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Research Report

The role of perceptual load in visual awareness

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ABSTRACT

Does awareness depend on attention? This is a fundamental issue for understanding the relationship of attention and awareness, yet previous research provided mixed results. Here, I describe new research that shows that the effects of attention on awareness depend on the level of perceptual load in the attended task. Awareness reports in both the inattentional blindness and change blindness paradigms were found to depend on the extent to which an attended primary task loads attention. Neuroimaging results revealed the involvement of frontoparietal attention network in awareness and transcranial magnetic stimulation experiments confirmed a causal role for frontoparietal activity in awareness. These results clarify the role of attention and associated frontoparietal activity in visual awareness within the framework of load theory of attention.

1. Introduction

Would focusing attention on a current task prevent intrusions of task-irrelevant stimuli into awareness? This fundamental issue has intrigued psychologists for many years and has led to an enduring controversy between early selection views suggesting that attention can prevent irrelevant distractors from reaching awareness (Broadbent, 1958; Neisser and Becklen, 1975) and late selection views suggesting that attention affects later processes such as response selection and memory but does not affect perceptual awareness (Deutsch and Deutsch, 1963; Tipper, 1985).

A possible resolution to this debate has been offered within a hybrid perceptual load model (Lavie, 1995; Lavie et al., 2004). According to this model, focusing attention on a task at hand can prevent perception of task-irrelevant stimuli (early selection) when the processing of task-relevant stimuli involves a high level of perceptual load that consumes all available capacity. By contrast, when processing of the task-relevant stimuli places lower demands on the perceptual system, any spare capacity from the task-relevant processing spills over involuntarily, resulting in the perception of irrelevant stimuli (late selection).

Although perceptual load model has the clear implication that intrusions of irrelevant distractors into awareness should not occur in situations of high perceptual load in the relevant task, previous tests of this theory (see Lavie, 2005 for review) have mainly used either indirect measures of distractor effects on RTs or assessed neural activity in sensory cortices related to the distractor perception and awareness but with one exception (Rees et al., 1997) have typically not included measures of the extent to which distractors have in fact entered visual awareness.

In the present article I describe new research on the effects of perceptual load on visual awareness in studies that assess awareness within the "Inattentional Blindness" (Mack and Rock, 1998) and "Change Blindness" (Rensink et al., 1997) paradigms. I then describe research on the implications of these behavioral findings for the neural mechanisms of awareness. I begin with a short review of the existing behavioral and neuroimaging evidence for perceptual load theory.

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1.1. *Existing evidence for perceptual load theory: RT experiments*

Increased perceptual load means that either the number of items that need to be perceived is increased, or that for the same number of items, perceptual identification is more demanding on attention with high load. The role of perceptual load in determining distractor processing was first established in behavioral experiments (Lavie, 1995; Lavie and Cox, 1997) using the response competition paradigm (Eriksen and Eriksen, 1974). The response competition paradigm was chosen for the first behavioral load experiments because it has been widely accepted as a conventional measure of distractor perception within modern research of early and late selection debate (Miller, 1991; Yantis and Johnston, 1990, for review, see Lavie and Tsal, 1994). However, as I discuss below, this paradigm does not allow direct conclusions about conscious awareness. In a typical response-competition task subjects make speeded responses indicating whether a central target letter is one of two pre-specified letters (e.g. 'X' or 'N') while attempting to ignore a peripheral distractor letter. Slower responses in the presence of a distractor with an incongruent identity (distractor 'X' for target 'N') compared with a congruent distractor (distractor 'X' for target 'X') or a neutral distractor (e.g. a distractor 'L' that was not associated with any of the task responses) indicate that the distractor identity was perceived at least to the extent of recognizing the association of distractor identity and (incongruent or congruent) response.

Perceptual load experiments showed that response competition effects from distractors with incongruent (vs. congruent) identity were found on target RTs when the target task involved low perceptual load (e.g., just one target letter was present, any additional task requiring only simple presence/absence detection) but were eliminated when the target task involved high perceptual load (search for the target among many similar letters (Lavie and Cox, 1997), or having to discriminate precise location and size for an adjacent shape, (Lavie, 1995)). These results clearly show that high perceptual load reduces processing of the distractor identity. However, since they are based on measures of the distractor congruency effects on target RTs, they do not specifically address the effects of perceptual load on subjective conscious perception. It remains entirely possible, for example, that subjects were not aware of the distractors' identity not only under conditions of high perceptual load, where target RTs were unaffected by the distractor identity but also under conditions of low perceptual load, where target RTs varied as a function of the distractor identity, because the identity effects on RTs in the conditions of low perceptual load might just reflect implicit unconscious recognition of the response association for the distractor instead of conscious representation of its identity. Conversely, it is also logically possible that the distractor reached awareness under both conditions of low and high perceptual load. The elimination of distractor congruency effects on target RTs with high load on this alternative account could be due to effects of load on processes other than conscious awareness, such as response selection. Although there is evidence against two specific suggestions (a) that reduced distractor congruency effects with high load are merely due to the associated slowing of responses with load (Lavie and DeFockert, 2003) and (b) that perceptual load increases active suppression of the distractor responses under high load (Lavie and Fox, 2000), the RT load studies leave open the general possibility that perceptual load effects are on responses rather than on conscious awareness. The new research I describe on the effects of perceptual load on direct measures of conscious awareness (in the sections on the role of perceptual load in inattentional blindness and change blindness) can provide more conclusive evidence on this issue.

1.2. *Neuroimaging*

Converging results from neuroimaging tests of perceptual load theory (Mesulam, 1981; Miller, 1991; Milner and Goodale, 1995; Mitchell et al., 2004; Most et al., 2001; Nobre et al., 2003; Neisser and Becklen, 1975; O'Connor et al., 2002; Ooi and He, 1999; Pessoa et al., 2002; Pinsk et al., 2003; Pisella et al., 2004; Rees et al., 1997, 1999; Schwartz et al., 2005, Yi et al., 2004) clearly show that load effects on distractor processing cannot be merely due to effects on RTs. These studies demonstrated that high load eliminates visual cortex activity related to task-irrelevant distractors. For example, Rees et al. (1997) found that neural activity related to motion (vs. stationary) distractors in visual cortex (e.g., MT) was found in conditions of low load in a relevant task on words at fixation (detection of the letter case) but was eliminated by high load in the relevant task (involving more complex word discrimination). Other studies found that visual cortex activity related to a task-irrelevant checkerboard dependant on the level of load in a relevant task, decreasing as load was increased (O'Connor et al., 2002; Tong et al., 1998). Rees et al. (1999) showed that fixated words did not elicit greater activity than letter strings when ignored during performance of a high load task of monitoring a rapid superimposed picture stream for repetitions. Yi et al. (2004) similarly showed that when subjects attempt to ignore pictures of places presented in the background, while monitoring for face repetitions at fixation, parahippocampal activity related to the place backgrounds is substantially reduced by increasing the load in the face identification task.

These results convincingly show that neural activity in areas of visual cortex that are related to perception of the task-irrelevant stimuli is determined by the level of load in task-relevant processing. However, apart from a study by Rees et al. (1997), this research typically has not assessed the effects of distracters on visual awareness. Rees et al. (1997) did accompany their neuroimaging experiment with assessment of the subjective duration of motion after-effects from the motion distractors presented either during low load or high load tasks. They found that the subjective duration of the motion after effect was significantly reduced by high load for each subject (all t's > 1.9; all P values ≤ 0.05, Fig. 1). This result is encouraging for the suggestion that perceptual load determines awareness at least in the case of visual motion.

To establish the role of perceptual load in visual awareness, it is important to examine whether perceptual load effects on awareness can generalize across various measures of visual awareness. Below I describe more recent experiments that test the effects of perceptual load on explicit

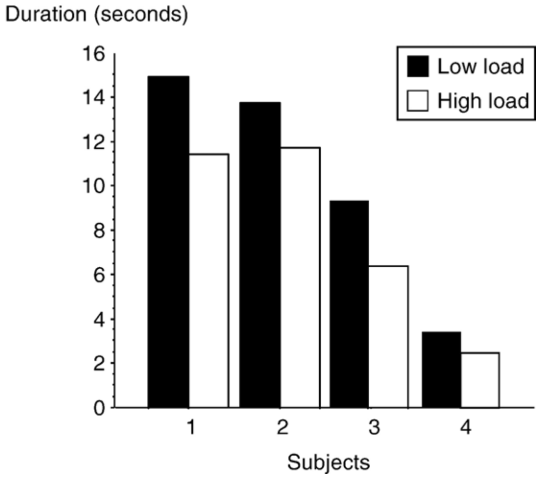

Fig. 1 – The effect of load on the subjective duration of MAE. Mean subjective duration reports of MAE are shown for each subject following adaptation to the visual motion stimulus under either high or low visual load.

reports about subjective awareness in the inattentional blindness and in the change blindness paradigms.

2. The role of perceptual load in "inattentional blindness"

In order to test whether conscious awareness of task-irrelevant stimuli depends on the level of perceptual load in task-relevant processing we ran a series of experiments that modified the typical "inattentional blindness" paradigm (Mack and Rock, 1998) to include manipulations of perceptual load in the relevant task (Cartwright-Finch and Lavie, 2005, in press).

Like in a typical inattentional blindness experiment, participants performed a task for a few (typically six) trials and then were presented with an additional task-irrelevant stimulus on the final critical trial. Immediately after the task-response participants were asked to report whether they detected this extra stimulus. On a subsequent control trial, the participants were requested not to perform the task, just detect instead whether there is any extra stimulus on the display. Importantly, unlike a typical inattentional blindness experiment, we did not rest our conclusions on a comparison of the critical trial and control trial, as these are confounded with expectation and intention, (see e.g. Braun, 2001). Performance on the control trial was just used as an exclusion criterion. To ascertain that any result of blindness in the previous trial is due to inattention only participants that could report the extra stimulus when attending to it in the final control trial were included in the analysis. Our comparisons instead were conducted on the rates of inattentional blindness observed for the task-irrelevant stimulus in the critical trial between the different levels of perceptual load in the relevant task. In this way, our comparisons did not confound varying levels of expectation. The task-irrelevant stimulus was equally unexpected at both levels of perceptual load. Instead, we manipulated "inattention" by varying the availability of attention to the critical stimulus via our manipulation of the level of perceptual load in the relevant task.

In one series of experiments, we used the cross task often used in inattentional blindness experiments. A cross was presented for 110 ms followed by a mask display on each trial. One cross arm was blue and the other green (hue differences chosen to be easily discriminated) and one cross arm was slightly longer than the other (length differences chosen to be hard to discriminate). In the conditions of low perceptual load subjects were asked to indicate which arm of the cross (vertical or horizontal) was blue. Such simple color discrimination task is known to impose low attentional load (Treisman and Gelade, 1980). In the conditions of high perceptual load, subjects were asked to indicate which arm of the cross (vertical or horizontal) was longer. As the difference in line-length was very subtle such task should demand considerably more attentional resources (Bonnel et al., 1987; Lavie, 1995) and have led to a reduction in effects of distracters on target RTs in previous load studies (for review see (Lavie, 2000; Lavie, 2005)). The novel question of interest in this study was whether perceptual load would also determine rates of inattentional blindness for an irrelevant stimulus presented on the critical trial. Fig. 2a presents the stimulus displays presented on the critical trials in these experiments. In these critical trials, a square (subtending 0.3° of visual angle) was unexpectedly presented in one of four peripheral locations in addition to the central cross. Subjects were interrogated about awareness of this stimulus immediately following their task response on that trial.

The results showed that perceptual load determined the rates of inattentional blindness in this task. For instance, in one such experiment, 11 of 20 subjects reported seeing the task-irrelevant stimulus in the low load condition but this rate was significantly reduced in the high load condition, χ^2 (1, $N = 40$) = 9.24, $P < 0.01$, where only 2 of 20 subjects reported seeing the task-irrelevant stimulus.

In another series of experiments, we replaced the cross task with a letter search task (Figs. 2b, c), similar to the one that has been shown to reduce interference effects on target RTs produced by an irrelevant distractor presented outside the search array (in the periphery, e.g., (Lavie, 1995; Lavie and Cox, 1997; Lavie and Fox, 2000) or even at fixation, see (Beck and Lavie, 2005)). As in the previous perceptual load studies, a circular array was presented for 200 ms in the center of the screen and subjects were asked to report whether the letter 'X or 'N' was present in the circle. In conditions of low perceptual load the search target (either X or N) was present in one of the circle positions with placeholders (small circles) presented in the other circle positions. In the high load condition other letters (J, P, U, S, F) occupied the non-target circle positions forcing the subjects to search for the target among these letters. The same task-irrelevant stimulus as used in the cross task was also unexpectedly presented in the periphery on the sixth trial in these experiments, and subjects were asked immediately after their letter-search response whether they saw this extra stimulus or not. The results showed that awareness of the unexpected task-irrelevant stimulus was determined by the level of perceptual load in the search task. For instance in one such experiment the rate of subjects who reported seeing the

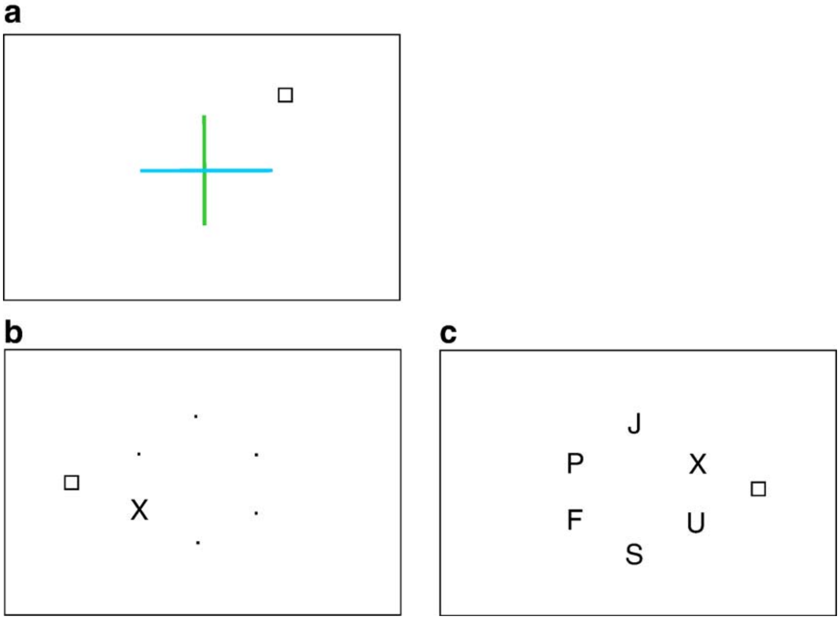

Fig. 2 – Load procedure in the inattentional blindness study of Cartwright-Finch and Lavie (2005, in press). An example of a stimulus display on a critical trial is shown for (a) the cross task under both conditions of perceptual load. In the low load condition, subjects were asked to indicate which arm was green. In the high load condition they were asked to indicate which arm was longer. (b) The letter search task in the low load condition and (c) the letter search task in the high load condition.

task-irrelevant stimulus was 16 of 18 in the low load condition and this was significantly reduced to 9 of 18 in the high load condition χ^2 (1, $N = 36$) = 6.42, $P < 0.02$.

Note that the level of awareness reports in the low perceptual load condition of this visual search experiment (88%) was higher than in the corresponding low perceptual load condition of the cross task experiment (55%). This is likely to be due to the greater similarity of the critical stimulus and the relevant task stimuli in terms of size and color (see Fig. 2). The similarity between the irrelevant stimulus and the relevant-task stimuli has already been shown to determine rates of inattentional blindness (Mack and Rock, 1998; Most et al., 2001). Critically regardless of the different levels of awareness in the low perceptual load condition, higher perceptual load has led to an equivalent reduction in the rate of awareness reports across both types of tasks (38% reduction in the search task, 45% reduction in the cross task).

Although the inattentional blindness measure is not based on RTs, it might still be affected by the slowing of task responses with higher perceptual load. Since slower task responses would involve a longer delay from presentation of the last critical display with the task plus the unexpected stimulus until questioning about awareness (which always followed responses) in the high (vs. low) load conditions, it could increase the likelihood of misses due to forgetting during the longer delay. This possibility was ruled out in an experiment that equated task RTs in high and low load conditions of the visual search task presented in Fig. 2 by forcing subjects to wait for 1 S following the task until they could make their task-response on all trials. In order to assess subjects RTs, we now ran a long block of 102 trials in total that included a random mix of low search load and high search load trials. The same unexpected task-irrelevant stimulus as that used in the short experiments was presented on the final trial of the block. The results showed that despite equivalent RTs in the low (335 ms) and high (334 ms) load conditions, load has significantly reduced the rate of awareness for the task-irrelevant stimulus again, from 15 of 18 subjects in the low load group to 8 of 18 subjects in the high load condition, χ^2 (1, $N = 36$) = 5.899, $P < 0.05$.

We conclude that the level of perceptual load in a current task determines awareness reports within the inattentional blindness paradigm. Greater inattentional blindness is found when a current task engages more attention with higher perceptual load.

Inattentional blindness measures, however, ask about awareness for an unexpected object. Although the effects of load on inattentional blindness cannot be due to varying the level of expectation, as the irrelevant stimulus was equally unexpected under all conditions of load, the conclusion from these inattentional blindness experiments remains restricted to cases of awareness for an unexpected object. Moreover, the retrospective measure of awareness with a surprise question following task responses involves a memory component. The effects of load may therefore be attributed to weaker encoding of the unexpected stimulus into memory with high load than low load.

It is therefore important to ask whether perceptual load can determine awareness in other paradigms that do not rely on a retrospective surprise question about an unexpected stimulus in their measure of awareness. The change blindness paradigm (Rensink et al., 1997) provides such a measure, as I describe next.

3. The role of perceptual load in "change blindness"

In the change blindness paradigm subjects are instructed in advance that their task is to detect whether a change occurred between two successive images and report about it immediately following the images. Thus, unlike inattentional blindness the event for which awareness is reported is expected and awareness reports are given immediately following the images. Indeed, under normal circumstances awareness reports will show very little failure to detect any change between the images. However, when the sensory transient that a change involved is interrupted, for example, when the two successive images are intervened with a blank interval that produces a 'flicker', observers will often fail to detect the change, exhibiting "change blindness" (Rensink et al., 1997).

Load on attention appears to play a critical role in change blindness. The images of natural scenes used to demonstrate change blindness should load attention as they are typically rich in detail and often fairly cluttered in this flicker task. Indeed, cuing the object that changes removes any difficulty to detect change (Rensink et al., 1997) suggesting that allocation of focused attention to the object of change is needed to detect a change in this paradigm, and the failure to detect changes when uncued is due to attention being loaded with the processing of other objects in the cluttered scene.

In line with this suggestion, it has also been found that objects that capture attention either by virtue of containing a singleton feature (Scholl, 2000) or by virtue of their significant socio-biological meaning (Ro et al., 2001) (e.g., human faces) do not suffer from change blindness as much as other objects that do not capture attention. However no study as yet has directly examined the effects of the level of load on attention on change detection.

Moreover, the duration of the cycling displays in all these experiments was sufficiently long to allow eye-movements and these were not monitored. It is therefore not clear whether the improved performance for the cued items or for singletons and faces was due to capturing of attention or to eye movements towards these items.

One line of experiments provided evidence for the role of attention in change detection in a paradigm that used short cycle durations that precluded alternative accounts in terms of eye movements. Wright et al. (2000) examined detection of orientation changes in Gabour patches, as a function of the number of Gabour patches displayed (display set size) and found a greater rate of change blindness with increased display set size (Wright et al., 2000). Although increased display set size should load attention it also involves greater crowding as well as greater load on decision making processes and on visual short-term memory. The effects of attentional load per se (without also involving crowding and effects on short-term memory and decision making) therefore remain unclear. Furthermore, it is not clear how much can be extrapolated from detection of simple orientation change in Gabour patches to detection of a more complex change between one meaningful object and another (e.g., a change of a face to another face) as has been typically measured in change blindness tasks.

In order to directly examine whether awareness of change in a more typical change blindness task depends on whether attention is available to focus on the changing object or is loaded with the processing of other objects we have modified a flicker change blindness task that requires subjects to detect a change of one object to another, to include a manipulation of perceptual load (Beck and Lavie, submitted for publication).

First, because the different natural scenes used in previous change blindness tasks may vary in the amount of clutter they involve, we simplified the visual displays used to include just two images from the same category (either both were faces or both were places) on each display. In this way, we examined change detection for meaningful 3D objects as in the typical change blindness studies whilst avoiding other variations in the displays (such as clutter) that could also affect the level of load on attention. Second, in order for any effects of perceptual load to be clearly attributed to availability of attention to the change blindness task rather than directly affecting the change detection task itself (c.f. manipulations of the changing display set size) we combined the change blindness task with another letter search task and varied the level of

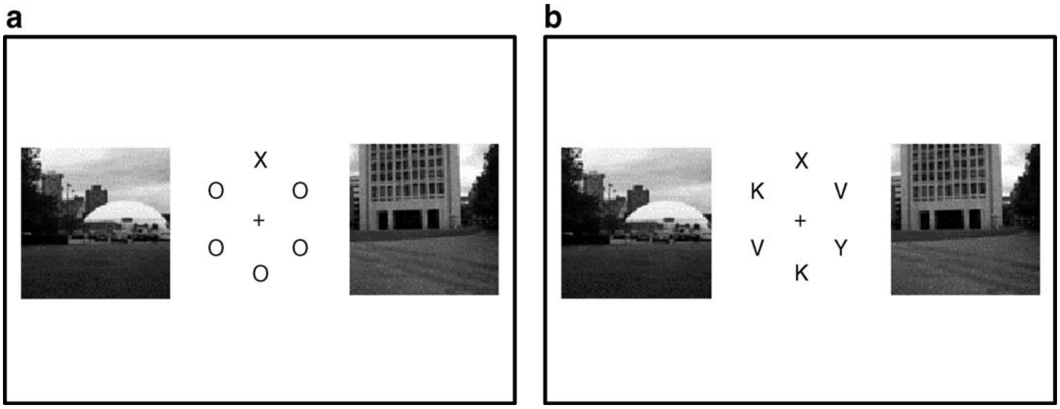

Fig. 3 – Load procedure in the change blindness study of Beck and Lavie (submitted for publication). An example of one stimulus display is shown for (a) the low load condition and (b) the high load condition. The circle of letters subtended 2.2° in diameter. The face and place images were positioned at 3.5° to the right and left of fixation.

perceptual load in the search task. The two images in the change blindness task flanked a central letter search array (Fig. 3). Subjects were asked to monitor the letters for an 'x', and press a key as soon as they can whenever this target appeared (on 31% of the trials). In the low load condition, all the five non-target letters were O's and in the high load condition they were drawn from the set of K, Y and V. A similar manipulation of perceptual load has been shown to reduce distractor interference effects in several previous studies (see Lavie, 2005 for review) and has been effective in inducing inattentional blindness as described earlier.

In this study, we asked whether the level of search load would also determine change blindness. Awareness of change was examined following a cycle of four displays (each presented for 500 ms) separated from each other by a blank interval (also presented for 500 ms) producing a "flicker". Since eye movements could occur in these display durations, we monitored fixation with an infrared eye tracker (ASL 310 Eye Tracking System) sampling horizontal eye positions at a rate of 40 Hz to ensure that our results can be attributed to effects of attention rather than eye movements.

The results showed that accuracy of change detection significantly declined from 69% on average in the low load condition to 58% on average in the high load condition, $t(5) = 7.3$, $P < 0.01$. To assess observers' sensitivity to change, we calculated d' values for each participant. These are presented in Fig. 4. Statistical analysis showed that sensitivity to the changes was significantly reduced from a mean d' of 1.54 in the low load conditions to a mean d' of 0.78 in the high load conditions, $t(5) = 6.49$, $P < 0.01$. Analysis of eye positions confirmed that subjects maintaining fixation just as well in the low load as in the high load conditions within ± 1° of visual angle from the display center in each condition. These results clearly rule out an account of the load effects on change detection in terms of a greater likelihood of eye movements to the peripheral images (see Fig. 3) under low load. Instead, the results suggest that the level of load on attention determines the level of awareness of change within change blindness paradigms.

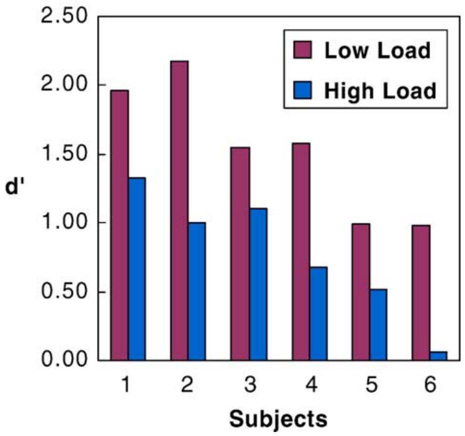

Fig. 4 – The effect of load on change detection Sensitivity. d' is plotted per each subject as a function of load in the primary letter search task.

4. Neural correlates of awareness in the change blindness paradigm

4.1. *Neuroimaging of change blindness*

The finding that awareness is determined by the level of perceptual load in a primary task has implications for the neural correlates of awareness. These should include neural structures associated with effects of attentional load in parietal and frontal cortex (Wojciulik and Kanwisher, 1999; Schwartz et al., 2005). To examine the neural correlates of awareness within the change blindness task, we have conducted an event-related fMRI study comparing activity during consciously detected changes and activity during undetected changes (Beck et al., 2001). The task was very similar to the behavioral study: subjects were asked to perform a primary letter search task searching for 'x' among six letters and report if one of the images changed. However, in this study, we did not manipulate load. Instead, we adjusted the level of load per subject, so that they detect change about 50% of the time. Again, since we used display durations (of 500 ms each) that permitted eye movements we monitoring fixation. The analysis of eye positions during scanning confirmed that fixation was typically well maintained at the display center, and that there were no systematical differences in eye positions between detected and undetected changes.

Fig. 5 shows areas with greater activity during detected changes than undetected changes. As can be seen in Fig. 5a, there were three main sites of activity related to detected changes: ventral stream activity in the fusiform gyrus, and dorsal stream activity in the classic attention network consisting of bilateral parietal lobe, and the right dorsolateral prefrontal cortex. The activity in this network is in line with the suggestion of our behavioral studies that attention plays a critical role in visual awareness.

In addition, activity in the fusiform gyrus diverged according to the type of change that was detected, when changes in faces were detected, there was greater activity in the areas of the fusiform gyrus previously associated with face perception, (Kanwisher et al., 1997); when place changes were detected greater activity was found in a region of the fusiform gyrus that is near but posterior to the 'parahippocampal place area' previously reported (Epstein and Kanwisher, 1998). By contrast, activity in the bilateral parietal lobe, and right dorsolateral prefrontal cortex was correlated with conscious detection for both types of change. In fact, masking procedure revealed that activity related to detected changes in common to both faces and places involved only the parietal and dorsolateral prefrontal sites, but none of the ventral areas. Thus, whereas the content of awareness depends on activity in category-specific regions of the ventral stream, frontoparietal activity plays a general role in awareness regardless of its content.

This general role fits with our hypothesis that frontoparietal structures associated with the effects of attentional load would also be involved in awareness, for if the frontoparietal activity reflects the allocation of attention, one would expect it to have a general involvement in

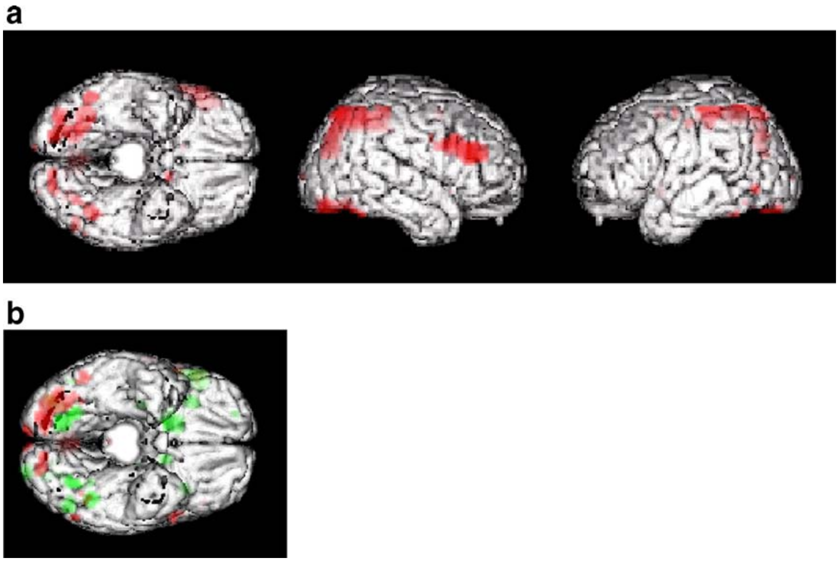

Fig. 5 – Brain areas showing greater activity during detected changes compared with undetected changes in Beck et al. (2001) study. The results are shown on three views (inferior (a and b), left lateral and right lateral) of a T1-weighted anatomical template brain upon which are superimposed loci where evoked activity was greater during consciously detected change compared to undetected change. (a) Activity related to conscious change detection (detected > undetected), pooled across stimulus category. (b) Activity related to category-specific conscious detection of change. Activity is superimposed in red for faces and green for places. A statistical threshold of z = 3.09 (P < 0.001, uncorrected) is used for display purposes.

determining whether any stimulus (regardless of content) enters awareness. Indeed, a growing body of research has implicated the frontoparietal cortex in visual awareness across a variety of tasks (e.g., binocular rivalry (Lumer et al., 1930), reversing perception of ambiguous figures (Kleinschmidt et al., 1998)) and percepts (ranging from percepts of gratings to meaningful high-level perceptual interpretations such as that of an old woman versus a young woman in Boring's (1930) "My wife and mother-in-law" ambiguous figure). Importantly, the allocation of attention to one percept or another has also been shown to determine awareness in these tasks (Ooi and He, 1999; Tsal and Kolbet, 1985; Mitchell et al., 2004).

It is worth noting that our suggestion that awareness-related frontoparietal activity reflects the allocation of attention does not necessarily mean spatial allocation of attention. The effects of load on attention are not confined to a spatial model (see (Lavie, 2005) for discussion). Take for example the effects of attentional load on change blindness I report in Section 3 although these may be interpreted as low load (vs. high load) allowing more spatial shifts of attention to the location of the changing image, they are also consistent with non spatial interpretations, for example, in terms of spending more processing time on the images in tasks of low load than high load. Moreover, frontoparietal cortex has been associated with the effects of attentional load both in spatial tasks (e.g. comparing high load versus low load in visual search tasks, (Corbetta et al., 1995; Nobre et al., 2003)) and nonspatial (Rapid Serial Visual Presentation at fixation) tasks (Schwartz et al., 2005; Wojciulik and Kanwisher, 1999).

4.2. *Transcranial Magnetic Stimulation during "change blindness"*

Although the consistent association of frontoparietal activity and awareness reports in a variety of imaging studies makes a compelling case for the suggestion of a role for frontoparietal cortex in determining awareness, functional imaging results merely show a correlation of neural activity and awareness. In order to examine whether the parietal lobe plays any causal role in awareness, we used Transcranial Magnetic Stimulation (TMS) to disrupt activity in either right or left parietal cortex during performance of a change detection task (Beck et al., in press). The sites of parietal stimulation were based on the peak coordinates from Beck et al.'s (2001) fMRI study (Beck et al., 2001). They were identified for each individual's anatomical MRI and co-registered with the coil using Brainsight software (Rogue Research, Montreal Canada). The task presented in Fig. 6 was similar to the one used in our behavioral and functional imaging experiments, except for the following changes.

As our hypothesis concerned a general effect of parietal stimulation, we no longer used two different image categories. In this study, we only presented female faces. Also, in order for TMS to directly affect performance of the change detection task, we removed the primary letter search task. (Otherwise any disruption effects could be indirectly due to effects of parietal TMS on the letter search task). Finally, for the TMS to be applied throughout the period of the change detection task, we used the so-called one-shot change detection procedure. Only one cycle of two faces—displays intervened by a 100 ms blank interval was presented on each

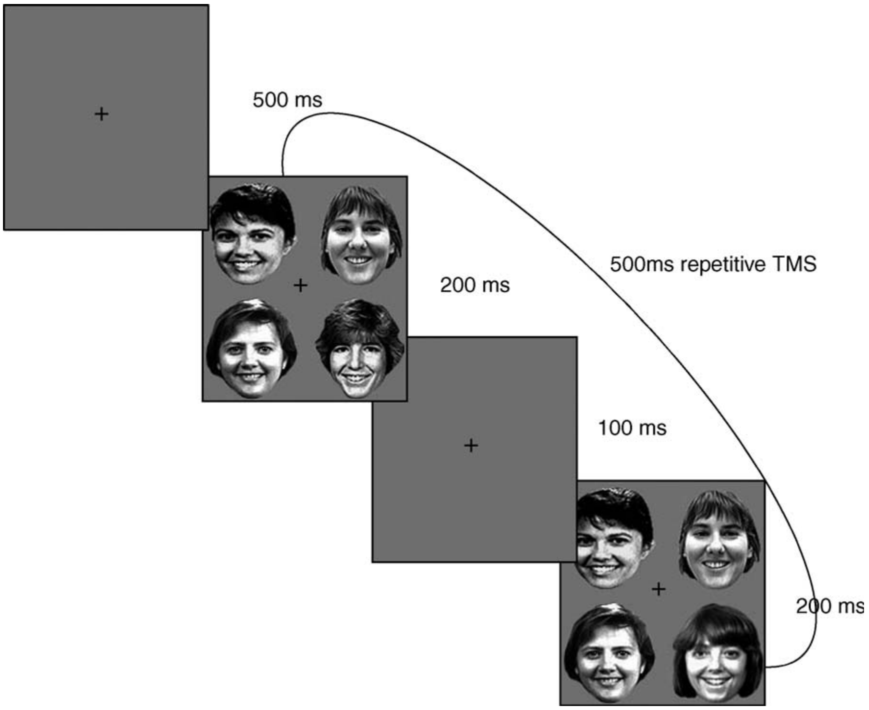

Fig. 6 – The procedure used in Beck et al. (in press).

trial, and repetitive TMS (1 Hz) was applied for 500 ms from the onset of the first display.

Initial pilot testing of this task with just two images and no other task concurred with the conclusion of our behavioral experiments that change detection critically depends on attentional load. With just two images and no other task to load attention change detection was at ceiling with minimal disruption effects due to TMS. We therefore added two more faces to the display to present four images in total, only one of which might change.

The results from nine subjects showed that right parietal TMS disrupted change detection regardless of the side of the change, producing significantly ($t \geq 2.34$, $P < 0.05$, in all statistical tests) slower RTs (M = 819 ms) and increased error rates (M = 37%) as well as reduced sensitivity of detection as assessed by d' (M = 1.55) compared to both left TMS (M RTs = 714 ms; M errors = 30%; M d' = 1.88) and a no TMS control condition (M RTs = 706 ms; M errors = 28%; M d' = 1.88). Whereas the left parietal TMS did not lead to any deficit compared to no TMS ($t < 1$ in all statistical comparisons of left TMS and no TMS conditions). These results demonstrate that right parietal cortex plays a causal role in change detection. The contrast between the right and left parietal TMS effects suggests that only the right parietal cortex, and not the left, is necessary for change detection. This suggestion is in accordance with the neuropsychological finding that the dramatic deficits in visual awareness documented in neglect patients, predominately follow right but not left parietal lesions (Vallar and Perani, 1986). It is important to note, however, that our findings do not preclude a role for the left parietal cortex in change detection under normal circumstances, when left parietal activity is undisrupted. Indeed, our functional imaging study implicated normal change detection with bilateral parietal activity. It therefore remains possible that under normal circumstances left parietal cortex also plays some causal role in change detection however because of the bilateral representation of space in the right but not left parietal cortex, (Heilman and Van Den Abell, 1980; Mesulam, 1981), when activity in the left parietal cortex is disrupted, the right parietal cortex can still take over and hence no deficit in representation is found.

The bilateral representation of space in the right parietal cortex may also account for our finding that right parietal TMS impaired detection in both the left and right sides of space. This finding is also in line with recent findings that neglect patients with a right parietal lesion show a general deficit in detecting a change in location on either side of space (Pisella et al., 2004).

Of course, our findings do not rule out a causal role in change detection for other structures. Specifically occipital cortex and right dorsolateral prefrontal (DLPFC) cortex have both been implicated in change detection in our functional imaging experiment. A causal role for occipital cortex in visual awareness is very well established (e.g., (Milner and Goodale, 1995; Tong et al., 1998) and a causal role for the right dorsolateral prefrontal cortex in change detection has also been recently established (Turatto et al., 2004). Turatto et al (2004) applied rTMS over the site of activity in right DLPFC found in Beck et al.'s 2001 study while subjects performed a one-shot face change detection task, very similar to that used by Beck et al. (in press). Similar to our findings with TMS over parietal cortex, Turatto et al. (2004) found that rTMS of DLPFC throughout the period of the change detection task also significantly increases the rate of changes missed.

5. Summary and conclusions

The extent to which a current task engages full attention under conditions of high perceptual load has been shown to determine neural processing of task-irrelevant stimuli as well as their interference effects on behavior. The present research shows that the level of perceptual load in a current task also determines the extent to which other task-irrelevant stimuli reach visual awareness. High load in a current task was found to increase the level of both "inattentional blindness" and "change blindness" reports. Neuroimaging results implicated frontoparietal cortex in visual awareness and transcranial magnetic stimulation experiments confirmed a causal role for frontoparietal activity in awareness. These findings support our proposal that visual awareness is the interactive result of activity in category-selective regions in visual cortex mediating the content of awareness and activity in frontoparietal cortex mediating attention to the stimuli presented and thus determining whether they reach awareness.

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