Vision Research 127 (2016) 152–164

Contents lists available at ScienceDirect

Vision Research

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

Unmasking saccadic uncrowding

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ARTICLE INFO

Article history:
Received 5 July 2016
Received in revised form 6 August 2016
Accepted 7 August 2016
Available online 2 September 2016

Keywords:
Crowding
Masking
Remapping
Perisaccadic perception
Neural modeling

ABSTRACT

Stimuli that are briefly presented around the time of saccades are often perceived with spatiotemporal distortions. These distortions do not always have deleterious effects on the visibility and identification of a stimulus. Recent studies reported that when a stimulus is the target of an intended saccade, it is released from both masking and crowding. Here, we investigated pre-saccadic changes in single and crowded letter recognition performance in the absence (Experiment 1) and the presence (Experiment 2) of backward masks to determine the extent to which saccadic "uncrowding" and "unmasking" mechanisms are similar. Our results show that pre-saccadic improvements in letter recognition performance are mostly due to the presence of masks and/or stimulus transients which occur after the target is presented. More importantly, we did not find any decrease in crowding strength before impending saccades. A simplified version of a dual-channel neural model, originally proposed to explain masking phenomena, with several saccadic add-on mechanisms, could account for our results in Experiment 1. However, this model falls short in explaining how saccades drastically reduced the effect of backward masking (Experiment 2). The addition of a remapping mechanism that alters the relative spatial positions of stimuli was needed to fully account for the improvements observed when backward masks followed the letter stimuli. Taken together, our results (i) are inconsistent with saccadic uncrowding, (ii) strongly support saccadic unmasking, and (iii) suggest that pre-saccadic letter recognition is modulated by multiple perisaccadic mechanisms with different time courses.

1. Introduction

Objects that fall on the fovea can be easily recognized whereas they may be difficult to recognize in the periphery due to factors such as the reduced photoreceptor density of the peripheral retina. Recognition is even more difficult when objects are closely surrounded by other objects, a phenomenon called crowding (Bouma, 1970; Chung, Levi, & Legge, 2001). The crowding strength is generally defined as a reduction in recognition performance due to the presence of flanking objects (Levi, 2008; Whitney & Levi, 2011). There are many accounts of crowding, but one account suggests that crowding results from the obligatory integration of features within a spatial window. The extent of this window, the critical distance, scales with eccentricity (Bouma, 1970; Chung et al., 2001). The crowding strength and the critical distance depend on temporal properties of the stimuli (Chung, 2016; Chung & Patel, 2011; Lev, Yehezkel, & Polat, 2014). Many other factors, such as attention (Freeman & Pelli, 2007; Grubb et al., 2013; Yeshurun & Rashal, 2010) and perceptual grouping (Manassi, Sayim, & Herzog, 2012, 2013) also affect crowding. Crowding is a major bottleneck for object recognition and a fundamental component of conscious spatial vision (Levi, 2008; Pelli & Tillman, 2008; Whitney & Levi, 2011).

While crowding impairs the recognition of an object, it leaves the detectability of its features unaffected (e.g., Levi, Hariharan, & Klein, 2002). Masking refers to the reduction in visibility of a (target) stimulus when it is presented in close spatiotemporal proximity to another (mask) stimulus (Breitmeyer & Ogmen, 2006). Masking and crowding are affected similarly by certain spatiotemporal properties of the stimuli such as stimulus onset asynchrony and duration (Chung et al., 2001; Lev & Polat, 2015); however, they also have distinct characteristics (Chung et al., 2001; Pelli, Palomares, & Majaj, 2004).

In this paper, we define flankers (i.e., stimuli crowding a target stimulus) as stimuli of the same object category (e.g., letters) as the target, although we note that flankers that belong to different object categories can also induce crowding (Chanceaux, Mathot, & Grainger, 2014; He & Tjan, 2004). Masks are defined as stimuli

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http://dx.doi.org/10.1016/j.visres.2016.08.003
0042-6989/

that do not have structures or features as those of the target (e.g., noise masks). Crowding can occur in the absence of masking, and vice versa. When flankers and masks are presented in combination, the net effect may not be equal to the sum of the individual effects. Certain types of masks reduce flankers' visibility, which in turn reduces crowding (Chakravarthi & Cavanagh, 2009). When a target is crowded *and* weakly masked, the combined deleterious effect is larger than the sum of their individual effects, known as "super-crowding" (Vickery, Shim, Chakravarthi, Jiang, & Luedeman, 2009). Crowding the "crowders" (i.e., flankers) or masking the masks can restore the recognizability or the visibility of a target (Manassi et al., 2013; Ogmen, Breitmeyer, Todd, & Mardon, 2006). The evidence reviewed here suggests that, although they can be dissociated in some settings, masking and crowding might share common neural mechanisms under certain conditions. Moreover, most stimuli used to study crowding and masking activate both mechanisms, therefore, it is difficult to disentangle their individual contributions to the final percept.

A powerful paradigm to study these processes is the pre-saccadic "uncrowding" and "unmasking", in which the presentation of the stimuli (i.e., target-mask or target-flanker displays) prior to an impending saccade reduces the impairments due to crowding and masking (De Pisapia, Kaunitz, & Melcher, 2010; Harrison, Mattingley, & Remington, 2013). Saccades constitute a fundamental aspect of normal vision; hence, it is essential to understand how visual processes operate under pre-saccadic conditions. As a consequence of saccades, retinal images are frequently displaced, yet we perceive a stable and coherent world. How does the visual system achieve perceptual stability? Among many proposals, much attention is received by those based on updating a highly detailed retinotopic map via shifts of neuronal receptive fields (RF) or attentional resources (Burr, Ross, Binda, & Morrone, 2010; Cavanagh, Hunt, Afraz, & Rolfs, 2010; Melcher & Colby, 2008; Wurtz, 2008). Neurons which shift their RFs in parallel to the direction of an impending saccade toward the retinal locations that they will occupy ("future field") after a saccade, commonly referred to as "remapping", have been found in several cortical and subcortical structures (Duhamel, Colby, & Goldberg, 1992; Nakamura & Colby, 2002; Sommer & Wurtz, 2006; Umeno & Goldberg, 1997; Walker, FitzGibbon, & Goldberg, 1995). However, recent studies indicate that these RF shifts in FEF and V4 occur toward the saccade target rather than the future field (Tolias et al., 2001; Zirnsak, Steinmetz, Noudoost, Xu, & Moore, 2014), leaving open the question of whether there is only one type of remapping or whether different areas show different patterns of remapping. In fact, a more recent study revealed both types of perisaccadic RF changes in monkey V4 cells, with remapping parallel to the saccade vector occurring earlier than convergence of RFs (Neupane, Guitton, & Pack, 2016).

Pre-saccadic modulations in crowding and masking have been associated with remapping (Harrison, Retell, Remington, & Mattingley, 2013; Hunt & Cavanagh, 2011). Admittedly, behavioral studies without explicit measurement of RFs cannot speak for or against this association, however, they provide a new avenue for inference about the underlying mechanisms and may potentially inform the theories based on neurophysiological data. Therefore, pre-saccadic uncrowding/unmasking paradigm is also important since it informs us whether or not, and to what extent RF modulations play a role in these phenomena. Here, we investigated how crowding, masking, saccade-related processes, including shifting RFs, contribute to pre-saccadic object recognition. In order to determine whether or not, and how saccadic eye movements modulate object recognition at the saccade target location, we carried out two experiments where observers reported the identity of a target letter presented in the peripheral retina. In separate and randomly interleaved blocks of trials, observers performed the task either during fixation (with the letters presented in the peripheral retina), or after a saccadic eye movement following the offset of a cue located at the location of the target letter. To quantify the changes in crowding strength due to impending saccades, the target letter was presented either alone or with two horizontally flanking letters. In Experiment 1, we specifically tested the hypotheses that (i) saccade targets are released from crowding, and (ii) perisaccadic mechanisms interact with the temporal order of the stimuli. In Experiment 2, we specifically tested the hypothesis that impending saccades reduce masking. By comparing the results from both experiments, we also tested the hypothesis that remapping (in the form of perceptual displacements) affects pre-saccadic masking but not crowding.

Saccades have been shown to result in increased detection thresholds (known as saccadic suppression) and enhanced discrimination performance (e.g., Bridgeman, Hendry, & Stark, 1975; Deubel & Schneider, 1996). In order to understand how mechanisms with such opposite effects might play a role in pre-saccadic object recognition, we used a simplified version of a dual-channel neural model of visual masking to account for the data in both experiments. This model could account for letter recognition performance during fixation, suggesting that masking and crowding might share common low-level mechanisms. Finally, by adding several independent saccadic mechanisms to this model, we sought to tease apart different components of pre-saccadic modulations in letter recognition.

2. Methods

2.1. Overview

In Experiment 1, we aimed to determine whether or not, and how pre-saccadic letter recognition is affected by the temporal order of presentation of a target and its flankers. The target letter was presented either alone (unflanked) or accompanied by two horizontally flanking letters with a varying flanker-target onset asynchrony (FTOA). A negative FTOA means that the flanker letters were presented before the target letter, a positive FTOA means that the target letter was presented first, and zero FTOA corresponds to the simultaneous presentation of the target and flanker letters.

In Experiment 2, we investigated whether or not, and how letter judgments are affected by saccades in the presence of backward noise-masks. Within a block of trials, a target letter was presented either alone or with two horizontally flanking letters. Each letter was always followed by spatially overlapping backward noise mask. By comparing the results between the flanked and unflanked conditions, we were able to determine whether crowding and masking interact. Moreover, by comparing the results of Experiment 2 and the zero FTOA condition in Experiment 1, we were able to determine whether or not saccadic uncrowding is just a manifestation of saccadic unmasking. In Experiment 2, the target and flanker letters were always presented simultaneously (i.e., with zero FTOA) but all letters were followed by noise-masks at their respective locations. In both experiments, timing of events was adjusted for each observer and block of trials such that in the majority of trials, target presentation was completed *before* saccade onset. This manipulation allowed us to investigate the time course of letter recognition performance before saccades. Note that our fixation and saccade conditions were identical in terms of retinal locations of the target and flanker letters.

2.2. Participants

Six observers (two males, four females) participated in the study. One of the observers was the first author (MNA), and the