

Delayed Reentrant Processing Impairs Visual Awareness: An Object-Substitution-Masking Study

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Abstract

In object-substitution masking (OSM), a sparse, common-onset mask impairs perception of a target when the mask's offset is later than the target's offset and spatial attention is dispersed. OSM is thought to reflect the interaction of feed-forward and reentrant processes in the brain: Upon stimulus presentation, a low-resolution representation of the target and mask progresses from sensory to anterior brain regions, triggering reentrant processing to confirm stimulus identity. It is hypothesized that dispersing spatial attention prolongs the required reentrant iterations, increasing the likelihood that only the lingering mask stimulus will remain physically present and thus substitute for the target in consciousness. However, empirically, it remains unclear whether substitution stems from delayed feed-forward or reentrant processing. Here, we demonstrate that delayed reentrant processing causes OSM, by showing that a task tapping high-level brain regions involved in reentrant processing leads to a spatially attended target being replaced by the mask. Our results confirm a key role for reentrant processing in conscious perception.

Keywords

object-substitution masking, consciousness, temporal attention, dual-task

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A glance at virtually any scene will provide the visual system with far more information than can be processed up to awareness. Even in simple displays, participants often fail to notice prominent objects if they are not attended (Most et al., 2001). Such failures of awareness demonstrate the illusory nature of people's visual experience, which seems so encompassing and yet excludes much of what goes on around them. Given this selectivity, it is not surprising that much scientific effort has been devoted to understanding the mechanisms underlying conscious perception.

To illuminate the processes that give rise to awareness, the fields of psychology and neuroscience have intensively investigated the sequence of events in visual information processing (e.g., Marr, 1982). Indeed, to fully characterize this sequence is to understand the path from sensation up to consciousness (Crick & Koch, 1990). Traditionally, it was assumed that visual processing proceeds in a feed-forward manner, from the retina up through the cortex, with the size of neurons' receptive fields, as well as the complexity of the features or operations they code for, increasing as information progresses along the various analytical pathways (see Hubel & Wiesel, 1977). Recently, however, there has been a shift in thinking with respect to the directionality of the flow of visual

information throughout the brain, and it is now generally accepted that feedback signals (reentrant, or top-down, processing) from anterior brain regions to primary visual cortex (V1) play a key role in conscious vision (e.g., Dehaene, Sergent, & Changeux, 2003; Di Lollo, Enns, & Rensink, 2000; Lamme & Roelfsema, 2000). This fits well with neuroanatomical studies demonstrating reentrant connections between extrastriate areas and V1 (Maunsell & van Essen, 1983; Mignard & Malpeli, 1991).

A key behavioral paradigm for studying the time course of visual processing is masking. In masking, two objects appear in close temporal and spatial proximity, and report accuracy for one of the objects (the target) varies as a function of its presentation duration, similarity to the second object (the mask), spatiotemporal distance from the mask, or some combination of these factors. Typically, masking (impaired target report) is greatest when the target is presented briefly, is similar in appearance to the mask, and appears in close spatiotemporal

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proximity to the mask. Masking is an important tool for studying mechanisms that give rise to awareness because a temporally trailing mask is thought to terminate visual analysis of the target (Breitmeyer & Ögmen, 2006), thus allowing researchers to tightly control the extent of stimulus processing.

The critical role of feedback processing in conscious perception has been highlighted recently by a phenomenon known as object-substitution masking (OSM; Di Lollo et al., 2000; Enns & Di Lollo, 1997). In a typical OSM paradigm, a target stimulus (e.g., a ring with a gap on the right or left), surrounded by a sparse mask (e.g., four dots adjacent to the corners of the target), appears among an array of distractors. The target and distractors are presented briefly (e.g., 30 ms), whereas the mask remains on display for a variable duration (~0–300 ms). Under these conditions, target identification decreases as mask duration increases up to approximately 300 ms, after which recovery is observed (Goodhew, Visser, Lipp, & Dux, in press). In addition, masking increases with the number of distractors in the display (Di Lollo et al., 2000).

Several characteristics distinguish OSM from other forms of masking (Di Lollo et al., 2000; Enns & Di Lollo, 1997). First, the target and mask have simultaneous onsets, and their contours do not overlap. This distinguishes OSM from backward and metacontrast masking, in which the onset of the mask follows the onset of the target (Breitmeyer, 1984; Kahneman, 1968). Second, there is a relatively large spatial separation between the target and mask. This differentiates OSM from metacontrast masking, in which the target is surrounded by a tightly fitting mask, and backward masking, in which the target and mask appear in the same spatial location. Finally, both backward and metacontrast masking can be obtained with centrally presented target and mask stimuli, whereas to date OSM has not been observed if the stimuli are centrally presented and are the subject of spatial attention (Enns & Di Lollo, 1997).

To explain these unique properties, Di Lollo et al. (2000) suggested that visual information progresses from primary visual cortex to higher-level brain regions via feed-forward pathways. From this information, anterior areas then generate a “perceptual hypothesis” pertaining to the identity of the visual input (e.g., a ring that has a gap on the right and is surrounded by four dots). Because of the large sizes of receptive fields in extrastriate regions and their reduced selectivity, high-resolution representations of the stimuli cannot be established. Thus, conscious identification requires iterative reentrant processing that compares the tentative perceptual hypothesis with stimulation in lower-level visual areas. Di Lollo et al. suggested that when spatial attention is dispersed (e.g., because of a large number of distractors), a greater number of iterative reentrant-processing loops are required to locate the target and confirm the preliminary perceptual hypothesis. In the OSM paradigm, by the time these loops are completed, only the mask remains on display, and consequently a conflict arises between the hypothesis and the stimulus input at the time of testing. To resolve this conflict, the system revises the hypothesis to include only the mask,

and as a result the mask is “substituted” for the target in consciousness.

This reentrant-processing account predicts that any manipulation that leads to more reentrant iterations (hypothesis testing) will result in stronger OSM, by increasing the chance that only the mask remains at the target location when it becomes the focus of this high-level confirmatory analysis. This prediction is consistent with evidence that (a) increasing the number of distractors, and therefore reducing the efficiency of spatial-attention deployment, increases OSM, and (b) precuing the target location or using a pop-out target to facilitate deployment of attention reduces OSM (Di Lollo et al., 2000). However, it is unclear whether these spatial manipulations affect reentrant processing or the initial feed-forward sweep, which could indirectly alter reentry by retarding hypothesis formation. This latter possibility is supported by evidence from behavioral and neuroimaging studies indicating that stimuli that are not at the focus of spatial attention are processed only to an early, precategorical level (e.g., Eger, Henson, Driver, & Dolan, 2004; Lachter, Forster, & Ruthruff, 2004). These findings suggest that information about spatially unattended targets may not reach anterior areas (i.e., feed-forward processing may be impaired).

In studies using other techniques, evidence that delayed reentry causes OSM has been similarly inconclusive. For example, Hirose et al. (2007) employed repetitive transcranial magnetic stimulation (TMS) to demonstrate that the functional disruption of V5/MT+, an extrastriate visual area with feedback projections to V1, reduced OSM. However, this result could have arisen because TMS of V5/MT+ impaired feed-forward processing, as this study did not use an event-related design to examine the time course of this disrupted masking. Similarly, using a dual-task paradigm, Dell’Acqua, Pascali, Jolicoeur, and Sessa (2003; see also Giesbrecht, Bischof, & Kingstone, 2003) found OSM at brief intertask intervals, which suggests that processing of the target for the first task may have delayed reentrant processing of the target for the second task. It should be noted, though, that because the target for each task in this study was presented at a different spatial location, the masking might again have reflected feed-forward effects.

To demonstrate that delayed reentrant processing gives rise to OSM in a dual-task manipulation, masking must occur at brief intertask intervals when all stimuli are spatially attended (i.e., appear in the same location). This follows from numerous studies that have shown that in dual-task paradigms, when all stimuli are at fixation, a nonreported second target is still processed to the level of identity (e.g., Luck, Vogel, & Shapiro, 1996; Maki, Frigen, & Paulson, 1997; Marois, Yi, & Chun, 2004). This indicates that unlike spatial manipulations, dual-task manipulations do not impede preliminary access to anterior brain regions (i.e., the initial feed-forward sweep). In addition, OSM must be greater under dual-task stimulus-presentation conditions when participants ignore the first task than when they respond to it, because this ensures that the

effect is not due to low-level visual processes (Raymond, Shapiro, & Arnell, 1992). To this end, we employed a demanding first task (T1) in a dual-task paradigm to prolong reentrant processing for a target in a second task (T2), while presenting the stimuli for the two tasks in the same spatial location to test whether OSM would be observed for a spatially attended target.

Method

To test whether delaying reentrant signals from high-level brain regions can affect OSM for a spatially attended stimulus, we presented participants with two tasks that had a varied stimulus onset asynchrony (SOA). We hypothesized that if T1, an arithmetic task known to tap parietal and prefrontal brain regions involved in reentrant processing (Dehaene et al., 2003; Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999; Miller & Cohen, 2001), engaged anterior brain areas at short SOAs, then reentrant processing of the target for T2 would be impaired, thus making it susceptible to OSM. In contrast, at long SOAs, T1 processing would be completed prior to the presentation of T2. Thus, reentrant processing in this condition could begin immediately, and OSM would be reduced (Dehaene et al., 2003; Pashler, 1994).

Participants

Nineteen (10 female, 9 male) University of Queensland students participated. The university's ethics board approved the protocol.

Stimuli and apparatus

Stimuli were presented on a Pentium computer using Presentation software (Version 12.20, Neurobehavioural Systems, www.neurobs.com). All stimuli appeared centrally on a black background, and participants sat, without head restraint, approximately 70 cm from the screen. The digits for T1 were white and subtended $0.38^\circ \times 0.61^\circ$ of visual angle. The Landolt Cs used for T2 ($\sim 0.46^\circ$) were gray and had a gap (0.16°) on the left, right, top, or bottom side. Four gray dots (each 0.08°) formed a notional square around the Landolt C, with the edge of the dots separated from the edge of the target by 0.08° .

Procedure

The single-task and dual-task conditions were identical in what was presented, but differed with respect to whether participants performed T1 or not. Participants completed both conditions, which were blocked and presented in a counterbalanced order across participants. Twenty practice trials preceded each block.

As shown in Figure 1, each trial began with a small white fixation cross in the center of the screen. Participants pressed the space bar to start the trial, and the screen went blank for

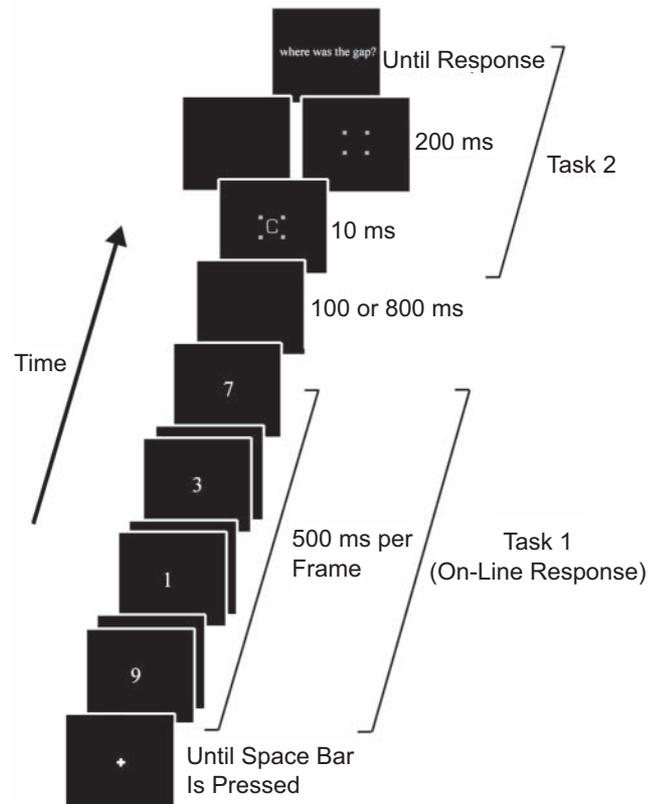


Fig. 1. Tasks and design. On dual-task trials, participants performed Task 1, an arithmetic calculation (digit 1 + digit 2 – digit 3 + digit 4), as quickly and as accurately as possible and then performed Task 2, reporting the location of the gap in the Landolt C (top, bottom, left, or right) with no time pressure. On single-task trials, participants ignored Task 1.

500 ms before the onset of T1. Four digits were presented sequentially in the center of the screen, for 500 ms each. The first three digits had an interstimulus interval of 500 ms. After the fourth digit, there was a blank screen for either 100 ms (Lag 100) or 800 ms (Lag 800). Following this blank screen, the Landolt C appeared for 10 ms in the same spatial location as the digits, surrounded by four dots. This display was followed by either a 200-ms blank screen (simultaneous mask offset) or the four dots alone for 200 ms (delayed mask offset). Finally, a prompt appeared, and remained on display until the participant made an unspeeded response using the left, right, up, or down arrow key. The sequencing of lag and mask-offset conditions was pseudorandomly determined across trials.

On dual-task trials, participants were first required to perform the following calculation: digit 1 + digit 2 – digit 3 + digit 4. They then made a speeded response as to whether the answer was odd or even. Response keys for this task were “z” and “?,” and their mapping was counterbalanced across participants. Participants were required to respond to the arithmetic task prior to indicating the orientation of the gap in the Landolt C. The digits for each trial were selected randomly from 1 through 9, with the constraints that (a) there were no

repetitions of a digit within the four-digit sequence for a given trial, (b) the calculation did not yield a negative number, and (c) the answer was even on half of the trials. On single-task trials, participants were told that they should ignore the four digits and respond only to the Landolt C.

Results and Discussion

Participants were excluded if their T2 accuracy exceeded 90% in the dual-task delayed-offset condition (2 participants) or was at or below 50% in the single-task simultaneous-offset condition (2 participants). Inclusion of these participants did not change the pattern of results.

T2 accuracy

Dual-task trials were included in the analysis only if the response to the arithmetic task was correct, to ensure that

participants processed T1 in this condition (Raymond et al., 1992). Figure 2a plots mean T2 accuracy as a function of lag, mask offset, and task block. A repeated measures analysis of variance with these variables as factors revealed a significant three-way interaction, $F(1, 14) = 4.60$, $p < .05$, $\eta_p^2 = .25$, demonstrating that OSM (simultaneous-offset T2 accuracy – delayed-offset T2 accuracy) differed across lags and task blocks. Specifically, although OSM at Lag 100 was significant in the single- and dual-task blocks, $t_s(14) > 5.10$, $p_s < .0002$, $\eta_p^2_s > .64$, and although OSM was greater at Lag 100 than that at Lag 800 in both task blocks, $t_s(14) > 3.30$, $p_s < .005$, $\eta_p^2_s > .44$, OSM was larger at Lag 100 for the dual-task blocks than for the single-task blocks, $t(14) = 2.30$, $p < .05$, $\eta_p^2 = .28$ (see Fig. 2b). This result confirms that OSM can be elicited for items that appear at a spatially attended location when participants are engaged in a task that taps higher-level brain regions involved in reentrant processing (prefrontal and parietal areas).

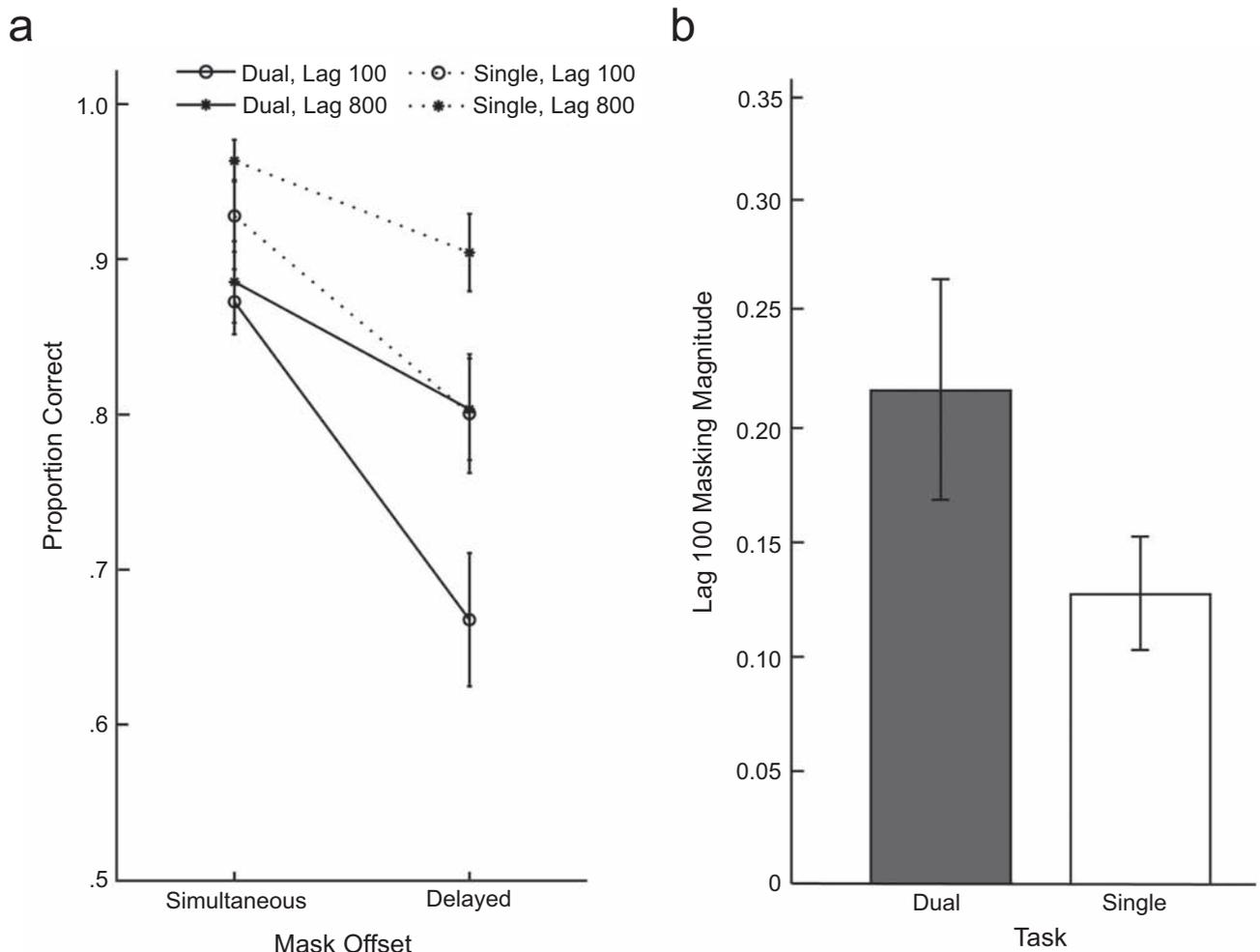


Fig. 2. Results: (a) Task 2 performance (proportion correct), given a correct response on the first task, as a function of task type (dual vs. single), lag (Lag 100 vs. Lag 800), and mask offset (simultaneous vs. delayed) and (b) the magnitude of object-substitution masking (performance on simultaneous-offset trials – performance on delayed-offset trials) at Lag 100 for the dual- and single-task conditions. Error bars represent standard errors of the mean.

It is somewhat surprising that significant OSM was also observed for the single-task blocks (see Fig. 2b). This result demonstrates that mere presentation of the digits, without a response requirement, was sufficient to elicit OSM for a spatially attended target. Similar results have been found in previous dual-task studies and may indicate that participants sometimes process T1 to some degree even when instructed not to do so (Chun, 1997). This T1 processing may have prevented accurate binding of target features during encoding (Bouvier & Treisman, 2010). In addition, forward masking of the T2 target may have affected performance. In any case, because OSM was larger in the dual-task blocks than in the single-task blocks, it is clear that participants' engagement in a high-level task influenced OSM magnitude over and above any low-level masking.

T1 accuracy and reaction time

Reaction time on the arithmetic task ($M = 2,439$ ms; measured from the offset of digit 4) was not influenced by mask offset or lag ($ps \geq .07$, $\eta_p^2 s < .28$). However, accuracy on this task was superior at Lag 800 (86%) relative to Lag 100 (83%), $F(1, 14) = 4.56$, $p = .05$, $\eta_p^2 = .246$, a pattern that mirrors the T2 accuracy data. T1 accuracy was not influenced by mask offset.

Conclusion

In recent years, theorists have argued that reentrant processing plays a vital role in the conscious perception of stimuli (Dehaene et al., 2003; Di Lollo et al., 2000; Lamme, Supèr, & Spekreijse, 1998). To date, however, there has been limited evidence for a key prediction of these accounts: that delayed reentrant feedback from higher-level brain regions to sensory areas limits consciousness. In this study, by pairing a task known to tap prefrontal and parietal regions involved in executive processes (Dehaene et al., 1999) with a standard OSM paradigm thought to reflect reentrant processing (Di Lollo et al., 2000), we obtained support for this prediction. Specifically, if reentrant processing is prolonged, then OSM can be observed for a spatially attended object.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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