Brief Communications

Subliminally Presented and Stored Objects Capture Spatial Attention

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When objects disappear from view, we can still bring them to mind, at least for brief periods of time, because we can represent those objects in visual short-term memory (VSTM) (Sperling, 1960; Cowan, 2001). A defining characteristic of this representation is that it is topographic, that is, it preserves a spatial organization based on the original visual percept (Vogel and Machizawa, 2004; Astle et al., 2009; Kuo et al., 2009). Recent research has also shown that features or locations of visual items that match those being maintained in conscious VSTM automatically capture our attention (Awh and Jonides, 2001; Olivers et al., 2006; Soto et al., 2008). But do objects leave some trace that can guide spatial attention, even without participants intentionally remembering them? Furthermore, could subliminally presented objects leave a topographically arranged representation that can capture attention? We presented objects either supraliminally or subliminally and then 1 s later re-presented one of those objects in a new location, as a “probe” shape. As participants made an arbitrary perceptual judgment on the probe shape, their covert spatial attention was drawn to the original location of that shape, regardless of whether its initial presentation had been supraliminal or subliminal. We demonstrate this with neural and behavioral measures of memory-driven attentional capture. These findings reveal the existence of a topographically arranged store of “visual” objects, the content of which is beyond our explicit awareness but which nonetheless guides spatial attention.

Introduction

Typically, visual short-term memory (VSTM) tasks require participants to search voluntarily their stored representations. Their task is usually to decide whether a probe item was part of a preceding memory array (Fabiani et al., 2003; Vogel and Machizawa, 2004; Astle et al., 2009; Kuo et al., 2009). VSTM has been shown to retain a topographic organization (Fabiani et al., 2003; Astle et al., 2009; Kuo et al., 2009; Luria et al., 2010). Recent experiments have shown that the voluntary selection of an item from memory leads to event-related potentials (ERPs) that are relatively more negative over posterior scalp contralateral versus ipsilateral to the original object location between 200 and 300 ms (Fabiani et al., 2003; Astle et al., 2009; Eimer and Kiss, 2009; Kuo et al., 2009; Dell’Acqua et al., 2010). The effect resembles the lateralized ERP differences obtained when participants search for objects in perceptual input, known as the N2pc (Luck and Hillyard, 1994; Woodman and Luck, 1999), which is thought to reflect spatially specific biases on visual cortices (Hopf et al., 2004) after target selection processes in areas such as the posterior parietal cortex (Fuggetta et al., 2006) and frontal eye fields (Cohen et al., 2009).

In addition to being voluntarily deployed while actively searching memory, attention can be captured involuntarily by the contents of VSTM (Awh and Jonides, 2001; Olivers et al., 2006; Soto et al., 2008). We therefore asked whether, just as voluntary selection from VSTM recruits spatial-biasing neural mechanisms, the involuntary capture of attention by items stored in VSTM might also elicit an N2pc. We also explored whether subliminally presented objects leave a topographically organized trace that cannot be accessed consciously but that can nonetheless capture our attention. Across a series of experiments, we demonstrate that indeed this is the case. To test whether the contents of a past subliminal display could exert a spatial bias on attention, we presented participants with a supraliminal or subliminal “memory” array of line shapes and, after 1 s, presented them with a test probe. On a proportion of trials, the test probe was one of the original memory array shapes, presented earlier that trial. Regardless of whether the memory array had been presented subliminally or supraliminally, when one of the shapes in the array reappeared as the test probe, participants’ attention was drawn back to the original location of that shape. This was evidenced by a clear neural marker of spatial biasing, the N2pc: a greater negativity contralateral to the original location of that shape in both subliminal and supraliminal arrays (experiment 1).

We also observed the direct behavioral consequences of this memory-driven attentional bias using a dot-probe experiment (experiment 3). Despite this effect on spatial attention, during the subliminal condition, participants were unable to recognize consciously the test probe as being one of the memory-array shapes (experiment 1) and showed no conscious bias as to the most likely location of the test probe in the previous array (experiment 2).

Materials and Methods

All the experiments described had the same basic trial structure. We presented a memory array of two items either subliminally (63 ms) or supraliminally (243 ms), sandwiched between two pattern masks com-

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Experiment 1: neural consequences of memory-driven attentional capture on a perceptual judgment task. The electrophysiological recording session started and concluded with an explicit-memory search task. This was designed to assess the liminality of the memory-array shapes. Participants’ \( n = 13 \); mean age of 25.1 years; six males) task was to decide whether the test probe had been present in the original memory array. On half of the trials, the test probe appeared in the memory array. They responded with their right hand, with their index finger corresponding to “present” and their middle finger corresponding to “absent.” d’ indexed participants’ sensitivity to the presence of the test probe in the preceding memory array.

During an electrophysiological recording session, participants performed 40 blocks of 10 trials. The trial sequence was identical to that used in the explicit-memory search task. This time, participants’ task was to judge the symmetry along the vertical midline of the test probe. The mean that the task was unrelated to the contents of the memory array. On two-thirds of trials, the test probe was one of the shapes in the preceding memory array. These trials contributed to the ERP analyses.

The electroencephalogram was recorded continuously (1000 Hz analog-to-digital rate; 0.1–300 Hz bandwidth; right-mastoid reference), subsequently re-referenced to the algebraic average of the right and left mastoids, and low-pass filtered at 40 Hz. Trials contaminated by blinks or eye movements were removed. The electroencephalogram was recorded continuously (1000 Hz analog-to-digital rate; 0.1–300 Hz bandwidth; right-mastoid reference), subsequently re-referenced to the algebraic average of the right and left mastoids, and low-pass filtered at 40 Hz. Trials contaminated by blinks or eye movements were removed. The electroencephalogram was recorded continuously (1000 Hz analog-to-digital rate; 0.1–300 Hz bandwidth; right-mastoid reference), subsequently re-referenced to the algebraic average of the right and left mastoids, and low-pass filtered at 40 Hz. Trials contaminated by blinks or eye movements were removed. The mean that the task was unrelated to the contents of the memory array. On two-thirds of trials, the test probe was one of the shapes in the preceding memory array. These trials contributed to the ERP analyses.

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trials, participants were faster and more accurate to respond to facilitated behavioral performance (Fig. 2A) when the probe appeared, we found a reliable main effect of contralaterality between 230 and 280 ms (F_{1,12} = 10.34, p = 0.007). That is, we observed a negativity contralateral to the original location of the test probe item in the memory array. This effect did not interact with electrode or liminality (p values <0.34). Analyses of simple effects confirmed that, when the memory array was supraliminal, we observed the probe-locked N2pc effect (F_{1,12} = 4.70, p = 0.05) (Fig. 1B, left). Thus, although the N2pc has been observed previously when participants search memory actively (Kuo et al., 2009), this neural marker also occurs when the contents of memory are irrelevant to the task at hand (Olivers et al., 2006). Surprisingly, we also observed the N2pc effect when the arrays were subliminal (F_{1,12} = 5.03, p = 0.04) (Fig. 1B, right). This suggests that attention was still directed to the original location of those probe-matching objects (Luck and Hillyard, 1994; Woodman and Luck, 1999), even when participants had been unable to perceive them consciously.

**Behavior during the electrophysiological session**

As was outlined in Materials and Methods, we incorporated a test of liminality into the electrophysiological recording. When the memory array had been supraliminal, congruence between the memory arrays suggests that participants were attempting to process the contents of the arrays and used this information to speed response selection to the test probe, resulting in a large number of errors on incongruent trials. If participants were able to detect at least part of one shape in the subliminal condition, we would expect the same effect. However, in this case, there was no effect of whether the probe was congruent or incongruent on either reaction times (511 and 516 ms, respectively, F_{1,12} = 0.83, p = 0.38) or error rates (90 and 92%, respectively, F_{1,12} = 0.74, p = 0.41) (Fig. 2B). The lack of this behavioral priming effect in the subliminal condition is strong evidence that participants could not detect the contents of the subliminal arrays during the electrophysiological recording session.

**Experiment 2: location decision task**
The electrophysiological effects elicited by subliminal stimuli in experiment 1 might have been driven by a conscious bias toward which memory array shape was most likely to have been the test probe. This bias might not be measured by our previous tests of liminality but might nonetheless drive the N2pc that we observed. We produced a d’ measure of participants’ sensitivity to the location of the test probe within the memory array. When the array was presented for 243 ms, participants’ d’ scores were significantly greater than zero (d’ = 3.96, t_{11} = 8.358, p < 0.001). When the array was presented for 63 ms, participants’ d’ scores were not significantly greater than zero (d’ = 0.15, t_{11} = 1.591, p = 0.143). In addition to being unable to identify consciously the subliminal memory array shapes or to categorize their symmetry along the vertical midline, participants showed no conscious bias as to the most likely location of a particular test probe.

**Experiment 3: behavioral effects of memory-driven attentional capture**

Having ruled out explanations related to participants consciously perceiving the items in the subliminal arrays, we assessed the direct behavioral consequences of the spatial attentional bias we suggested had driven our electrophysiological findings. We conducted a dot-probe experiment to test the spatiotopic allocation of attention directly. If participants’ attention was drawn back to the original location of test probes, then they ought to be faster to make arbitrary judgments about dot-probes appearing in that original location relative to a control location (Fukuda and Vogel, 2009). This was indeed the case. The judgment was significantly faster when the dot had appeared in the “attended” location congruent than to incongruent probes (411 and 524 ms, respectively, F_{1,12} = 34.07, p < 0.001; 93 and 62% correct, respectively, F_{1,12} = 17.72, p = 0.001). That performance was affected to such a great extent by the congruence of the memory arrays suggests that participants were attempting to process the contents of the arrays and used this information to speed response selection to the test probe, resulting in a large number of errors on incongruent trials. If participants were able to detect at least part of one shape in the subliminal condition, we would expect the same effect. However, in this case, there was no effect of whether the probe was congruent or incongruent on either reaction times (511 and 516 ms, respectively, F_{1,12} = 0.83, p = 0.38) or error rates (90 and 92%, respectively, F_{1,12} = 0.74, p = 0.41) (Fig. 2B). The lack of this behavioral priming effect in the subliminal condition is strong evidence that participants could not detect the contents of the subliminal arrays during the electrophysiological recording session.

**Figure 1.** A. Trial order schematic. B. Grand-averaged event-related potentials comparing posterior recordings contralateral and ipsilateral to the location of the probe-matching item in the memory array, locked to the onset of the test probe. Each waveform is the average of three electrodes (P07/8, P7/8, and O1/2). We found a reliable main effect of contralaterality between 230 and 280 ms. This was also present as a simple main effect of contralaterality in both the supraliminal and subliminal conditions. There was no interaction between contralaterality and liminality or with liminality and electrode. Topographical plots show contralateral minus ipsilateral voltage in the left hemisphere; the right hemisphere shows the mirror of this. C. Participants’ mean d’ on the explicit-memory search task, for each duration of the memory array, before and after the electrophysiological recording session.
had been supraliminal or subliminal (unaffected by whether the memory array had been supraliminal or subliminal (p = 0.55). There was a significant effect of matching versus mismatching location in both the supraliminal (493 vs 510 ms, respectively, F(1,12) = 4.95, p = 0.046) and the subliminal condition (505 vs 517 ms, respectively, F(1,12) = 6.50, p = 0.025). There were no significant differences in accuracy between match and mismatch trials in either the subliminal (95 vs 96%, respectively, p = 0.579) or the supraliminal condition (95 vs 93%, respectively, p = 0.307).

To validate our manipulation of liminality in this dot-probe experiment, as in the electrophysiological recording session, we immediately preceded and followed the experiment with the forced-choice explicit-memory search task. Before running the dot-probe experiment, participants’ performance was not significantly better than chance in the “subliminal” condition (d’ = -0.16, t(12) = -0.650, p = 0.528) but was in the “supraliminal” condition (d’ = 1.75, t(12) = 4.744, p < 0.001). After the dot-probe experiment, their performance was still not significantly better than chance when the arrays were presented for 63 ms (d’ = -0.07, t(12) = -0.266, p = 0.795) but was significantly better than chance when the arrays were presented for 243 ms (d’ = 2.16, t(12) = 6.937, p < 0.001).

Discussion

Recent functional imaging studies have demonstrated that retaining simple features of perceptual objects recruits early visual cortices; decoding the voxel-based activity within visual cortical areas V1, V2, and V3 can reveal accurately the particular items being intentionally stored in VSTM (Harrison and Tong, 2009; Serences et al., 2009). This would support the view that VSTM is mediated by domain-general control areas, such as posterior parietal and/or prefrontal cortex, interacting with brain regions involved in the original perception of the items (Passingham and Sakai, 2004). Consistent with this view, the contents of VSTM can be biased by the top-down allocation of attention, according to a particular task goal, as indexed by an N2pc (Astle et al., 2009; Kuo et al., 2009).

The current results demonstrate that the relationship between this posterior biasing mechanism and the contents of VSTM is bidirectional: not only do spatial biases influence the contents of memory, the contents of memory also drive spatial attentional biases when a match occurs with a currently perceived item. In both cases, spatial biases appear to modulate the current level of excitability in neural activity in visual areas, which participate in the coding of perceptual as well as memory arrays (Kuo et al., 2001; Kuo et al., 2009). The task performed on the dot was completely unrelated to the perceptual match between the memory-array items and the test probe. That we observed a behavioral facilitation effect to a novel stimulus appearing in the same location cannot be imputed to simple perceptual priming and must instead result from the allocation of spatial attention. Furthermore, that the memory-based attentional capture effects survive pattern noise masking and occur over relatively lengthy intervals would also rule out visual priming as a likely explanation.

The dot-probe result also rules out one final alternative explanation for the electrophysiological result that the N2pc effect, rather than reflecting some spatially specific attentional process, actually indexes some form of object-based priming (Kristjansson et al., 2001; Kuo et al., 2009). The task performed on the dot was completely unrelated to the perceptual match between the memory-array items and the test probe. That we observed a behavioral facilitation effect to a novel stimulus appearing in the same location cannot be imputed to simple perceptual priming and must instead result from the allocation of spatial attention. Furthermore, that the memory-based attentional capture effects survive pattern noise masking and occur over relatively lengthy intervals would also rule out visual priming as a likely explanation.

It has been demonstrated recently that incoming stimuli that participants fail to perceive can nonetheless capture attention (Ansorge et al., 2009). Here we show that previously presented stimuli that participants failed to perceive, and therefore unsurprisingly failed to recognize subsequently, can also capture spatial attention. In short, the subliminally presented stimuli leave a trace that retains the original spatial layout of the memory array and the particular configuration of lines that constitute each item. This trace is sufficient to drive spatial attention. However, the subliminal shapes are not assigned to higher-order categories, with the traces left by the subliminal memory arrays not affecting the symmetrical versus asymmetrical judgment on the test probe. An additional question, then, is what type of storage is responsi-
able for this effect? The traditional view of VSTM is of a capacity-limited, time-limited store. Because this store is topographically organized, it could be producing the effects that we observed. However, the traditional view of VSTM usually specifies that only items that participants intentionally retain are stored (Luria et al., 2010) and can capture attention (Olivers et al., 2006). It seems unlikely that our participants were intentionally storing the items; the memory array objects were essentially irrelevant for the task performed and, in some cases, were not consciously detectable. That said, it has been shown recently that large quantities of information may be retained in a fragile form of VSTM (Sligte et al., 2008) and that the existence of these fragile object representations can be evidenced using alternative means of probing “recognition,” such as retrospective attentional cuing (Griffin and Nobre, 2003; Landman et al., 2003). The traces reported here are more robust than those stored in fragile VSTM (Sligte et al., 2008), because they survive combined forward and backward pattern masking. Nonetheless, like fragile VSTM, there seems to exist some form of item retention that cannot be evidenced by conventional recognition tests but that is nonetheless available. Our findings imply the existence of a previously undiscovered quality of VSTM or a parallel unconscious store which is also topographically organized. Either way, we demonstrate that objects that participants fail to perceive nonetheless leave a topographically organized trace and guide attention.

References


