield, and yet the object-centered “left” continued to be at a disadvantage. Similarly, Driver, Baylis, Goodrich, and Rafal (1994) presented their patients with a gap detection task, wherein the gap was always positioned along the viewer’s vertical midline. Critically, the object’s vertical axis could rotate by $\pm 45^\circ$. Consistent with stimulus-centered neglect, Driver et al. (1994) found a disadvantage for the left side of the object’s vertical axis. Furthermore, the case studies by Humphreys and Riddoch (1994) reported patients for whom viewer-centered and object-centered neglect were in opposite directions (i.e., viewer-centered right neglect and object-centered left neglect). These findings argue for the presence of multiple, dissociable spatial frames of reference in the human brain, while also suggesting that the asymmetric deficit in neglect could affect multiple representational levels.

Although it has been shown that visual processing under VWM load resembles some symptoms of left neglect, this has only been shown within the viewer-centered, egocentric spatial frame of reference (i.e., neglect of the observer’s left side). It is not known whether this load-induced deficit can also affect the “left” segment of space within a scene-centered or object-centered frame of reference, similar to what has been observed in patient studies. To test this possibility, the present study examines two different tasks under low and high VWM load. Like in previous studies, the critical stimuli were always presented during the retention period of a memory task (Emrich et al., 2011; Todd et al., 2005). Experiment 1 examined object recognition with laterally presented objects (left, right, above, and below fixation). Additionally, in Experiment 1, the stimulus-centered reference frame was manipulated by changing the orientation of the memory display, presented at fixation (upright or rotated by $\pm 90^\circ$). With this manip-

ulation, objects above or below fixation were positioned on the left or right, relative to a stimulus-centered reference frame (e.g., with $+90^\circ$ rotation, an object above fixation would be located to the left of the stimulus-centered reference frame).

In Experiment 2, participants performed a visual search task under high and low VWM loads. The search task required reporting the presence/absence of a circle with a gap on the left or right side among distractors with gaps in their top or bottom halves. Thus, when present, the target feature (gap) could appear either on the left or right side of the object. An object-centered cost predicts a higher cost of VWM load for left-gap objects relative to the right-gap objects. Together, the two experiments test whether the cost of VWM load is strictly confined to the viewer-centered left, or whether it spreads to the higher-level object reference frames. Confirming the latter prediction would provide support for the notion that high VWM load and the associated suppression in the attentional network in healthy observers is a working model of unilateral neglect.

Experiment 1A: Object Recognition Under Low Load

This experiment involved an object recognition task performed under low VWM load. On any given trial, two images of objects were presented left and right of a centrally presented VWM stimulus with the possibility that one of them is later probed (see Figure 1). Before encountering the lateral objects, participants saw a central VWM stimulus (a snowman) that was either upright or rotated by $\pm 90^\circ$. With the upright orientation, the stimulus-centered left/right were identical with the viewer-centered left/right. With rotated orientations, the viewer-centered above/below were the stimulus-centered left/right (with $+90^\circ$ rotation) or right/left (with -90° rotation). Examining performance in this task under low VWM load would reveal any preexisting bias on either the viewer-centered or object-centered left side. We did not manipulate VWM load within-participants, in order to avoid fatigue during the experiment (as described later, the experiment consisted of 540 test trials, which took just under an hour to complete).

Method

Participants. Thirty University of Toronto undergraduate students (20 female; M age = 19.4 years, $SD = 2.8$) participated in the experiment in exchange for course credit. Participants reported normal or corrected-to-normal vision, and they were unaware of the purpose of the study. All experimental protocols were approved by the local Research Ethics Board of the University of Toronto.

Apparatus and stimuli. The experiment was run in Matlab (MathWorks, Natick, MA) using the Psychophysics toolbox (Brainard, 1997; Pelli, 1997), version 3.0.8. Stimuli were presented on a 19-in. CRT monitor set at $1,024 \times 768$ pixels resolution and 85 Hz refresh rate. The viewing distance from the monitor was fixed at 45 cm, using a chin/head rest.

The memory display consisted of three colored circles (radius = $.6^\circ$, center-to-center distance = 3°) appearing as buttons of a white snowman, presented against a black background (see Figure 1). Thus, the colored circles were always presented along one midline (vertical midline, in the upright orientation). The image of the snowman fit within a centrally

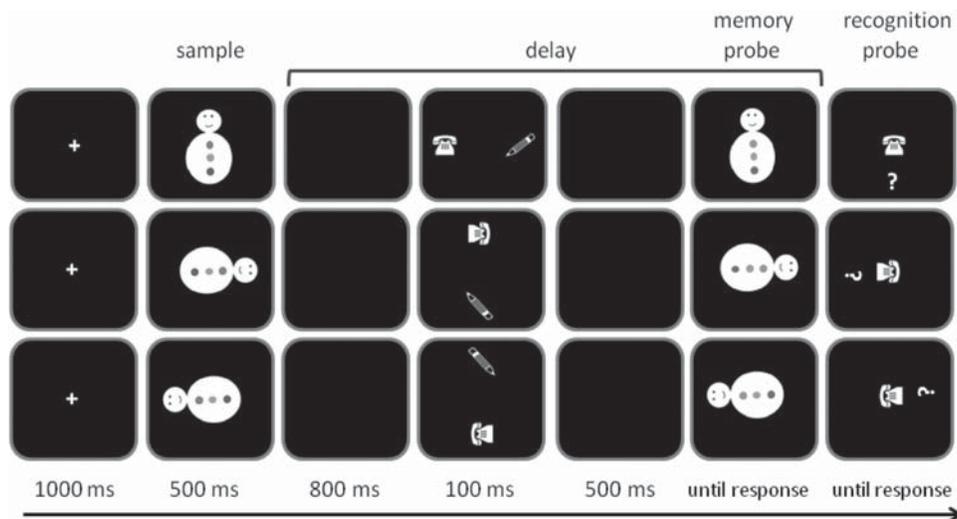


Figure 1. Trial schematic for Experiment 1B. In Experiment 1A, the snowman buttons in the sample display were all gray (no memory task), and in the probe display, only one button would turn to blue. The three rows represent the reference frame rotations of 0 (top), +90 (middle), and -90 (bottom) degrees.

presented rectangle ($8^\circ \times 16^\circ$ for upright conditions, $16^\circ \times 8^\circ$ for rotated conditions). In Experiment 1A, the snowman buttons in the initial (sample) display were all gray and, therefore, participants were not required to memorize any color. In the probe display of the memory task, one of the three snowman buttons changed to blue and participants were required to report the location of this button (see Procedure).

Visual objects used in the recognition task were 12 wingding characters (☎, ✍, ☞, ⌚, 📺, 🗑, 🦋, 🦄, 🕒, 📷, 📺, 📺), each expanded to fit within a $4^\circ \times 4^\circ$ square. Objects were presented in white against a black background. The object recognition sample displays consisted of two objects, presented laterally (center deviating 5° from fixation). In the upright condition, the two objects were presented left and right of fixation, whereas in the rotated conditions, the two objects were presented above and below fixation (i.e., congruent with the orientation of the snowman). For the object recognition probe display, a single object was presented at fixation, still preserving the trial orientation, accompanied by a question mark (see Figure 1).

Procedure. Each trial began with the presentation of a central fixation cross ($1.2^\circ \times 1.2^\circ$) for 1,000 ms and participants were required to wait for the onset of the snowman. The snowman remained on the screen for 500 ms and informed the participants about the display orientation during that trial (upright, or rotated by $+90^\circ$ [i.e., clockwise] or -90° [i.e., counterclockwise]). Half of the trials consisted of the memory task only. In these memory-only trials, the presentation of the first snowman (i.e., memory sample) was followed by a 1,300-ms blank screen (i.e., delay/retention period), after which the snowman was presented for a second time (i.e., memory probe) with one button having turned blue. Participants were instructed to localize the blue button using three keys (“Q” key for *top*, “A” key for *middle*, “Z” key for *bottom*). Importantly, the localization had to be relative to the body of the snowman (i.e., the *top* button was always the one closest to the snowman’s head). The memory probe remained on the screen until

a response was recorded. Given that participants simply had to indicate the location of a blue circle, the memory load on these trials was minimal. The rationale behind this design was to test for recognition performance with our particular visual displays under low load conditions.

As such, the other half of the trials included the object recognition task embedded in the low-load memory task. In these trials, the retention period, instead of being a continuous 1,300-ms blank screen, consisted of a 800-ms blank screen, followed by a 100-ms exposure to an object recognition sample display, followed by another 500-ms blank screen (total retention period = 1,400 ms). In addition, in these trials, upon recording the memory response, the object recognition probe was displayed and participants were required to report whether the probe object had been presented during the delay/retention period of that trial. Object recognition responses were made using the right hand (“</>” keys for yes/no, respectively). No feedback was provided regarding accuracy in the memory or recognition tasks.

Design. Each participant performed 10 practice trials and 540 experimental trials. The three possible orientations were equally likely (upright, $+90^\circ$, or -90° rotation). As mentioned previously, all trials included the memory task, but only half of them (270 experimental trials) included a recognition task. The recognition task was less frequently presented in order to encourage participants to give priority to the memory task. During the recognition probe, presenting each one of the laterally presented objects was as probable as presenting a new object. Therefore, only on one third of the object-recognition trials, the probe was a new object that was not presented during the retention period. Participants were not informed that the “yes” response on the recognition task was more likely to be correct. Postexperiment debriefings, as well as examining false-alarm errors (see Results), confirmed that participants were unaware of this pattern.

Results and Discussion

Memory task. Accuracy in this task was defined as proportion of correct localizations of the color change in the memory probe display. Mean accuracy and response times (RTs) were both submitted to a repeated-measures ANOVA, with orientation (-90° , upright, $+90^\circ$) as the independent factor (see Figure 2). First, for accuracy data, the analysis revealed a significant effect of orientation, $F(2, 58) = 10.89, p < .001, \eta_p^2 = .273$. Accuracy was significantly higher with upright ($M \pm SE = 96\% \pm 2\%$) and -90° ($96\% \pm 1\%$) orientations, compared with the $+90^\circ$ ($94\% \pm 1\%$) orientation (respectively, $t[29] = 3.44, SE = .005, p < .001$, and $t[29] = 3.79, SE = .005, p = .002$), but did not differ between the upright and -90° orientations ($p > .7$).

For RT data, we also found a main effect of orientation, $F(2, 58) = 73.13, p < .001, \eta_p^2 = .716$. Matching the accuracy data, responses were slower with $+90^\circ$ rotation ($M \pm SE = 665 \pm 19$ ms), compared with both the upright condition (597 ± 18 ms), $t(29) = 11.72, SE = 5.86, p < .001$, and the -90° condition (621 ± 19 ms), $t(29) = 6.65, SE = 6.73, p < .001$. Additionally, the upright orientation resulted in faster responses compared with the -90° orientation, $t(29) = 5.33, SE = 4.51, p < .001$. In short, both accuracy and RT data suggest lower efficiency in processing the $+90^\circ$ orientation relative to the other two orientations.

Object recognition. Performance in the recognition task was analyzed using trials with a correct response on the memory task. This is particularly crucial when examining performance under high load (Experiments 1B and 2). Recognition trials were further divided, based on the correct response, into “hit trials” (i.e., when the probe object was presented during the retention period) and “rejection trials” (i.e., when the probe object was not presented during the retention period) trials. Because hit trials were more frequent than rejection trials, it was important to ensure participants were not biased toward false positives. Comparing the two trial types revealed significantly higher accuracy on rejection trials (94%) compared with hit trials (88%), $t(29) = 3.05, SE = .02, p < .01$, inconsistent with a tendency toward false positives. We therefore proceeded with analyzing the hit rates,¹ by submitting them to a 3×2 repeated-measures ANOVA (see Figure 2). The two factors were orientation (-90° , upright, $+90^\circ$) and the location of the probed object during the retention period (left vs. right). Object location was always defined relative to the snowman. For instance, the viewer-centered “above” was defined as “left” with $+90^\circ$ rotation, whereas it was defined as “right” with -90° rotation. This ANOVA revealed a significant main effect of orientation, $F(2, 58) = 4.36, p = .017, \eta_p^2 = .131$. Neither the main effect of object location, $F(1, 29) = 1.25, p = .27, \eta_p^2 = .041$, nor the interaction, $F(2, 58) = 2.27, p = .11, \eta_p^2 = .073$, reached significance. Compared with the upright condition (M hits $\pm SE = 90\% \pm 2\%$), hit rates were lower with both -90° rotation ($87\% \pm 2\%$), $t(29) = 2.72, SE = .011, p = .01$, and with $+90^\circ$ rotation ($87\% \pm 2\%$), $t(29) = 2.45, SE = .011, p = .021$. Hit rates did not differ across the two rotated orientations (-90° and $+90^\circ$), $t < 1$.

Mean RTs were also submitted to the same 3×2 ANOVA (see Figure 2), which revealed a main effect of orientation, $F(2, 58) = 4.20, p = .02, \eta_p^2 = .126$, and a main effect of object location, $F(1, 29) = 18.63, p < .001, \eta_p^2 = .391$. The two-way interaction was not significant, $F < 1$. For the main effect of orientation, paired-sample t tests revealed only a significant difference between the

$+90^\circ$ rotation (688 ± 25 ms) and the upright orientation (657 ± 22 ms), $t(29) = 2.80, SE = 11.04, p < .01$. More importantly, the main effect of object location was indicative of faster responses when the probed objects had appeared on the left side of the snowman ($M \pm SE = 652 \pm 23$ ms) compared with objects that had appeared on the right side (692 ± 23 ms). We suspected this leftward advantage to be primarily driven by the upright orientation. Interestingly, however, the leftward advantage in RTs remained significant even when excluding the upright condition, $t(29) = 3.62, SE = 9.62, p = .001$. In other words, examining the rotated orientations alone, object recognition was faster for objects on the snowman’s left (662 ± 23 ms) than for objects on the right (697 ± 26 ms).

The central finding of Experiment 1A is that we did not find any significant asymmetry in terms of a leftward disadvantage in object recognition accuracy when VWM was not taxed. In fact, we found an RT benefit for objects that were encoded from the left periphery, which may indicate a leftward attentional bias.² A leftward attentional bias has been previously reported in healthy observers, taken to support a right-hemisphere dominant view of visual attentional functions (e.g., Jewell & McCourt, 2000; Rhodes & Robertson, 2002; Toba, Cavanagh, & Bartolomeo, 2011). Thus, Experiment 1A confirmed that in the absence of a working memory load, the attentional mechanisms maintain their regular function: shifting attention to salient information with a slight bias toward preferring the left side of both egocentric and allocentric space. In the next experiment, we test whether a reliable bias in the opposite direction can be induced under high VWM load.

Experiment 1B: Object Recognition Under High Load

This experiment consisted of the object recognition task used in Experiment 1A with an additional high VWM load component. Based on previous findings, we hypothesized that this high VWM load will be associated with a bias against objects located on the left side of space. This perceptual disadvantage under high VWM load could be present only at the viewer-centered left side (i.e., objects located to the left side of the snowman in the upright condition). Alternatively, the leftward disadvantage could travel with rotated orientations of the snowman. If so, a general stimulus-centered disadvantage should be found, such that even objects that are located physically along the midline of the display but appear

¹ Because only a single false alarm score corresponded to hit rates for the two lateral locations (left/right), subtracting that number from the hit rates would not change the results of our analysis. Therefore, after ensuring that observers were not biased toward false alarms, we used hit rates in the subsequent analyses.

² A second possibility is that the leftward bias is a stimulus–response (S-R) compatibility effect (Lu & Proctor, 1995), because the hit key was positioned to the left of the rejection key. This is unlikely because object recognition was performed in response to a probe stimulus, appearing at fixation. Therefore, the probe itself could not activate the left response. The possibility remains, however, that there could be a S-R compatibility effect between the response location and the location of the remembered object. Importantly, there is no reason to expect this S-R compatibility effect to be reversed under VWM load (as we found in Experiment 1B). Therefore, based on the fact that the recognition probe was spatially neutral and the sensitivity to VWM load, the most plausible account of the leftward benefit/cost in the two experiments is the asymmetry in the allocation of attention under low/high load.

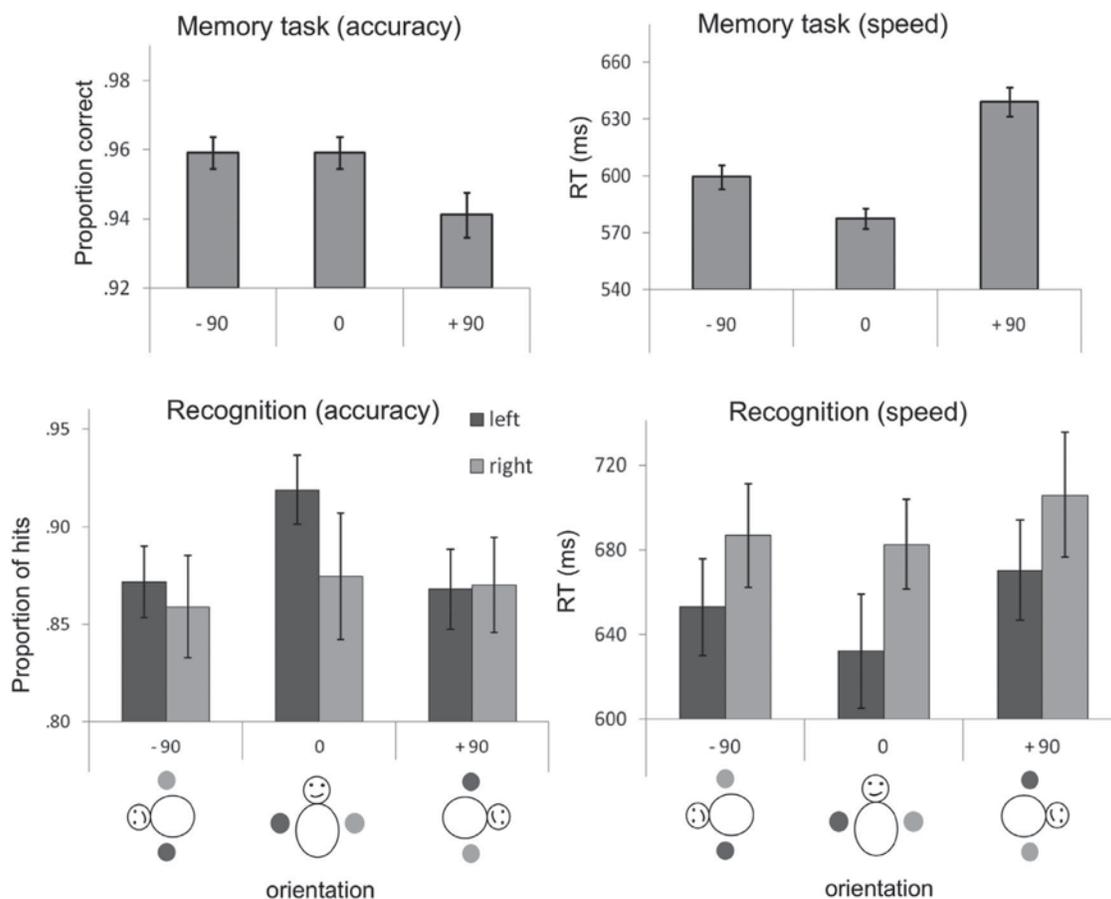


Figure 2. Performance accuracy and RT data in Experiment 1A. The panels above and below represent performance in the memory task and the object recognition task, respectively. Error bars indicate within-subjects 95% confidence intervals (Cousineau, 2005).

left of the reference object (i.e., the snowman) will be affected by this processing bias.

Method

Participants. Thirty new undergraduate students (22 females; M age = 19.5 years; SD = 1.7) at the University of Toronto participated in the experiment in exchange for course credit. Participants reported normal or corrected-to-normal vision, and they were unaware of the purpose of the study.

Apparatus, stimuli, and procedure. The general set-up and procedure was identical to Experiment 1A, except for the displays used in the memory task. The snowman buttons in the sample display were colored uniquely (randomly drawn from the following set: red [RGB values = 255,0,0], green [0,255,0], blue [0,0,255], purple [255,0,255], yellow [255,255,0], green-blue [0,255,255], brown [140,70,20], and gray [128, 128, 128]). We instructed participants to memorize the three colors shown on the memory sample display. In the probe display of the memory task, one of the three buttons would change into a different color. Thus, there was a color change on every trial and participants were required to report the location of this button (top/middle/bottom).

Participants were told that the nonchanging colors would not switch locations.

Design. Similar to the previous experiment, each participant performed 10 practice trials and 540 experimental trials. The three possible orientations were equally likely (upright, +90°, or -90° rotation). All trials included the memory task, but only half of them (270 experimental trials) included the object recognition task, in order to encourage participants to give priority to the memory task. In the object recognition trials, probing one of the laterally presented objects was as probable as presenting a new object, similar to Experiment 1A. Thus, only on one third of the object recognition trials the probe was a new object that was not presented during the retention period. Participants were not informed that the “yes” response on the recognition task was more likely to be correct, and the following results below postexperiment debriefings confirmed that they remained unaware of this pattern.

Results and Discussion

Memory task. Accuracy in this task was defined as proportion of correct localizations of the changed color in the memory probe display. Mean accuracy and RTs were both submitted to a

repeated-measures ANOVA, with orientation (-90° , upright, $+90^\circ$) as the independent factor (see Figure 3). First, for accuracy data, although we observed a trend toward lower accuracy in the $+90^\circ$ condition (80%) compared with the upright (83.6%) and the -90° condition (84%), this pattern did not reach significance, $F(2, 58) = 2.40, p = .100, \eta_p^2 = .076$.

For RT data, we did find a main effect of orientation, $F(2, 58) = 27.40, p < .001, \eta_p^2 = .486$. Congruent with the pattern in accuracy data, responses were slower with $+90^\circ$ rotation ($M \pm SE = 889 \pm 28$ ms), compared with both the upright condition (832 ± 24 ms), $t(29) = 6.95, SE = 8.20, p < .001$, and the -90° condition (834 ± 25 ms), $t(29) = 5.68, SE = 9.56, p < .001$. The upright and -90° orientations did not result in significantly different RTs ($p > .7$).

Object recognition. Trials of this task were first divided, based on the correct response, into “hit trials” (when the probe

object had in fact been presented during the retention period) and “rejection trials” (when the probe object was new) trials. It is very important to establish that participants were not biased toward false positives, which would lead to a lower percentage of correct rejection, relative to the hit rate. Comparing the two trial types revealed no significant difference between correct rejection trials (76%) compared with the hit rates (77%), $p > .5$, inconsistent with a tendency toward false positives. We therefore proceeded with analyzing the mean hit rates, by submitting them to a 3×2 repeated-measures ANOVA. The two factors were orientation (-90° , upright, $+90^\circ$) and the location of the probe object during the retention period (left vs. right of the snowman). This ANOVA revealed a main effect of orientation, $F(2, 58) = 9.92, p < .001, \eta_p^2 = .255$, a main effect of object location, $F(1, 29) = 12.58, p < .001, \eta_p^2 = .303$, but no interaction, $F(2, 58) = 1.91, p = .157, \eta_p^2 = .062$. Compared with the upright condition (M hits $\pm SE = 78\% \pm$

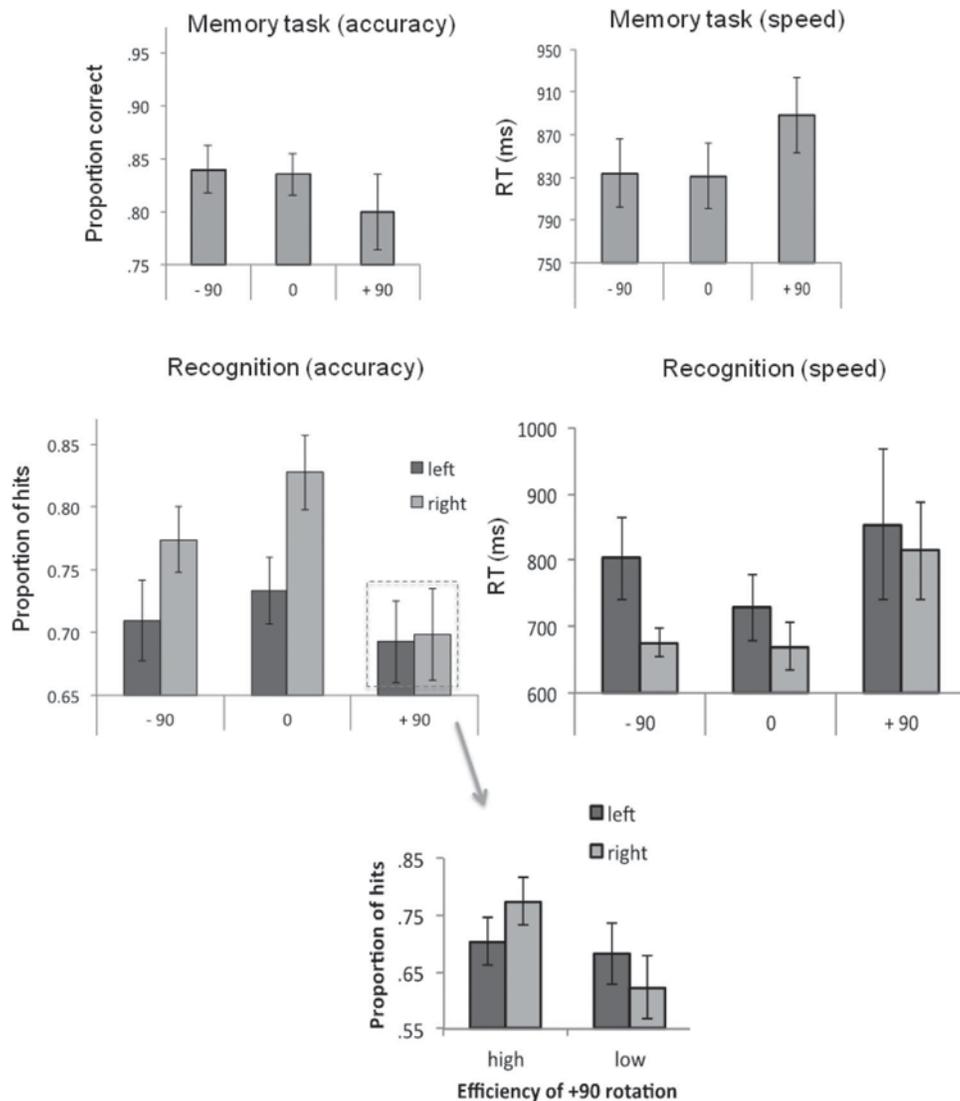


Figure 3. Performance accuracy and RT data in Experiment 1B. Recognition accuracy in the $+90^\circ$ orientation condition is depicted separately as a function of efficiency (high vs. low; median split on mean IES) in the memory task. Error bars indicate within-subjects 95% confidence intervals (Cousineau, 2005).

2%), hit rates were lower with both -90° rotation ($74\% \pm 3\%$), $t(29) = 2.15$, $SE = .019$, $p = .040$, and with $+90^\circ$ rotation ($70\% \pm 3\%$), $t(29) = 4.33$, $SE = .020$, $p < .001$. Hit rates also differed significantly across the two rotation conditions (-90° and $+90^\circ$), $t(29) = 2.41$, $SE = .019$, $p = .023$. Furthermore, object recognition was less accurate on the left ($71\% \pm 2\%$) side of the snowman compared with the right side ($77\% \pm 3\%$). To ensure that the main effect of object location was not solely driven by the upright condition (i.e., viewer-centered neglect), we examined the effect of location after excluding the upright trials. Even when the upright condition was excluded from analysis, the stimulus-centered leftward disadvantage was still observed, with lower hit rates for objects presented on the left side ($70\% \pm 3\%$) compared with objects presented on the right side, ($74\% \pm 3\%$), $t(29) = 2.40$, $SE = .014$, $p = .023$.

Mean RTs were also submitted to a similar 3×2 ANOVA, which revealed a main effect of orientation, $F(2, 58) = 4.31$, $p = .018$, $\eta_p^2 = .130$, and a marginally significant main effect of object location, $F(1, 29) = 4.02$, $p = .054$, $\eta_p^2 = .430$. The two-way interaction did not reach the significance level, $F(2, 58) = 2.54$, $p = .088$, $\eta_p^2 = .080$. For the main effect of orientation, paired-sample t tests revealed significantly faster RTs with upright orientation (700 ± 40 ms) compared with the -90° (740 ± 39 ms), $t(29) = 2.41$, $SE = 16.52$, $p = .023$, and $+90^\circ$ (834 ± 91 ms), $t(29) = 2.48$, $SE = 54.07$, $p = .019$, orientations. The -90° and $+90^\circ$ orientations did not significantly differ ($p > .1$). More importantly, the marginally significant effect of object location was consistent with the pattern observed in accuracy data. Specifically, responses were slower for objects on the left side of the snowman (795 ± 72 ms) compared with objects that had appeared on the right side (720 ± 40 ms). To ensure this pattern was not solely driven by the upright condition, we examined the rotated orientations alone and found the leftward disadvantage in RT data still approaching significance, $t(29) = 1.80$, $SE = 46.15$, $p = .082$. Objects presented on the stimulus-centered left received slower responses (745 ± 40 ms) compared with when they had appeared on the right side (680 ± 37 ms).

Despite the evidence for a stimulus-centered leftward disadvantage, Figure 3 also illustrates that the leftward disadvantage was not obtained with $+90^\circ$ orientation ($ps > .4$ for both accuracy and RT data). Considering this observation, it is important to note that participants were consistently slower and less accurate in the memory task, as well as the recognition task, when faced with $+90^\circ$ orientation. This raises the possibility that perhaps adopting the reference frame of the $+90^\circ$ -rotation displays was challenging, and, consequently, without adopting the reference frame, no stimulus-centered disadvantage should be expected. In particular, if adopting the $+90^\circ$ reference frame is difficult, participants may start to adopt this frame only when faced with the memory probe display, consistent with slower and less accurate responses during the $+90^\circ$ orientation. Assuming some degree of individual difference in adopting this reference frame, we performed the following analysis, examining object recognition performance on trials with $+90^\circ$ orientation as a function of performance efficiency in the memory task.

To divide participants based on how efficiently they adopted the $+90^\circ$ reference frame, we used the Inverse Efficiency Score (IES = $RT/[\text{percent correct}]$; Townsend & Ashby, 1983) on the memory task, which takes into account both accuracy and speed of

localizing the color change with the $+90^\circ$ orientation. After calculating mean IES for each participant on the memory task, we divided them into two equal groups of 15 and examined stimulus-centered neglect in the $+90^\circ$ separately for the high-efficiency ($M \pm SE = 903 \pm 27$ ms) and low-efficiency ($1,128 \pm 135$ ms) groups. We submitted the hit rates to a mixed ANOVA with location (left vs. right) and efficiency (high vs. low) as within- and between-subjects factors, respectively (Figure 3; bottom panel). This analysis revealed no main effect of location, $F < 1$, or efficiency, $F(1, 28) = 2.25$, $p = .145$, $\eta_p^2 = .074$, but a significant interaction, $F(1, 28) = 4.26$, $p = .048$, $\eta_p^2 = .132$. Interestingly, we found a significant leftward disadvantage with the high-efficiency group, $t(14) = 2.24$, $SE = .032$, $p = .042$, but no significant effect of object location with the low-efficiency group, $t(14) = 1.09$, $SE = .055$, $p = .295$. It appears that participants who adopted the $+90^\circ$ orientation reference frame efficiently did show stimulus-centered neglect, with lower hit rates for objects presented on the left ($M \pm SE = 70\% \pm 5\%$) compared with objects presented on the right ($77\% \pm 5\%$). Therefore, the stimulus-centered neglect seems to depend on efficiently adopting the reference frame of the stimulus (here, the rotated snowman).

The reason for the apparent inefficiency of processing the $+90^\circ$ orientation is unclear. It has been suggested that clockwise rotation relies on the right hemisphere, more so than the counterclockwise rotation (Burton, Wagner, Lim, & Levy, 1992; Corballis & Sergeant, 1988). One possibility, therefore, is that the inefficient performance with $+90^\circ$ orientation is due to a within-hemispheric interference. Specifically, assuming that the right hemisphere structures may be more dominantly engaged in maintaining items in VWM (e.g., Sheremata et al., 2010), as well as with attentional orienting toward the lateral objects (e.g., Posner, Walker, Friedrich, & Rafal, 1984), it may be more economical to delay the adoption of the $+90^\circ$ reference frame until encountering the memory probe. This possibility is consistent with the observation that object recognition performance was also worse with -90° orientation compared with the $+90^\circ$ orientation (i.e., without adopting the reference frame objects would be encoded less successfully). A second possible source of inefficiency in processing the $+90^\circ$ orientation is related to stimulus-response (S-R) mapping in the memory task. Specifically, the arrangement of the three keys “Q”/“A”/“Z” may correspond more readily to the buttons of the snowman in the -90° orientation compared with the $+90^\circ$ orientation.³ This S-R mapping explanation, however, cannot account for the object recognition performance difference across the two rotated orientations. Regardless of the reason for the inefficiency, when separating the participants into two equal groups of high and low efficiency, significant object-centered neglect was found for the half of the participants who were highly efficient in the memory task, whereas no such object-centered neglect was observed for the low-efficiency group of participants. This finding is consistent with the object-centered disadvantage being a direct result of adopting the object-centered reference frame.

Comparing object recognition under low and high load. To confirm the effect of VWM load on inducing transient neglect, we compared object recognition performance across Experiments 1A and B. Submitting the accuracy and RT data from both experi-

³ We thank an anonymous reviewer for pointing out this possibility.

ments to mixed $3 \times 2 \times 2$ ANOVAs (within-subject factors: orientation and object location; between-subjects factor: load), revealed significant Load \times Location interactions for both accuracy, $F(1, 58) = 10.56, p = .002, \eta_p^2 = .154$, and RTs, $F(1, 58) = 8.92, p = .004, \eta_p^2 = .133$. Importantly, these Load \times Location interactions remained significant even after excluding the upright orientation (accuracy: $F[1, 58] = 4.13, p = .047, \eta_p^2 = .067$; RT: $F[1, 58] = 6.24, p = .015, \eta_p^2 = .097$), suggesting that the interaction is not solely based on transient neglect being anchored to an egocentric reference frame.

To summarize, Experiments 1A and 1B confirmed that under high VWM load, objects on the left side of space receive a processing disadvantage compared with the objects presented to the right side. Furthermore, this leftward disadvantage is sensitive to the spatial reference frame of the stimuli, such that objects above or below fixation are at a disadvantage if they coincide with the left side of the central stimulus (i.e., the snowman). These findings provide the first indication that VWM load can provoke a transient stimulus-centered neglect.

Experiment 2: Visual Search

In accounting for the findings of Experiment 1, we propose that the objects presented on the left side were at a disadvantage during the initial phase of attentional allocation (i.e., encoding phase). This, however, remains an inference, as responses were measured at the recognition phase (i.e., retrieval phase). Therefore, in order to overcome this limitation and explore object-centered transient neglect without relying on retrieval responses *after* the encoding period, we also used a visual search task in which responses are made *during* the retention period.

In addition to examining the cost of VWM load within the viewer-centered and object-centered reference frames, a benefit of using the visual search task was that it allowed us to examine the possible interaction between the two reference frames. A previous

study by Reuter-Lorenz, Drain, and Hardy-Morais (1996) with healthy observers reported different object-centered attentional biases within the left and right hemifields. Specifically, the authors found a leftward object-centered advantage in the left hemifield and a rightward object-centered advantage in the right hemifield. Because the two brain hemispheres are thought to contribute predominantly to the contralateral side of space, these findings were taken to indicate how each hemisphere also expresses an object-centered spatial bias in the contralateral direction. That is to say, healthy observers seem to have a small object-centered left “neglect” within the right hemifield (Reuter-Lorenz et al., 1996). In the present study, although it may be possible to observe an object-centered left neglect in both hemifields, it is likely for the VWM load manipulation to accentuate the already-existing object-centered neglect within the right hemifield.

In this experiment, we examined detection of visual targets based on the location of a critical feature. We expected to observe a spatially asymmetric disadvantage induced by VWM load on search that could reveal itself in a scene-centered and/or object-centered manner. We hypothesized that the spatial attributes of a target can interact with the cost of VWM load on search. In addition, this experiment also tested whether the potential object-based neglect is modulated by the hemifield from which an object is selected.

Method

Participants. Thirty new University of Toronto undergraduate students (18 females; M age = 19.3 years, $SD = 3.2$) participated in this experiment for course credit. They all reported normal or corrected-to-normal vision and were unaware of the purpose of the experiment.

Stimuli and procedure. The sequence of events in a sample trial is depicted in Figure 4. Each trial began with the presentation of a central fixation cross ($.6^\circ \times .6^\circ$) for 1,000 ms. Subjects were

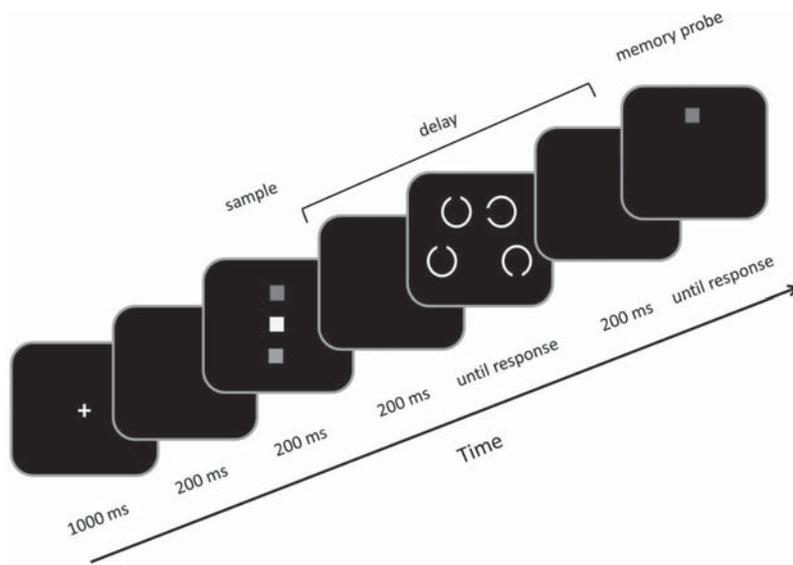


Figure 4. Experiment 2. Schematic illustration of the sequence of events during a sample high-load, target-present search trial.

instructed to look at this fixation cross at the beginning of each trial. The fixation cross was followed by a blank screen (200 ms) and then by the first display of the memory task (200 ms). This display consisted of either 1 (low load) or 3 (high load) colored squares (side = .8° of visual angle; center-to-center distance between adjacent squares = 3°) presented along the vertical midline (to minimize horizontal shifts of attention). On high-load trials, all three squares were presented with unique colors (chosen randomly from white, red, green, blue, yellow, brown, gray, and green-blue), whereas on low-load trials a colored square was presented at one of the three equiprobable locations. Subjects were instructed to try to commit these colors to memory to be able to successfully respond to the memory probe display. The sample memory display was then followed by a blank screen (200 ms) and then by the search display. The search display consisted of four circles (diameter = 2°), each having a small gap that was either in the top or bottom half, or on the left or right side (gap size = 0.5°). Distractors were defined as circles with either top or bottom gaps, whereas a target was defined as a circle with a gap either on the left or right side. The search items were always symmetrically arranged around the vertical midline, with two circles in the left and two circles in the right hemifield. In each hemifield, the two circles were not vertically aligned, to minimize the potential for gestalt grouping (e.g., a circle positioned in the top half with a bottom gap grouped with a lower circle with a top gap). In each hemifield, one circle deviated 7° from the vertical midline, and the other deviated 3° from the midline. Therefore, with a symmetrical arrangement of the display, the search items were either presented in a V- or an inverted V-shaped pattern. The two arrangements were equally likely. The search display remained on the screen until a key-press response was recorded (15 subjects pressed the “?” key on the keyboard for target present and “z” for target absent, and another 15 subjects had the reverse key assignment). Immediately after a response to the search task was recorded, subjects were presented with a blank screen (200 ms), followed by the memory probe display. The probe consisted of a single colored square and subjects decided whether this color was the same (“?” key response) as one of the colors they saw on the first display or whether it was a different color (“z” key response). For same-color trials, the repeated color was presented at the same location. On low-load trials, the sample and probe colors were presented at the same location.

Design. Each subject performed 20 practice trials and 384 test trials. VWM load (low vs. high), target presence, target hemifield (left vs. right), and target gap-side (left vs. right) were randomized and equally probable. That is, a search target was present on only half of the trials. Among the target-present trials, the target was equally probable to appear on the left or the right hemifield, and to have a gap on the left or right side.

Results and Discussion

First, examining performance in the memory task alone revealed higher accuracy with low load ($M \pm SE = 90\% \pm 2\%$) compared with high load ($83\% \pm 2\%$), $t(29) = 4.78$, $SE = .02$, $p < .001$. In examining the influence of memory load on search, we only included trials with correct responses to the memory task. Accuracy in the search task was sufficiently high (97% and 98% under low and high load, respectively) to justify limiting the analyses to

the RT data. Prior to the analysis of RTs, we also removed trials with incorrect responses to the search task (2.6% of trials), and RTs 3 standard deviations above or below the total mean (2.0% of trials in total). The remaining RT data were submitted to a $2 \times 2 \times 2$ repeated-measures ANOVA, with load (low vs. high), target hemifield (left vs. right), and target gap-side (left vs. right) as factors (Figure 5; data for target-absent trials are shown in this figure but were not included in the analysis.). Among the main effects, only the effect of load was significant, $F(1, 29) = 43.71$, $MSE = 3.19 \times 10^5$, $p < .001$, $\eta_p^2 = .601$. Search was faster under low load ($M \pm SE = 1,363 \pm 71$ ms) compared with search under high load ($1,845 \pm 116$), replicating previous findings (e.g., Solman, Cheyne, & Smilek, 2011). No main effect of target hemifield or target gap-side was found, $F_s < 1$. Furthermore, neither the Load \times Hemifield, $F < 1$, nor the Load \times Gap-Side, $F(1, 29) = 2.04$, $MSE = 1.68 \times 10^4$, $p = .16$, $\eta_p^2 = .070$, interactions reached significance level. The two-way interaction between target hemifield and gap-side, however, reached significance, $F(1, 29) = 6.50$, $MSE = 4.7 \times 10^4$, $p = .016$, $\eta_p^2 = .183$, replicating the findings of Reuter-Lorenz et al. (1996). That is, responses were faster when there was congruence between hemifield and gap-side (i.e., either both “left” or both “right”) compared with when the two were incongruent ($1,568 \pm 92$ ms and $1,639 \pm 88$ ms, respectively), indicative of an object-centered spatial bias within each hemifield. Finally, there was a three-way interaction, $F(1, 29) = 6.31$, $MSE = 2.2 \times 10^4$, $p = .018$, $\eta_p^2 = .18$, which revealed a load-induced left neglect that was confined to the right hemifield. In the right

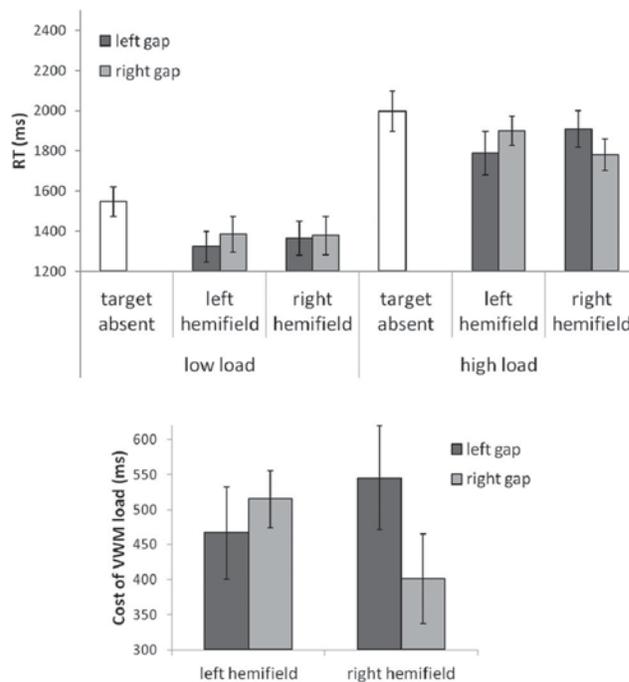


Figure 5. The top graph shows visual search RT data in Experiment 2 graphed as a function of visual working memory load and visual target characteristics (presence, hemifield, and gap location). The bottom graph summarizes these data by presenting the cost of memory load as a function of visual target hemifield and gap location. Error bars indicate within-subjects 95% confidence intervals (Cousineau, 2005).

hemifield, a larger cost of load was found for left-gap targets (545 ± 80 ms) compared with right-gap targets (401 ± 80 ms), $t(29) = 2.43$, $SE = 59.30$, $p = .022$. In the left hemifield, by contrast, the cost of load did not differ significantly for left-gap (467 ± 89 ms) and right-gap (515 ± 73 ms) targets, $t(29) = 1.19$, $SE = 40.81$, $p = .24$. Interestingly, we observed an object-centered leftward bias in the left hemifield that persisted even under high VWM load.

The most important finding of Experiment 2 is that stimulus-centered neglect was only observed in the right hemifield. Within the left hemifield, there exists an a priori bias toward the left side of attended objects (Reuter-Lorenz et al., 1996). Importantly, this object-centered leftward bias persists under both low and high load, removing the transient object-centered neglect. Therefore, although transient object-centered neglect appeared along the vertical meridian (Experiment 1) for objects selected from the right hemifield, it was not observed for objects that were selected from the left hemifield.

It is worth pointing out that the pattern of interaction graphed in Figure 5 (lower panel) cannot be attributed to a higher cost of retinal eccentricity under VWM load. If load simply accentuates the cost of high retinal eccentricity, then we would expect a leftward processing advantage within the right hemifield. By contrast, we found a rightward advantage within the right hemifield, inconsistent with the Load \times Retinotopy interaction. Instead, this pattern is consistent with the asymmetric object-centered attentional bias within the two hemifields (Reuter-Lorenz et al., 1996), suggesting that this type of attentional bias is sensitive to VWM load. Nonetheless, we further examined the potential role of horizontal target eccentricity and its potential interaction with VWM load. As stated previously, a target object could deviate 3° or 7° from fixation. Using these two levels of eccentricity, we submitted the RT data to a 2×2 ANOVA with load (low vs. high) and eccentricity (near fixation vs. far) as factors. This ANOVA only revealed a main effect of load, $F(1, 29) = 44.61$, $p < .001$, $\eta_p^2 = .61$, but no main effect of target eccentricity nor an interaction, $F_s < 1$. In other words, when disregarding the role of gap location and target hemifield, horizontal target eccentricity did not seem to influence performance. This observation supports the claim that VWM load affected attentional processes, instead of accentuating the effect of eccentricity.

Unlike in Experiment 1, we did not observe an overall left-hemifield disadvantage. This is likely due to the opportunity to make eye movements to both hemifields. The present findings therefore suggest that the load-induced neglect is not associated with a failure to explore the left side of space. Instead, the load-induced neglect seems to be akin to perceptual neglect, which is dissociated from motor neglect and remains despite restoring normal exploratory behavior in patients (Danckert & Ferber, 2006).

General Discussion

Converging evidence indicates a resemblance between the behavioral and the neural cost of high VWM load and unilateral neglect (Emrich et al., 2011; Todd et al., 2005). At the neural level, memory load has been shown to cause suppressed activity in the right TPJ, an area intimately associated with neglect (Corbetta & Shulman, 2011; Karnath et al., 2001). Behaviorally, this suppression correlates with a disadvantage for objects presented in the left hemifield (Emrich et al., 2011). The present study examined the

possibility of a load-induced leftward disadvantage within stimulus-centered reference frames, similar to stimulus-centered neglect in patient studies (Behrmann & Moscovitch, 1994; Driver & Halligan, 1991; Driver et al., 1994; Humphreys & Riddoch, 1994; Tipper & Behrmann, 1996; Walker, 1995). Consistent with a stimulus-centered spatial cost, in Experiment 1, we found reduced hit rates and slowed RTs for objects seen at the stimulus-centered left side. In Experiment 2, we found a hemifield asymmetry in this transient neglect: under high VWM load, a leftward object-centered neglect was found in the right hemifield but not in the left hemifield. Together, these results indicate that the cost of VWM load may affect visual perception within multiple spatial frames of reference, similar to the deficit in neglect patients.

Among the disorders of visual perception following brain damage, spatial neglect is one of the most extensively studied (Corbetta & Shulman, 2011; Kerkhoff, 2001; Vallar, 1998). The study of neglect, although important from the perspective of rehabilitation and recovery, has also revealed important insights concerning the nature of visual-spatial attention in the healthy brain. For instance, the dissociation between neural representations of the near-body and the far-from-body space was inferred from the observation that neglect can selectively impair one of the two representations of space (e.g., Halligan & Marshall, 1993). Dissociations were also found between spatial sensory and motor maps (e.g., Bisiach, Geminiani, Berti, & Rusconi, 1990), and between the neural representation of the body (e.g., Farnè, Iriki, & Làdavas, 2005), the environment (Farah, Brunn, Wong, Wallace, & Carpenter, 1990; Làdavas, 1987), and objects (e.g., Driver & Halligan, 1991). Object-centered neglect is not found in all neglect patients, consistent with the existence of dissociable maps of space (Behrmann & Moscovitch, 1994; Farah et al., 1990; Hillis & Rapp, 1998).

The present findings support the idea that visual perception under VWM load resembles characteristics of spatial neglect, and therefore it could provide a useful alternative method to the lesion method. The lesion method has several disadvantages, including the nonselectiveness of lesions and individual differences in localization of brain functions (e.g., Rorden & Karnath, 2004). Examining visual perception under VWM load as a model of neglect can circumvent these limitations. Furthermore, it would be easier to determine the kind of neglect symptoms that are reliably associated with high VWM load. For instance, we found that the left-hemifield impairment disappears when observers have the opportunity to make eye movements (Experiment 2). Based on this observation, the load-induced impairment does not seem to affect the oculomotor exploration of the left side of space (motor neglect) but does impair encoding of the left segment of space/stimulus, akin to perceptual neglect (Danckert & Ferber, 2006).

Assuming that object-centered and viewer-centered spatial representations are indeed dissociable, why do we find a leftward disadvantage in both frames using the single manipulation of memory load? Could both kinds of spatial disadvantage be attributed to suppressed activity in the right TPJ? The accounts of object-centered neglect in patient studies do not base the explanation on a single region deficit. Instead, object-centered neglect is thought to be a deficit in the interaction between regions devoted to object perception (inferior temporal lobe [IT]), regions devoted to spatial representation of the environment (posterior parietal cortex [PPC]), spatial attention and VWM (right TPJ; Corbetta & Shulman, 2011; Milner & Goodale, 2006, pp.196–197). Walker (1995)

proposed that object-centered neglect may arise from activity in regions in which representations of objects and space converge (i.e., prefrontal cortex). It is therefore possible that the interaction between the right TPJ and multiple areas devoted to representation of, and attention to, space causes an imbalance in processing in several of those areas. Alternatively, suppression of the TPJ may interfere with the interaction between regions of object representation (IT) and regions of spatial orienting (PPC). This impaired interaction may affect distribution of spatial attention after an object is selected.

Aside from implications for neglect, the present study is relevant to the current debate about the role of VWM in perception. Initial studies argued that perception may be independent of working memory, and the cost of working memory on perceptual tasks was attributed to a cost for processes that precede (e.g., delayed initiation of visual search) or follow (e.g., delayed response selection) perception (Woodman, Luck, & Schall, 2007; Woodman, Vogel, & Luck, 2001). Later studies showed that when the costs on initiation and response selections are taken into account, there still remains an effect of memory load on visual processes (Solman et al., 2011). For instance, without the contribution of VWM, observers may fail to inhibit previously visited information on the display (Al-Aidroos, Emrich, Ferber, & Pratt, 2012; Emrich, Al-Aidroos, Pratt, & Ferber, 2010). The present findings are in agreement with the contribution of VWM to online perception, because the cost of VWM load is modulated based on the perceptual features of items (e.g., object location; location of the target feature).

The spatially asymmetric cost of memory load is also consistent with a greater contribution of the right hemisphere to VWM functions (Sheremata et al., 2010). Does this right-hemisphere dominance also influence the interaction between memory and online perception? It is believed that the contents of VWM can bias the allocation of attention, guiding attention toward features similar to those in memory (Soto, Heinke, Humphreys & Blanco, 2005). Based on the right-hemisphere dominance of VWM functions, we could expect a greater memory-driven attentional bias in the left hemifield. This question was recently addressed by Du and Abrams (2010), who found that distractors that match a target feature produce a significantly greater cost when they are presented in the left hemifield. By contrast, stimulus-driven attentional capture did not differ across the two hemifields. Therefore, the content of working memory may also exert a spatially asymmetric influence on online perception.

In sum, VWM load seems to induce a cost for the left side on multiple spatial frames of reference. This observation supports the notion that visual perception under working memory load may serve as a model of perceptual neglect. Furthermore, the present study reveals an important interaction between visual perception and working memory, which stands in contrast to viewing the two mechanisms as independent.

References

Al-Aidroos, N., Emrich, S. M., Ferber, S., & Pratt, J. (2012). Visual working memory supports the inhibition of previously processed information: Evidence from preview search. *Journal of Experimental Psychology: Human Perception and Performance*, *38*, 643–663. doi: 10.1037/a0025707

- Behrmann, M., & Moscovitch, M. (1994). Object-centered neglect in patients with unilateral neglect: Effects of left-right coordinates of objects. *Journal of Cognitive Neuroscience*, *6*, 1–16. doi:10.1162/jocn.1994.6.1.1
- Bisiach, E., Geminiani, G., Berti, A., & Rusconi, M. L. (1990). Perceptual and premotor factors of unilateral neglect. *Neurology*, *40*, 1278–1281. doi:10.1212/WNL.40.8.1278
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*, 433–436. doi:10.1163/156856897X00357
- Burton, L. A., Wagner, N., Lim, C., & Levy, J. (1992). Visual field differences for clockwise and counterclockwise mental rotation. *Brain and Cognition*, *18*, 192–207. doi:10.1016/0278-2626(92)90078-Z
- Corballis, M. C., & Sergent, J. (1988). Imagery in a commissurotomy patient. *Neuropsychologia*, *26*, 13–26. doi:10.1016/0028-3932(88)90027-9
- Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neuroscience*, *3*, 292–297. doi: 10.1038/73009
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 201–215. doi:10.1038/nrn755
- Corbetta, M., & Shulman, G. L. (2011). Spatial neglect and attention networks. *Annual Review of Neuroscience*, *34*, 569–599. doi:10.1146/annurev-neuro-061010-113731
- Cousineau, D. (2005). Confidence intervals in within-subject designs: A simpler solution to Loftus and Masson's method. *Tutorials in Quantitative Methods for Psychology*, *1*, 42–45.
- Danckert, J., & Ferber, S. (2006). Revisiting unilateral neglect. *Neuropsychologia*, *44*, 987–1006. doi:10.1016/j.neuropsychologia.2005.09.004
- Driver, J., Baylis, G. C., Goodrich, S. J., & Rafal, R. D. (1994). Axis-based neglect of visual shapes. *Neuropsychologia*, *32*, 1353–1365. doi: 10.1016/0028-3932(94)00068-9
- Driver, J., & Halligan, P. W. (1991). Can visual neglect operate in object-centred co-ordinates? An affirmative single-case study. *Cognitive Neuropsychology*, *8*, 475–496. doi:10.1080/02643299108253384
- Du, F., & Abrams, R. A. (2010). Visual field asymmetry in attentional capture. *Brain and Cognition*, *72*, 310–316. doi:10.1016/j.bandc.2009.10.006
- Emrich, S. M., Al-Aidroos, N., Pratt, J., & Ferber, S. (2010). Finding memory in search: The effect of visual working memory load on visual search. *The Quarterly Journal of Experimental Psychology*, *63*, 1457–1466. doi:10.1080/17470218.2010.483768
- Emrich, S. M., Burianová, H., & Ferber, S. (2011). Transient perceptual neglect: Visual working memory load affects conscious object processing. *Journal of Cognitive Neuroscience*, *23*, 2968–2982. doi:10.1162/jocn_a_00028
- Farah, M. J., Brunn, J. L., Wong, A. B., Wallace, M. A., & Carpenter, P. (1990). Frames of reference for allocating attention to space: Evidence from the neglect syndrome. *Neuropsychologia*, *28*, 335–347. doi: 10.1016/0028-3932(90)90060-2
- Farnè, A., Iriki, A., Ládavas, E. (2005). Shaping multisensory action space with tools: Evidence from patients with cross-modal extinction. *Neuropsychologia*, *43*, 238–248. doi:10.1016/j.neuropsychologia.2004.11.010
- Halligan, P. W., & Marshall, J. C. (1993). When two is one: A case study of spatial parsing in visual neglect. *Perception*, *22*, 309–312. doi: 10.1068/pp.220309
- Hillis, A. E., & Rapp, B. (1998). Unilateral spatial neglect in dissociable frames of reference: A comment on Farah, Brunn, Wong, Wallace, and Carpenter (1990). *Neuropsychologia*, *36*, 1257–1262. doi:10.1016/S0028-3932(98)00009-8
- Humphreys, G. W., & Riddoch, M. J. (1994). Attention to within-object and between-object spatial representations: Multiple sites for visual

- selection. *Cognitive Neuropsychology*, *11*, 204–241. doi:10.1080/02643299408251974
- Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: A review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia*, *38*, 93–110. doi:10.1016/S0028-3932(99)00045-7
- Karnath, H.-O., Ferber, S., & Himmelbach, M. (2001). Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature*, *411*, 950–953. doi:10.1038/35082075
- Kerkhoff, G. (2001). Spatial hemineglect in humans. *Progress in Neurobiology*, *63*, 1–27. doi:10.1016/S0301-0082(00)00028-9
- Làdavias, E. (1987). Is the hemispatial deficit produced by right parietal lobe damage associated with retinal or gravitational co-ordinates? *Brain*, *110*, 167–180. doi:10.1093/brain/110.1.167
- Lu, C.-H., & Proctor, R. W. (1995). The influence of irrelevant location information on performance: A review of the Simon and spatial Stroop effects. *Psychonomic Bulletin & Review*, *2*, 174–207. doi:10.3758/BF03210959
- Milner, A. D., & Goodale, M. A. (2006). *The visual brain in action* (2nd ed.). Oxford, UK: Oxford University Press. doi:10.1093/acprof:oso/9780198524724.001.0001
- Pelli, D. G. (1997). The video toolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442. doi:10.1163/156856897X00366
- Posner, M. I., & Dehaene, S. (1994). Attentional networks. *Trends in Neurosciences*, *17*, 75–79. doi:10.1016/0166-2236(94)90078-7
- Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25–42. doi:10.1146/annurev.ne.13.030190.000325
- Posner, M. I., Walker, J. A., Friedrich, F. J., & Rafal, R. (1984). Effects of parietal injury on covert orienting of attention. *The Journal of Neuroscience*, *4*, 1863–1874.
- Reuter-Lorenz, P. A., Drain, M., & Hardy-Morais, C. (1996). Object-centered attentional bias in the intact brain. *Journal of Cognitive Neuroscience*, *8*, 540–550. doi:10.1162/jocn.1996.8.6.540
- Rhodes, D. L., & Robertson, L. C. (2002). Visual field asymmetries and allocation of attention in visual scenes. *Brain and Cognition*, *50*, 95–115. doi:10.1016/S0278-2626(02)00014-3
- Rorden, C., & Karnath, H.-O. (2004). Using human lesions to infer a function: A relic from a past era in the fMRI age? *Nature Reviews Neuroscience*, *5*, 813–819. doi:10.1038/nrn1521
- Rushworth, M. F., Paus, T., & Sipila, P. K. (2001). Attention systems and the organization of the human parietal cortex. *The Journal of Neuroscience*, *21*, 5262–5271.
- Sheremata, S. L., Bettencourt, K. C., & Somers, D. C. (2010). Hemispheric asymmetry in visuotopic posterior parietal cortex emerges with visual short-term memory load. *The Journal of Neuroscience*, *30*, 12581–12588. doi:10.1523/JNEUROSCI.2689-10.2010
- Solman, G. J. F., Cheyne, J. A., & Smilek, D. (2011). Memory load affects visual search processes without influencing search efficiency. *Vision Research*, *51*, 1185–1191. doi:10.1016/j.visres.2011.03.009
- Soto, D., Heinke, D., Humphreys, G. W., & Blanco, M. J. (2005). Early, involuntary top-down guidance of attention from working memory. *Journal of Experimental Psychology: Human Perception and Performance*, *31*, 248–261. doi:10.1037/0096-1523.31.2.248
- Tipper, S. P., & Behrmann, M. (1996). Object-centered not scene-based visual neglect. *Journal of Experimental Psychology: Human Perception and Performance*, *22*, 1261–1278. doi:10.1037/0096-1523.22.5.1261
- Toba, M.-N., Cavanagh, P., & Bartolomeo, P. (2011). Attention biases the perceived midpoint of horizontal lines. *Neuropsychologia*, *49*, 238–246. doi:10.1016/j.neuropsychologia.2010.11.022
- Todd, J. J., Fougny, D., & Marois, R. (2005). Visual short-term memory load suppresses temporo-parietal junction activity and induces inattention blindness. *Psychological Science*, *16*, 965–972.
- Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature*, *428*, 751–754. doi:10.1038/nature02466
- Townsend, J. T., & Ashby, F. G. (1983). *The stochastic modeling of elementary psychological processes*. Cambridge, UK: Cambridge University Press.
- Vallar, G. (1998). Spatial hemineglect in humans. *Trends in Cognitive Sciences*, *2*, 87–97. doi:10.1016/S1364-6613(98)01145-0
- Walker, R. (1995). Spatial and object-based neglect. *Neurocase*, *1*, 371–383. doi:10.1080/13554799508402381
- Woodman, G. F., Luck, S. J., & Schall, J. D. (2007). The role of working memory representations in the control of attention. *Cerebral Cortex*, *17*, i118–i124. doi:10.1093/cercor/bhm065
- Woodman, G. F., Vogel, E. K., & Luck, S. J. (2001). Visual search remains efficient when visual working memory is full. *Psychological Science*, *12*, 219–224. doi:10.1111/1467-9280.00339

Received January 16, 2013

Revision received May 20, 2013

Accepted June 18, 2013 ■