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Perceptual Load Modulates Visual Cortex Excitability to Magnetic Stimulation

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Muggleton N, Lamb R, Walsh V, Lavie N. Perceptual load modulates visual cortex excitability to magnetic stimulation. *J Neurophysiol* 100: 516–519, 2008. First published May 21, 2008; doi:10.1152/jn.01287.2007. Much recent research has shown that the level of perceptual load in a task determines the perception of task-irrelevant stimuli and associated neural activity, but the mediating neural mechanisms remain unclear. Here we show that increasing the level of perceptual load in a static letter search task results in an increase in the intensity of transcranial magnetic stimulation over V5/MT required to elicit the perception of a moving phosphene. These findings suggest that the neural mechanisms mediating the effects of perceptual load involve reduced visual cortex excitability in task-unrelated areas.

INTRODUCTION

The load theory of attention (Lavie 1995, 2005) provides a compelling resolution to the fundamental controversy in psychology research over whether or not perception depends on the allocation of attention. This issue has long been debated between views of perception as a limited capacity process that requires focused attention and views of perception as an automatic involuntary process with unlimited capacity that does not depend on the allocation of attention (Driver 2001; Kahneman and Treisman 1984 for reviews). Load theory reconciles these opposing views by proposing that, although perceptual capacity is limited, perceptual processing proceeds automatically and involuntarily on all stimuli within capacity, irrespective of whether they are relevant or irrelevant to the task at hand, as long as capacity is available.

The critical tests of load theory concern task-irrelevant distractor processing. Load theory predicts that high perceptual load in the task will exhaust attentional capacity, leaving no capacity for the perception of any task-irrelevant stimuli. By contrast, in tasks of low perceptual load, the resources not used for task-relevant processing are automatically allocated to the irrelevant stimuli that are consequently perceived. These predictions have been confirmed in many studies (Lavie 1995; Schwartz et al. 2005; Yi et al. 2004 for review) showing that irrelevant distractors are nevertheless perceived and elicit BOLD changes in tasks of low perceptual load and that these behavioral and neural effects of distractors are diminished in tasks of high perceptual load.

This research resolves the controversy over the effects of attention on perception, but the underlying neural mechanisms remain to be elucidated. Here we tested an account of the effects of load in terms of a modulation of the excitability of visual cortex, measured by transcranial magnetic stimulation

(TMS). According to this account, the reduction in distractor-related activity with high perceptual load may be explained by a reduction in the ongoing excitability in sensory neural populations that mediate perception of task-irrelevant stimuli.

Notably the previous demonstrations of the effects of perceptual load indicate that different stimuli, processed in different brain areas, share a common capacity-limited resource. For example, the first imaging study of load theory (Rees et al. 1997) showed that the level of perceptual load in a lexical task concerning static words determined the BOLD response in V5/MT related to processing a task-irrelevant motion stimulus.

In this study, we thus hypothesized that high perceptual load in a static letter search task would reduce the excitability of sensory neurons in the task-irrelevant area V5/MT. The level of cortical excitability in V5/MT was measured in human observers by applying a single-pulse TMS over the right V5/MT and assessing the intensity of stimulation required to elicit moving phosphenes (Stewart et al. 1999). The threshold in terms of the magnetic stimulator intensity required to induce the perception of V5 phosphenes provides a measure of neural excitability (Aurora and Welch 1998; Battelli et al. 2002; Boroojerdi et al. 2000) in area V5/MT.

Perceptual load in the letter search task was manipulated by varying the search set size from one (low load) to six (high load). This load manipulation is well established and has successfully increased the demand on attention in many previous studies (Lavie 2005 for review). Immediately following the visual search response (or before the search response in *experiment 4*), subjects were required to indicate whether a phosphene was present or absent. The coil was positioned to produce a moving phosphene in a location peripheral to the letter circle. Phosphene threshold was expressed as the percentage of stimulator output that elicits phosphenes on 50% of the trials (with correct search task responses) determined with a staircase procedure.

METHODS

Subjects

Six subjects participated in *experiments 1–4*. Three of these also participated in *experiment 5* with three further subjects.¹ All subjects were UCL students; age range, 24–33 yr. All gave informed consent

¹ A 2×2 mixed model ANOVA with the between-subject factor of subject group (old, new) and working memory load (low, high) confirmed no difference in the effect of working memory load on the new versus old subjects ($F < 1$ for the interaction).

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before participation. The study was approved by the UCL ethics committee.

TMS

A single TMS pulse was delivered over V5/MT in the right hemisphere at the onset of each task display using a 70-mm figure-eight coil with a Magstim Super Rapid stimulator (Magstim Company). V5/MT was localized using a functional method in which the center of the coil is placed on the surface of the skull such that the stimulation elicits phosphene that intrude on the center of the visual field (Stewart et al. 1999).

The starting location for stimulation was 2 cm dorsal and 4 cm lateral from theinion. The coil was moved slightly to find a region from which the moving phosphene induced appear at a position that does not overlap with search letters positions (typically to the left of the letters level with the display center). The average coil position was 3 cm dorsal and 5 cm lateral from theinion. The site of stimulation was co-registered with high-resolution structural MRI scans for each subject. For each individual, the location of stimulation was transformed into normal space (Talairach coordinates) using the FSL software package (FMRIB), and good agreement was found with the location of V5/MT reported in imaging studies (mean stimulation location: 41, -66.7, -1.4, compared with 44, -67, 0 reported by Dumoulin et al. 2000). Once the TMS location was determined, the coil was clamped in place for the duration of the experiment and was oriented with its handle held horizontally and pointing in posterior to anterior direction.

Tasks

E-Prime was used to run the experiment and control the TMS timing and intensity. Viewing distance was held at 57 cm with a head and chin rest.

The load task used was similar to that used in previous perceptual load studies. A visual search display was presented for 100 ms on each trial. Participants searched for the letter X or N and pressed 0 for X and 2 for N on the keyboard number pad. The instructions emphasized performance accuracy in the task. The target X or N was equally likely and was presented in any of six possible locations equally spaced on a circle (with a 1.4° radius) on each trial. In the high load conditions, the nontargets were K, H, V, Z, and W. In the low load conditions, the nontargets were dot place holders (subtending 0.1°). Each letter subtended 0.7° × 0.9°. Letter configurations were selected at random from all available permutations on each trial. Ten blocks were run (5 for each of the load conditions) in a different random order for each subject. Blocks lasted for as many trials as required to determine the phosphene threshold. (The average number of trials per block varied from 16 to 21 between the different experiments.)

Phosphene thresholds were determined using a modified binary-search paradigm (MOBS) (Tyrell and Owens 1988), an adaptive threshold finding algorithm. TMS intensity was increased or decreased according to the subject's report on the previous trial. Only correct trials contributed toward threshold determination.

In *experiment 1*, TMS was delivered at the onset of the visual stimulus. Following the load task response, phosphene reports were made by pressing either the 0 (for yes) or 2 (for no) keys. *Experiments 2–5* followed the same procedure as *experiment 1* with the following exceptions.

In *experiment 2*, the load task was not performed; instead, following the search displays, subjects pressed either 0 or 2 at random and then made their phosphene detection response. In *experiment 3*, the TMS pulse was delivered 500 ms from the onset of the visual stimulus. In *experiment 4*, the order of the judgments was reversed. Subjects indicated the presence or absence of a phosphene first followed by the load-task response.

In *experiment 5*, working memory (WM) load was manipulated using the procedure reported by Lavie et al. (2004). A memory set with either six digits (in the 5 high-WM load blocks) or one digit (in the 5 low-load blocks) was presented for 500 ms at the start of each trial followed by a mask presented for 500 ms. Following a blank retention interval of 1.5 s, a single pulse was administered. Phosphene report was made using the same keys as before and was followed by a memory probe of one digit (presented until response). The subject pressed the 2 key to indicate that the memory probe was present in the memory set or the 0 key to indicate that it was absent.

RESULTS

The search task accuracy results confirmed the effectiveness of the perceptual load manipulation in this study. Search accuracy was significantly reduced in the high load condition (75%) compared with the low load condition [98%; $t(5) = 11.997$, $P < 0.001$ for the difference]. As predicted from the hypothesis that high perceptual load reduces cortical excitability in task-irrelevant areas, the V5 phosphene threshold was significantly increased in the high load compared with the low load condition [$t(5) = 2.773$, $P = 0.039$; Fig. 1, *experiment 1*].

Experiment 2 confirmed that the effect of perceptual load on the phosphene threshold was not caused by any difference in the visual stimuli between the load conditions. Phosphene thresholds for the two load conditions did not differ [$t(5) = 0.981$, $P = 0.37$] when subjects were presented with the same stimuli as in *experiment 1* but did not perform the visual search task (Fig. 1, *experiment 2*). A comparison of the difference in phosphene thresholds between the two load conditions in *experiment 1* and *experiment 2* confirmed a significant reduction in the effect of load on the phosphene threshold in *experiment 2* [$t(5) = 2.56$, $P = 0.025$].

In *experiment 3*, we sought to rule out general—nonperceptual—effects of task difficulty such as effects on the overall level of arousal or response criterion. The search task of *experiment 1* was used, but TMS was now delivered 500 ms from onset of the search display (Fig. 1, *experiment 3*)—a time window selected to encompass postperceptual processes such as response selection (Pashler and Johnston 1998). As in load theory, the effects of perceptual load are caused by perceptual capacity limits rather than general task difficulty; we predicted that perceptual load would not affect neural excitability at this late postperceptual time window.

The results supported this prediction. The search data confirmed a significant effect of perceptual load on the letter search accuracy [the accuracy was reduced in the high load

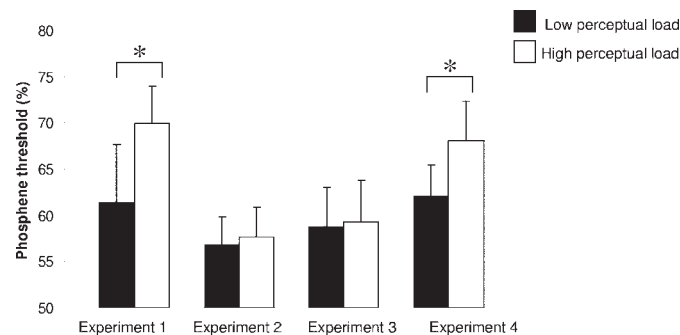


FIG. 1. Phosphene threshold (% stimulator intensity) as a function of perceptual load in *experiments 1–4*. The error bars indicate SE. *Significant load effect ($P < 0.05$).

condition ($M = 79\%$) compared with the low load condition ($M = 98\%$), $t(5) = 6.452$, $P < 0.001$]. However, the phosphene thresholds for the two load conditions no longer differed [$t(5) = 0.928$, $P = 0.39$], and a comparison of the load effects on the phosphene stimulation threshold between *experiment 1* and *experiment 3* confirmed a significant reduction in the effect of load on the phosphene threshold in *experiment 3* [$t(5) = 2.33$, $P = 0.034$].

Experiment 4 ruled out response-priority and memory-based accounts for the effects of load on the phosphene thresholds. In this experiment, the order of report was reversed: Subjects made the phosphene report first and the search response second. As in *experiment 1*, the search performance accuracy was significantly reduced in the high-load ($M = 72\%$) compared with the low-load ($M = 93\%$) conditions [$t(5) = 9.156$, $P < 0.001$], and the phosphene threshold was again significantly higher in the high compared with low-load conditions [$t(5) = 5.028$, $P = 0.004$; Fig. 1, *experiment 4*]. The effect of load on the phosphene threshold did not differ between *experiment 1* and *experiment 4* [$t(5) = 0.827$, $P = 0.446$], despite the different order of phosphene and search responses. This comparison reinforces the fact that the phosphene stimulation threshold is determined by perceptual load rather than processes associated with the response order (such as the likelihood of memory decay).

Experiment 5 confirmed the specificity of the perceptual load effect by distinguishing it from the effect of working memory load (see Lavie et al. 2004). In this experiment, a single pulse was delivered over V5/MT while subjects rehearsed a memory set of either one digit (low WM load) or six digits (high WM load). Task performance confirmed that the manipulation of WM load was effective. Accuracy was significantly reduced in the high-load condition ($M = 71\%$) compared with the low-load condition [$M = 96\%$; $t(5) = 4.683$, $P = 0.005$], an effect of comparable magnitude to that found with perceptual load in the previous experiments. However, in contrast to the effects of perceptual load, the phosphene thresholds did not significantly differ between the low ($M = 49\%$) and high ($M = 51\%$) WM load conditions ($t < 1$). A comparison of the effect of WM load on the phosphene threshold with that of perceptual load (*experiment 1*) confirmed the significant reduction in the effect of WM load compared with that of perceptual load [$t(5) = 2.69$, $P = 0.023$].²

DISCUSSION

The results of these five experiments provide clear support for our prediction that the level of perceptual load in a letter search task would determine visual cortex excitability in a task-irrelevant area, in this case V5/MT. Furthermore, by finding the effect of perceptual load irrespective of whether the phosphene report was made before or after the search task responses and by establishing that there were no changes in the phosphene threshold as a function of differences in the visual stimuli, WM load and thus general task difficulty and general demands on cognitive control resources, or when the phos-

phene was induced at a later postperceptual time window, we can exclude any effects not specific to perceptual load.

Our findings suggest that previous demonstrations of the effects of perceptual load on behavioral and neural responses related to task-irrelevant stimuli are caused by a change in the excitability of task-unrelated sensory cortices. The finding that phosphene thresholds are unaffected by WM load not only reinforces the specificity of the effect to perceptual load but also has implications for the load theory. It suggests that the increase in distractor processing previously found with high WM load (De Fockert et al. 2001) may not be caused by enhanced cortical excitability (but rather indicate effects of WM load on later postsensory processes, such as those related to the distractor effects on response selection).

The effects of perceptual load were found in response to direct stimulation of V5/MT—bypassing the retina and LGN—and therefore preclude accounts of the modulation of V5/MT phosphene threshold in terms of forward gating by the LGN. Accounts of the modulation of V5/MT phosphenes by load in terms of modulation of the recursive projections from V5/MT to V1 as well as superior colliculus (SC) and the LGN remain possible. These accounts can accommodate previous findings that high perceptual load modulates lateral geniculate nucleus activity related to task-irrelevant stimuli (O'Connor et al. 2002) and that high perceptual load modulates activity related to irrelevant motion distractors in a network of motion responsive areas including V5/MT, V1/V2, and the SC (Rees et al. 1997). Whether the effects of perceptual load on visual cortex reflect modulations of feedforward or backprojections is an important question for future research.

GRANTS

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² Although the phosphene thresholds in *experiment 5* seem to be lower overall than those in the corresponding low perceptual load condition in *experiment 1*, this difference was not statistically significant [$t(10) = 1.399$, $P = 0.19$] and is thus likely to be caused by random variations between the different subjects groups in the different experiments.

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