Consciousness and Cognition xxx (2017) xxx–xxx

Contents lists available at ScienceDirect

Consciousness and Cognition

journal homepage: www.elsevier.com/locate/concog

Early visual processing allows for selective behavior, shifts of attention, and conscious visual experience in spite of masking

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A R T I C L E I N F O

Article history:
Received 28 October 2016
Revised 20 January 2017
Accepted 24 January 2017
Available online xxxx

A B S T R A C T

Object-substitution masking (OSM) occurs when a briefly displayed target in a search array is surrounded by a mask, which remains onscreen after the target has disappeared. It has been suggested that OSM results from a specific interference with reentrant visual processing, while the initial feedforward processing is left intact. Here, we tested the prediction that the fastest saccadic responses towards a masked target, supposedly triggered before the onset of reentrant processing, are not impaired by OSM. Indeed, saccades faster than 350 ms "escaped" the influence of the mask. Notably, participants' judgements of subjective awareness indicated that stimulus processing during this early stage is not entirely devoid of conscious awareness. Furthermore, the N2pc event-related potential component indicated shifts of spatial attention towards the masked targets on trials with correct fast saccades, suggesting that both target detection and spatial attention can be based on the computations accomplished during the initial feedforward sweep.

1. Introduction

The perceptual and neural mechanisms necessary for visual awareness are greatly debated, but several theories assume that, among other mechanisms, reentrant processing plays a key role in the process (Dehaene & Changeux, 2011; Lamme, 2006; Overgaard & Mogensen, 2014; Tononi & Koch, 2015). Visual brain areas are heavily interconnected, and most of these connections are reciprocal. The term "reentrant processing" or "recurrent processing" refers to neural activity arising due to feedback from higher areas and lateral connections, allowing the integration of information from outside the neuron's classical receptive field, reducing ambiguity and increasing tolerance to variability in low level features. The role of reentrant processing has been demonstrated by a number of physiological and psychophysical studies, which suggest that reentrant processing is crucial for figure-ground segmentation and contour integration (Bullier, 2001; Scholte, Jolij, & Lamme, 2006), as well as for selective attention (Macknik & Martinez-Conde, 2009). Several authors have proposed that reentrant processing is also crucial for visual awareness, implying that information processed during the feedforward sweep remains unconscious if

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http://dx.doi.org/10.1016/j.concog.2017.01.021
1053-8100/

Please cite this article in press as: Crouzet, S. M., et al. Early visual processing allows for selective behavior, shifts of attention, and conscious visual experience in spite of masking. *Consciousness and Cognition* (2017), http://dx.doi.org/10.1016/j.concog.2017.01.021

reentrance is disrupted, e.g. by masking or TMS (Boehler, Schoenfeld, Heinze, & Hopf, 2008; Di Lollo, Enns, & Rensick, 2000; Lamme, 2006; Silvanto, Lavie, & Walsh, 2005).

In psychophysics, the interplay between feedforward and reentrant processing has been studied using visual masking (Bachmann, 2006; Breitmeyer & Ogmen, 2006). Specifically, object substitution masking (OSM), stands as particularly relevant to that aim. OSM occurs when a briefly presented target in a search array is surrounded by small dots that remain visible after the target disappears (Di Lollo et al., 2000). This delayed offset of the four-dot mask strongly reduces target visibility. Thus, unlike pattern masking or meta-contrast masking, the masking effect results from the delayed mask *offset* rather than its delayed *onset*. In fact, Francis and Cho (2007) have demonstrated that any delay between target and mask onset obliterates the masking effect and that models of backward masking do not account for this finding. Therefore, OSM is also referred to as "common onset masking". Di Lollo et al. (2000) proposed that the representation of the target-plus-mask initially proceeds undisturbed through the feedforward sweep, and that OSM occurs when a mismatch arises between the reentrant signal representing target-plus-mask and the new incoming information at the lower level representing the mask alone. This mismatch results in the replacement of the target-plus-mask representation with the mask-alone representation. While it is still debated whether the performance impairment under OSM is due specifically to object substitution, authors agree that OSM affects some later processes beyond the initial feedforward signal (Di Lollo, 2014; Francis & Hermens, 2002; Goodhew, Pratt, Dux, & Ferber, 2013; Põder, 2013). Thus, in contrast to other forms of backward masking, OSM has been claimed to selectively disrupt reentrant processing while leaving the initial feedforward sweep intact (Di Lollo et al., 2000; Enns, 2004).

Numerous studies have used OSM as a proxy for a selective disruption of reentrant processing. The reasoning is that if performance on a task is impaired by OSM, this task is assumed to require reentrant processing. By contrast, if performance is not impaired, it is assumed that this task is based on the unimpaired feedforward sweep (e.g. Bouvier & Treisman, 2010; Dux, Visser, Goodhew, & Lipp, 2010; Koivisto, 2012; Ro, Breitmeyer, Burton, Singhal, & Lane, 2003). For example, several studies have demonstrated that even when the target cannot be consciously identified under OSM, its low-level, unbound stimulus features can be detected (Bouvier & Treisman, 2010; Chen & Treisman, 2009) consistent with the notion that these processes do not require recurrent processing.

Recently, a number of event-related potentials (ERP) studies have investigated target processing under OSM by investigating the N2pc component of the ERP. The N2pc (N2-posterior-contralateral) is a negative-going deflection of the ERP at posterior channels contralateral to a relevant stimulus with an onset latency of approximately 200 ms, which indicates top-down selection of a stimulus according to its task-relevant properties (Eimer, 1996). For example, Woodman and Luck (2003) found that even though OSM reduced target visibility, the N2pc was not reduced by OSM and was equivalent on trials with correct and incorrect responses. Similar findings were reported in subsequent studies (Harris, Ku, & Woldorff, 2013; Prime, Pluchino, Eimer, Dell'Acqua, & Jolicœur, 2011; Woodman, 2010). Taken together, these findings confirm a central tenet of the object-substitution account by showing that early target processing is yet undisturbed by the mask and allows for target detection and a subsequent shift of attention (see Woodman & Luck, 2003). Thus, the perceptual impairment under OSM occurs only later when information transfer to higher-level processing is disrupted by the mask. However, given that the first feedforward sweep reaches occipito-temporal areas within the first 100 ms (Schmolesky et al., 1998) and given that the N2pc occurs only after 200 ms, "early processing" as indicated by an intact N2pc under OSM may not be identical with feed-forward activation in low-level sensory areas.

However, most demonstrations of intact task performance or differential electrophysiological effects would be equally consistent with the notion that OSM represents simply a weak form of perceptual impairment that affects all stages of stimulus processing, and that the residual information surviving this impairment is sufficient to perform certain rather simple tasks such as detecting simple visual features. This interpretation is supported by a large number of behavioral experiments (e.g. Overgaard, 2006; Overgaard, Fehl, Mouridsen, Bergholt, & Cleeremans, 2008; Overgaard & Sandberg, 2012) and ERP experiments (Tagliabue, Mazzi, Bagattini, & Savazzi, 2016) showing that consciousness should not be conceived of as a dichotomous "either-or" but as a gradual phenomenon. Theoretically, the idea that the ability to solve tasks of different degrees of complexity relates to the degree of consciousness has been predicted by the REF-CON framework (see Overgaard & Mogensen, 2014).

The hypothesis that OSM is associated with an intact feedforward sweep, while later recurrent processing is disrupted, predicts a specific temporal pattern of task performance that cannot be explained by a weak perceptual impairment: the accuracy of behavioral responses under OSM should strongly depend on the time when these responses are initiated. Specifically, OSM should not affect the accuracy of particularly fast responses, which were already initiated during the first, intact feedforward sweep and before recurrent processing was disrupted by the mask. By contrast, if the response is delayed, e.g. because the target was not located rapidly enough in the search display, the mask may disrupt recurrent processing before a response is initiated. Thus, OSM should primarily impair the accuracy of slow responses, which were initiated after the mask had already disrupted recurrent processing. To test this hypothesis, we recently established a masking paradigm in which two critical items (one target and one lure) are embedded in a search array and surrounded by four-dot masks. Unlike previous OSM studies that emphasized response accuracy over speed, we asked observers to make a saccade as fast as possible towards the target item. We found that OSM and backward masking impaired performance predominantly for slower saccades, while the fastest saccades under masking were as accurate as comparably fast saccades without a mask. This sparing of the fastest saccades cannot be explained by a generic, time-independent performance impairment. Rather, it suggests that early processing stages, which may coincide with the early feedforward sweep, are not impaired by masking. By contrast, a