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Causal evidence for subliminal percept-to-memory interference in early visual cortex

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ABSTRACT

There has been recent interest in the neural correlates of visual short-term memory (VSTM) interference by irrelevant perceptual input. These studies, however, presented distracters that were subjected to conscious scrutiny by participants thus strongly involving attentional control mechanisms. In order to minimize the role of attentional control and to investigate interference occurring at the level of sensory representations, we developed a paradigm in which a subliminal visual distracter is presented during the delay period of a visual short-term memory task requiring the maintenance of stimulus orientation. This subliminal distracter could be either congruent or incongruent with the orientation of the memory item. Behavioral results showed that the intervening distracter affected the fidelity of VSTM when it was incongruent with the memory cue. We then assessed the causal role of the early visual cortex in this interaction by using transcranial magnetic stimulation (TMS). We found that occipital TMS impaired the fidelity VSTM content in the absence of the memory mask. Interestingly, TMS facilitated VSTM performance in the presence of a subliminal memory mask that was incongruent with the memory content. Signal detection analyses indicated that TMS did not modulate perceptual sensitivity of the masked distracter. That the impact of TMS on the precision of VSTM was dissociated by the presence vs. absence of a subliminal perceptual distracter and its congruency with the VSTM content provides causal evidence for the view that competitive interactions between memory and perception can occur at the earliest cortical stages of visual processing.

Introduction

The interplay between visual short-term memory (VSTM) and perception is being the subject of much recent interest. One line of research has concentrated on how engagement in VSTM/mental imagery modulates the detection of concurrently viewed visual stimuli (e.g. Craver-Lemley and Reeves 1987, 1992; Farah 1985; Soto et al., 2010). A second line of research has assessed how incoming perceptual input may influence the fidelity of the representations held in VSTM. This form of VSTM-perception interaction is the focus of our study. Psychophysical studies indicate that the appearance of an irrelevant stimulus during the delay period of a VSTM task interferes with VSTM performance (cf. memory masking; Magnussen et al. 1991, 2003; Magnussen and Greenlee, 1992). This interference could be due to the memory masker diverting attentional resources from the critical feature in held VSTM. In line with this, the strength of VSTM interference is a function of the amount of attention paid to the irrelevant percept (Rutman et al., 2010; Sreenivasan and Jha, 2007).

In prior studies of memory interference by perception observers were consciously aware of the visual distracters and the competitive interactions between perception and memory were resolved by top-down attentional control mechanisms originating in the prefrontal cortex (Zanto et al., 2011). Here we ask whether interference in VSTM by perception may be observed at the level of sensory cortex, under conditions that minimize attentional modulation. We developed an experimental paradigm where memory maskers were presented in a subliminal fashion. In this paradigm, subjects were asked to maintain the orientation of a grating in memory and subliminal distracter was presented during the delay period. We reasoned that if conscious awareness is a dispensable feature in the interaction between VSTM and perception then the fidelity of the representations held in VSTM (and subsequent VSTM performance) ought to be influenced by the presence of concurrent subliminal input. Here we report that masking of VSTM content can be triggered by unconsciously perceived items that are incongruent with the VSTM content. Next we assessed the causal role of the early stages of cortical visual processing. A number of studies have linked VSTM with engagement of neurons in the early visual cortex tuned for the critical feature held in VSTM (e.g. orientation, Harrison & Tong, 2009; see also Serences et al., 2009; Cattaneo et al., 2009). We applied a pulse train (3 pulses at 10 Hz) of transcranial magnetic stimulation (TMS) to the occipital pole when the subliminal distracter appeared during the delay of the VSTM task. We reasoned that if VSTM and perception interact in the early visual cortex then the impact of TMS on VSTM performance should depend on the congruency between the perceptual input and the VSTM content. In other words, if eatly visual cortex is involved in the interaction between VSTM and perception, the

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amount of occipital TMS-induced VSTM interference ought to rely on whether or not the perceptual input and the VSTM content engage the same neural channels in this region (i.e. whether the neurons coding for the orientation of the percept match or mismatch the VSTM content). In contrast, we hypothesized that if the early visual cortex plays a causal role in VSTM but the subliminal distracter effect occurs beyond this region, then occipital TMS ought to disrupt VSTM performance regardless of whether the perceptual distracter is congruent or incongruent with the VSTM content. This prediction would follow if perceptual input and the VSTM content did not engage the same neural channels in the early visual cortex and thus there would be no competitive interaction between the incongruent distracter and VSTM content. Finally, no effect of TMS on VSTM performance would be expected in any of the conditions if the early visual cortex does not play a causal role in VSTM.

General methods

Participants

Eighteen observers provided informed consent to take part in the study, which was approved by the Hammersmith Research Ethics Committee. There were 8 healthy participants (5 males; mean age 35 years) in the behavioral Experiment 1, and 10 participants (6 males; mean age 27 years) in the TMS study.

Experimental procedure

The stimuli were presented on a 15-inch monitor with a display resolution of 800×600 pixels. Stimuli and task were controlled by E-prime v2.0 (Psychology Software Tools Inc., Pittsburgh, USA; http://www.pstnet.com/eprime.cfm). Each trial began with a black fixation point appearing in the middle of the screen for 1000 ms, followed by a blank screen for 500 ms. The memory cue then appeared for 200 ms (see Fig. 1 for the timeline of an experimental trial). The memory cue was a grating contrast with a 0.9 Michelson contrast and could be tilted 30, 40, 50° to the left or right. The stimuli consisted of a sinusoidal luminance-modulated grating with a spatial frequency of 1 cycle/degree.

Participants were asked to maintain an image of the grating during a subsequent 2-second maintenance period. During this period, a low contrast grating (Michelson contrast 0.1) was presented on 66% of trials. for a duration of 13 ms, and was followed by a 80 ms mask (a black circle covering the area of the grating). On “No distractor” trials, only the mask appeared (the mask thus appeared on all trials). The visual distracter appeared 1000 ms after the onset of the cue. The orientation of the distracter was either the same or opposite (i.e. congruent or incongruent) to that of the memory cue. In other words, if the memory cue was tilted 30° to the left, then the orientation of the distracter could be either 30° (congruent condition) to the left or 30° to the right (incongruent condition). 1000 ms after the offset of the mask, another high contrast grating appeared for 300 ms as a memory probe test. The memory probe grating was tilted 10° either to the left or right relative to the memory cue observers had to indicate this by pressing a different response button during an unlimited time window. Accuracy was emphasized. In addition, subjects were asked to indicate whether they had perceived the visual distracter appearing during the maintenance period, using a 4-point scale, adapted from Overgaard et al. (2010) and Sandberg et al. (2010) and used in a recent TMS study by Koivisto et al. (2010): 1 = did not see it; 2 = maybe saw something; 3 = saw the stimulus but not its orientation; 4 = saw the stimulus and its orientation.

Cue orientation and congruency varied randomly on each trial. Observers were encouraged to be as accurate as possible during an unlimited time window. Fig. 1 shows the stimuli presented during the experimental trial. Observers received detailed instructions on the sequence of events on each trial. They performed training on the task with distracters that were consciously perceived (i.e. 100 ms exposure) and then followed by more training with a reduced duration (i.e. 13 ms) that rendered invisible the presence of the masked items.

Two TMS conditions were included in the TMS study (Experiment 1b): early visual cortex (EVC-TMS) and sham TMS (the control condition). For each combination of TMS condition and trial type (i.e. no visual distracter, congruent distracter and incongruent distracter) 48 trials were administered. The experiment was carried out in 8 blocks of 36 trials (with each block containing 12 congruent, 12 incongruent and 12 no distractor trials). The order of blocks was counterbalanced between subjects, such that half of the participants began with a sham TMS block, and the other half with

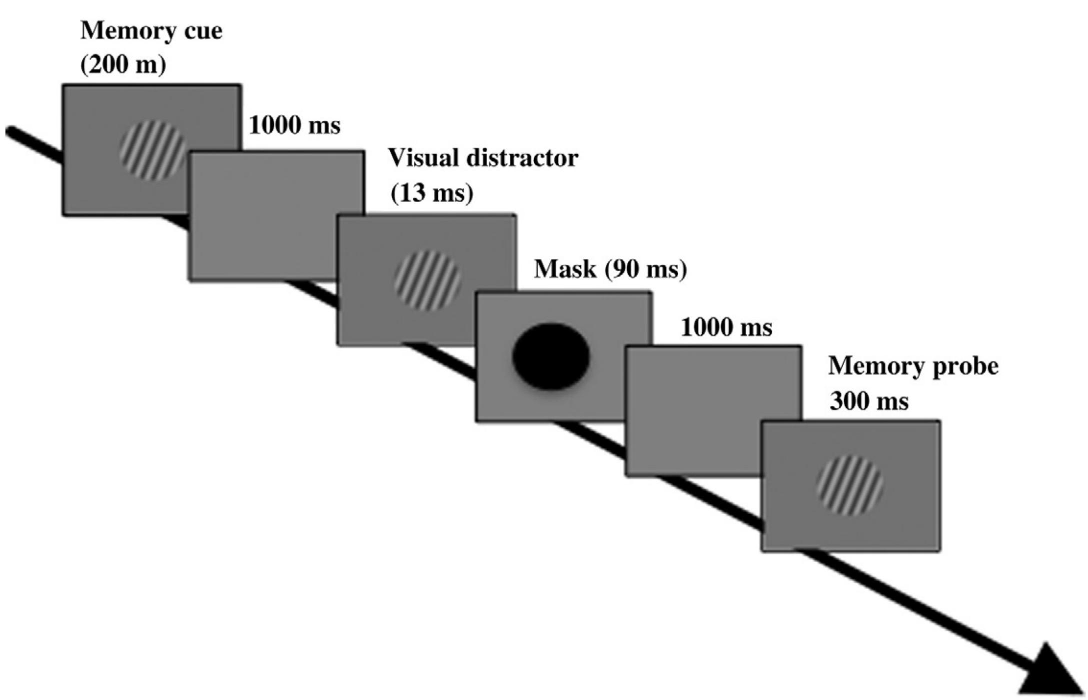

Fig. 1. (A) Illustration of the timeline of an experimental trial. An example of congruent condition is depicted. In the TMS experiment (Experiment 1b), a pulse train (consisting of three pulses applied at 10 Hz, i.e. pulse gap of 100 ms) was applied concurrently with the onset of the distracter on each trial.