Releasing crowding prior to a saccade requires more than "attention": response to van Koningsbruggen and Buonocore

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We thank van Koningsbruggen and Buonocore (2013) for their interest in our recent study, in which we investigated the relationship between eye movements and *visual crowding*, the phenomenon whereby a target object in peripheral vision is made difficult to recognize when closely flanked by distractor objects (Pelli and Tillman, 2008). We found that, just prior to a saccadic eye movement, the deleterious effects of crowding are reliably diminished at the saccade goal (Harrison et al., 2013a). As plausible explanations for such a pre-saccadic release from crowding, we discussed changes in the gain of visual neurons (e.g. Moore and Armstrong, 2003), a reduction in probabilistic positional uncertainty (Greenwood et al., 2009; van den Berg et al., 2012), and receptive-field shifts (Tolias et al., 2001) brought about by the known neurophysiological links between oculomotor and visual areas (for reviews, see Schall, 2002; Moore et al., 2003). Van Koningsbruggen and Buonocore have proposed two interesting alternative explanations for our results, and we respond to these here.

Pre-saccadic attention

The first explanation offered by van Koningsbruggen and Buonocore (2013) is that the pre-saccadic reduction in crowding we observed is due to allocation of visual attention to the saccade goal. Such effects of attention have been reported previously (Remington, 1980; Kowler et al., 1995; Deubel and Schneider, 1996). However, our results are unlikely to be due to attention shifts. First, observers knew the target's position and approximate timing in the no-eye movement and eye movement conditions so that attention could be allocated in the same manner on every trial, yet their ability to correctly discriminate the target improved during saccade preparation. Thus, saccade preparation affected crowding differently from the voluntary allocation of attention. Second, Yeshurun and Rashal (2010) found that critical distance, the area over which crowding occurs, decreases when a pre-cue is used to capture attention involuntarily at the upcoming location of a crowded target. We followed their method for modeling critical distance and found a much larger relative change in critical distance prior to a saccade than that found by Yeshurun and Rashal with attentional cues. These differences suggest a dissociation in perceptual changes caused by exogenous attention and eye movement preparation. Further support of such a dissociation comes from Rolfs and Carrasco (2012) who found a difference in the *temporal* profile of exogenous attention shifts and pre-saccadic perceptual enhancements. Third, pre-saccadic shifts of attention alone cannot explain our results from Experiment 2, in which performance improved prior to the saccade for the three smallest target-flanker separations, but not for the two largest separations. This interaction between saccade preparation and target-flanker separation drove the reported reduction in critical distance; critical distance would have been unchanged had target identification accuracy also improved at wider target-flanker separations, as may be predicted from an attentional account. Thus, our results are inconsistent with a straightforward attentional account. Instead, they point to important differences between perceptual changes associated with shifts of attention occurring with the eyes fixed versus those associated with saccade preparation.

Van Koningsbruggen and Buonocore (2013) also suggest that, if saccade preparation changes the area over which information is averaged, all stimuli should be more easily identified, however a previous study has shown that identification of objects near the saccade goal is reduced (Kowler et al., 1995). It is not clear why the release from crowding we observed at the saccade goal ought to similarly affect all objects in the visual field; crowding at locations other than the saccade goal may be alleviated, unchanged, or worsened - this is an empirical question. We found that the reduced area over which crowding occurs prior to a saccade corresponds closely to the precision of the saccade endpoint, suggesting changes in crowding are linked to the saccade goal rather than to a general change in visual processing throughout the visual field. In any case, relative to a no-eye movement condition, Kowler et al. (1995; Experiment 2) found no influence of an impending saccade on performance beyond the goal of the eye movement. Moreover, these earlier results are likely influenced by the working memory demands required of observers in that study -- perfect performance required observers to hold 8 briefly presented items and their locations in short-term memory. When the possible target locations were limited to two positions directly surrounding the saccade goal, Kowler et al. (Experiment 3) found above-chance accuracy around the saccade endpoint, which was again no different from the no-eye movement condition.

Target (un)masking

Van Koningsbruggen and Buonocore (2013) correctly assert that our use of forward and backward masks in Experiment 1, and forward masks in Experiment 2, might have influenced observers' ability to identify the target. They also point out that any effect of masking could be mitigated during saccadic preparation (De Pisapia et al., 2010; Hunt and Cavanagh, 2011), thereby leading to improved identification prior to a saccade regardless of whether there is a change in crowding. This is a potentially important limitation of our study, though as we describe below pre-saccadic unmasking cannot account for our results. In our experiments targets and flankers were preceded by dynamic white noise to reduce any spatial distortions that might occur around the time of saccade onset (e.g. Honda, 1989). Our continuous forward masks eliminated the abrupt transients associated with target and distractor onsets, and should have therefore minimized perceptual mislocalizations and unmasking (e.g. De Pisapia et al., 2010). Nonetheless, it is possible that the masks altered performance differentially for the no-eye movement and eye movement conditions. But unmasking cannot account for our results: why did unmasking fail to improve performance at the two widest target-flanker separations?

Final remarks

Although van Koningsbruggen and Buonocore (2013) interpreted our study within the literature on predictive remapping, we in fact made no such claim ourselves. In the electrophysiology literature, predictive remapping has been used to denote the pre-saccadic responses of cells in oculomotor and visual attention regions, such as the lateral intraparietal area, that predict the arrival of a stimulus within a neuron's receptive field following a saccade (e.g. Duhamel et al., 1992). Behaviorally, the term has been used to denote the changes in visual perception that seem to anticipate the consequences of an upcoming eye movement (e.g. Rolfs et al., 2011; Harrison et al., 2013b). We did refer to a study by Tolias et al. (2001), in which receptive fields of V4 neurons shrunk in size and shifted toward the saccade goal, providing a possible mechanism for the release from crowding prior to a saccade. In this case, a reduction in receptive-field size could imply an increase in resolution for object discrimination. However, Tolias et al. found that these changes in receptive field dynamics of V4 neurons prior to a saccade were distinct from predictive remapping – receptive fields shifted toward the saccade goal, *not* the relative predicted post-saccadic position. Our results therefore do not necessarily need to be interpreted with respect to the remapping literature. (For a unifying model of how these pre-saccadic effects may be related to one another, we refer readers to Hamker et al., 2008).

In summary, there are several reasons why pre-saccadic changes in visual attention are insufficient to explain a reduction in crowding before a saccade. The degree to which pre-saccadic changes in crowding apply to nearby locations, as well as the role of unmasking in these effects, are interesting questions posed by van Koningsbruggen and Buonocore (2013), and we look forward to discovering the answers.

References

De Pisapia N, Kaunitz L, Melcher D (2010) Backward masking and unmasking across saccadic eye movements. Current Biology 20:613–617.

Deubel H, Schneider WX (1996) Saccade target selection and object recognition: evidence for a common attentional mechanism. Vision Research 36:1827–1837.

Duhamel JR, Colby CL, Goldberg ME (1992) The updating of the representation of visual space in parietal cortex by intended eye movements. Science 255:90–92.

Greenwood JA, Bex PJ, Dakin SC (2009) Positional averaging explains crowding with letter-like stimuli. Proceedings of the National Academy of Sciences 106:13130–13135.

Hamker FH, Zirnsak M, Calow D, Lappe M (2008) The peri-saccadic perception of objects and space. PLoS Computational Biology 4:e31.

Harrison WJ, Mattingley JB, Remington RW (2013a) Eye movement targets are released from visual crowding. Journal of Neuroscience 33:2927–2933.

Harrison WJ, Retell JD, Remington RW, Mattingley JB (2013b) Visual Crowding at a Distance during Predictive Remapping. Current Biology 23:793–798.

Honda H (1989) Perceptual localization of visual stimuli flashed during saccades. Percept Psychophys 45:162–174.

Hunt AR, Cavanagh P (2011) Remapped visual masking. Journal of Vision 11(1):1–8.

Kowler E, Anderson E, Dosher B, Blaser E (1995) The role of attention in the programming of saccades. Vision Research 35:1897–1916.

Moore T, Armstrong KM (2003) Selective gating of visual signals by microstimulation of frontal cortex. Nature 421:370–373.

Moore T, Armstrong KM, Fallah M (2003) Visuomotor origins of covert spatial attention. Neuron

40:671–683.

Pelli DG, Tillman KA (2008) The uncrowded window of object recognition. Nature Neuroscience 11:1129–1135.

Remington RW (1980) Attention and saccadic eye movements. Journal of Experimental Psychology: Human Perception and Performance 6:726–744.

Rolfs M, Carrasco M (2012) Rapid Simultaneous Enhancement of Visual Sensitivity and Perceived Contrast during Saccade Preparation. Journal of Neuroscience 32:13744–13752.

Rolfs M, Jonikaitis D, Deubel H, Cavanagh P (2011) Predictive remapping of attention across eye movements. Nature Neuroscience 14:252–256.

Schall JD (2002) The neural selection and control of saccades by the frontal eye field. Philosophical Transactions of the Royal Society B: Biological Sciences 357:1073–1082.

Tolias AS, Moore T, Smirnakis SM, Tehovnik EJ, Siapas AG, Schiller PH (2001) Eye movements modulate visual receptive fields of V4 neurons. Neuron 29:757–767.

van den Berg R, Johnson A, Martinez Anton A, Schepers AL, Cornelissen FW (2012) Comparing crowding in human and ideal observers. Journal of Vision 12.

van Koningsbruggen MG, Buonocore A (2013) Mechanisms behind Perisaccadic Increase of Perception. Journal of Neuroscience 13:xxx–xxx.

Yeshurun Y, Rashal E (2010) Precueing attention to the target location diminishes crowding and reduces the critical distance. Journal of Vision 10:1–12.