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The spatial profile of mask-induced compression for perception and action

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ABSTRACT

Stimuli briefly flashed just before a saccade are perceived closer to the saccade target, a phenomenon known as saccadic compression of space. We have recently demonstrated that similar mislocalizations of flashed stimuli can be observed in the absence of saccades: brief probes were attracted towards a visual reference when followed by a mask. To examine the spatial profile of this new phenomenon of masked-induced compression, here we used a pair of references that draw the probe into the gap between them. Strong compression was found when we masked the probe and presented it following a reference pair, whereas little or no compression occurred for the probe without the reference pair or without the mask. When the two references were arranged vertically, horizontal mislocalizations prevailed. That is, probes presented to the left or right of the vertically arranged references were "drawn in" to be seen aligned with the references. In contrast, when we arranged the two references horizontally, we found vertical compression for stimuli presented above or below the references. Finally, when participants were to indicate the perceived probe location by making an eye movement towards it, saccade landing positions were compressed in a similar fashion as perceptual judgments, confirming the robustness of mask-induced compression. Our findings challenge pure oculomotor accounts of saccadic compression of space that assume a vital role for saccade-specific signals such as corollary discharge or the updating of eye position. Instead, we suggest that saccade- and mask-induced compression both reflect how the visual system deals with disruptions.

1. Introduction

Localizing objects, that is, registering *where* objects are in our environment is a fundamental task of the visual system. However, when probe stimuli are only briefly flashed, previous research has described systematic biases when observers are asked to localize the probe. Some of the most remarkable mislocalization effects have been reported around the time of saccadic eye movements. In complete darkness, stimuli flashed briefly before or in the early phase of a saccade are strongly mislocalized in the direction of the eye movement, independently of where in the visual field the probe is flashed (Honda, 1989, 1991; Matin, Matin, & Pearce, 1969; Matin, Matin, & Pola, 1970). In contrast, under conditions of dim illumination (e.g., in a dimly-lit room or with stimuli presented on a computer screen with a slightly illuminated background), the pattern of mislocalizations changes: flashed probes are perceived closer to the target of the saccadic eye movement (Honda, 1993, 1999; Lappe, Awater, & Krekelberg, 2000; Morrone, Ross, & Burr, 1997; Ross, Morrone, & Burr, 1997). That is, flashes presented between the fixation point and the saccade target are mislocalized in saccade direction, whereas flashes presented beyond the saccade target are mislocalized against saccade direction. Due to the convergence of localization responses on the location of the saccade target, the phenomenon has become known as saccadic compression of space (Ross et al., 1997).

As these mislocalization effects were discovered in the context of saccades, most authors have attributed their origin to saccade-specific phenomena. Specifically, the mislocalizations are assumed to be capturing intermediate stages in the transformation from pre- to post-saccadic coordinates under the direction of extraretinal signals related to the eye movement, for instance eye position signals, saccade vector information or corollary discharge (Dassonville, Schlag, & Schlag-Rey, 1992; Hamker, Zirnsak, Calow, & Lappe, 2008; Honda, 1993; Matin et al., 1970; Morrone et al., 1997; Richard, Churan, Guitton, & Pack, 2009; Teichert, Klingenhoefer, Wachtler, & Bremmer, 2010; VanRullen, 2004;

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Ziesche & Hamker, 2011). These coordinate shifts have been well documented in the property changes of receptive fields of visual neurons around the time of saccades (Duhamel, Colby, & Goldberg, 1992; but see Zirnsak, Steinmetz, Noudoost, Xu, & Moore, 2014). In general, these coordinate shifts ensure that we perceive the visual world around us as stable, in spite of drastically changing retinal input with every eye movement (see Bays & Husain, 2007; Cavanagh, Hunt, Afraz, & Rolfs, 2010; Melcher, 2011; Sommer & Wurtz, 2008 for recent overviews).

However, other findings have challenged the claim that the observed mislocalizations are exclusively related to and caused by eye movements. For instance, when the visual consequences of saccades are simulated by moving the stimuli and their background at saccadic speed while participants remain fixated, mislocalizations similar to those observed with real saccades can be observed (Honda, 1995; MacKay, 1970; Morrone et al., 1997; O'Regan, 1984; Ostendorf, Fischer, Gaymard, & Ploner, 2006). Although qualitatively similar, there are often differences in magnitude or in the time course of effects when comparing real saccades to "simulated" saccades, leaving the possibility that there is still an aspect that is inherently saccadic to the specific pattern of mislocalizations. In particular, saccadic compression of space, including a strong mislocalization component against saccade direction for stimuli presented beyond the saccade target, has been elusive when simulating saccades with image motion (Morrone et al., 1997; but see Ostendorf et al., 2006).

Recently, we have reported a mask-induced compression effect in the perceived locations of briefly flashed probes in a condition with neither image motion, nor saccadic eye movements (Zimmermann, Born, Fink, & Cavanagh, 2014; Zimmermann, Fink, & Cavanagh, 2013). Participants held fixation throughout a trial while first a visual reference stimulus was presented in the periphery, followed by a flashed probe and a whole-field random texture mask. Participants had to localize the probe and the reference was irrelevant to the task. Nevertheless, participants' localization responses were biased towards the reference stimulus, even though they remained as precise (i.e., similar variance in the localization responses) as in the unmasked control. Indicative of compression, the bias was found both for probes more foveal and for probes presented more peripheral than the reference: all appeared shifted toward the reference. Furthermore, strong compression was only observed when the mask was presented close in time to the probe, and when the reference stimulus' onset occurred in a time window 70–200 ms before the probe and mask.

These results shed an entirely new light on compression effects and point to contributions from mechanisms unrelated to saccades and retinal image motion. To better understand these mechanisms, the current experiments examine the two-dimensional profile of mask-induced compression induced with different reference stimulus configurations and test its robustness by comparing two response modes: mouse clicks to indicate remembered probe location, or saccades to the probe location. The basic procedure was similar to that used in our previous work (Zimmermann, Born, et al., 2014; Zimmermann et al., 2013): we presented a salient visual reference stimulus followed by a mask to induce compression in the perceived space of briefly flashed probes. In contrast to the previous studies, results were compared to a condition with references and no mask and a condition with a mask but no references. Compression in perceived probe locations was only found with both, references and mask. Further, we used two reference stimuli that were spatially separated either vertically (Experiment 1) or horizontally (Experiment 2). We found in both arrangements that perceived probe locations were compressed towards the references and that compression was stronger orthogonally to the axis joining the two reference stimuli as opposed to along that axis. Finally, when we compared mislocalizations in perception to the misdirection of fast, voluntary movements towards the probe (i.e., saccades), the distribution of saccade endpoints was compressed towards the references in the same way as the perceptual judgments, indicating that the saccade system is subject to the perceptual illusion. Note that when we use a saccade as a method of reporting the probe location, the mislocalization is still induced by the mask, not the saccade. The saccade follows the probe presentation by 270–280 ms (average saccade latency in the current experiments), as a measure of the mislocalization. At first glance, the introduction of the saccade confuses the attempt to evaluate mislocalization in the absence of saccades. But the saccade target in this technique was the probe itself. Thus, saccadic compression should not interact with the mask-induced compression towards the references, as saccadic compression is always toward the saccade target (the probe here) and, in any case, the delay between the probe and the saccade falls outside the range of delays where saccadic compression is seen (e.g., Ross et al., 1997).

2. Experiments 1a and 1b: vertically arranged pair of references

In the previous articles on mask-induced spatial compression (Zimmermann, Born, et al., 2014; Zimmermann et al., 2013), the perceived probe location was often shifted to the reference to the extent that it overlapped. This caused difficulty in differentiating between a shifted probe, seen flashed on top of the reference, and a probe that was just not seen at all. Thus, we cannot fully exclude that sometimes participants may have reported the reference location when they were unsure of what they had seen. Since our probes are set to be low contrast (or short duration), we needed to avoid any confusion between unseen probes and probes that are fully compressed, overlapping the reference stimulus. Our use of two reference stimuli in these new experiments addresses this issue as it allows a probe to be drawn into the gap between the two references. A trial with complete compression (all three stimuli will be seen) can then be easily differentiated from a missed probe (only two will be seen). Having two references also let us explore the spatial profile of compression.

2.1. Methods

2.1.1. Participants

The two experiments were run on eight participants each (Experiment 1a: six women, two men, including one author, mean age: 32.9 years; Experiment 1b: three men, five women, including the same author and one further participant from Experiment 1a, mean age: 32.0 years). One participant in Experiment 1b reported strabismus and therefore completed the experiment under monocular viewing conditions, with one eye patched and stimuli presented in the nasal hemifield. The response pattern for this participant was comparable to the others and inclusion/exclusion did not change the results of the statistical analysis. All other participants reported normal or corrected-to-normal vision. For all experiments reported in this study, observers gave written informed consent prior to participating and the procedures followed the principles laid down in the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.1.2. Apparatus

Subjects were seated 57 cm from a Compaq P1220 CRT monitor (Houston, TX, USA) with head stabilized by a chin- and head-rest. The visible screen diagonal was 22 inches, resulting in a visual field of 40.2 × 30.5°. Stimuli were presented with a monitor refresh rate of 120 Hz at a resolution of 1024 × 768 pixels. The experiment was programmed in Matlab (The MathWorks Inc., Natick, MA, USA)