Journal Club

Editor's Note: These short, critical reviews of recent papers in the *Journal*, written exclusively by graduate students or postdoctoral fellows, are intended to summarize the important findings of the paper and provide additional insight and commentary. For more information on the format and purpose of the Journal Club, please see http://www.jneurosci.org/misc/ifa_features.shtml.

Mechanisms behind Perisaccadic Increase of Perception

Martijn G. van Koningsbruggen[1,2] and Antimo Buonocore[1]
[1]Center for Mind/Brain Sciences, and [2]Department of Psychology and Cognitive Sciences, University of Trento, 38068 Rovereto, Italy
Review of Harrison et al.

Our peripheral vision is very limited. We can perceive isolated targets in our periphery, but when multiple stimuli are presented simultaneously our perception deteriorates drastically, a phenomenon known as crowding (Whitney and Levi, 2011). Crowded stimuli can still be detected, but can no longer be identified correctly. There is converging evidence that crowding results from averaging of target and distractor features, and that it is a higher level perceptual phenomenon (Chakravarthi and Cavanagh, 2009).

To analyze crowded peripheral information, we make several saccades every second to bring the relevant information into our central vision where visual acuity is optimal. Several neural processes are engaged around the time of saccades to maintain stable and continuous visual perception despite rapid movement of the image on the retina. One proposed mechanism for maintaining stability is predictive remapping of neurons' visual fields just before the eyes actually start to move (for review, see Melcher, 2011). With predictive remapping, the receptive field of some neurons shifts toward the location they will occupy after the eye movement (Duhamel et al., 1992). It is hypothesized that predictive remapping is driven by an efference copy of the motor command that is sent back to the oculomotor cortex, informing the brain about the upcoming eye movement.

A study by Harrison et al. (2013) investigated whether predictive remapping causes peripheral targets to be released from crowding just before an eye movement is made. In the first experiment, participants were asked to report the orientation of a small, peripherally-presented stimulus that was crowded by four vertically oriented stimuli (flankers). Both the target and flankers were presented for 24 ms. White noise stimuli were presented immediately preceding and following the flankers and targets, in the same location. Before the start of the main experiment, orientation of uncrowded peripheral targets was individually adjusted so that performance was 75% for all participants. Across different blocks, participants were instructed to either maintain central fixation or make an eye movement toward the target. On trials where subjects were instructed to maintain fixation, orientation discrimination was impaired by 15% for crowded targets compared with when the target was not crowded. In the eye movement blocks, the fixation offset served as the cue to make an eye movement. The crowded target display was presented at different time points relative to the predicted onset of an eye movement (all analyses were relative to the actual onset of the eye movement). When the eye movement was executed, only the white noise stimuli were visible, because the target and flankers were only presented for 24 ms. Subjects reported the orientation of the target after the eye movement was completed. The authors found that orientation identification of the peripheral crowded target increased when the target was presented 50 ms before a saccade was initiated. When the target was presented 150 or 100 ms before saccade onset, discrimination performance was higher than in the no saccade condition, but lower than 50 ms before saccade onset (although statistics are not reported). It is important to note that the retinal information was the same for both the fixation and saccade condition, because in the saccade condition the target disappeared before the eye movement began. Therefore, the authors argue that an extraretinal preparation of the saccade stops the obligatory averaging of visual features of both flankers and distractors, thereby releasing a target from crowding.

We would like to suggest two alternative hypotheses that can also explain these findings: the coupling of attention and eye movements, and perisaccadic unmasking. Deubel and Schneider (1996) showed that a shift of covert attention precedes every saccade. Their subjects were asked to report the identity of a crowded stimulus which was presented at either the saccade goal or small distance away from the saccade goal. Deubel and Schneider found that targets presented at the saccade goal were identified more reliably compared with targets presented 1.09° away from the saccade goal. These findings show that shifts of attention are tightly coupled to the planned eye movement landing position. Kowler et al. (1995) extended these findings by showing that performance is not only enhanced at the target location, but also suppressed at nearby locations.

Received April 12, 2013; revised May 30, 2013; accepted May 30, 2013.
We thank Jorien van Paaschen for helpful discussions.
Correspondence should be addressed to Dr. Martijn G. van Koningsbruggen, Department of Psychology and Cognitive Science, University of Trento, Corso Bettini 31, 38068 Rovereto, Italy. E-mail: martijn.van.koningsbruggen@gmail.com.
DOI:10.1523/JNEUROSCI.1567-13.2013
 0270-6474/13/3311327-02$15.00/0

Based on these findings, one would expect that if saccade preparation releases items in the peripheral vision from the compulsory averaging of visual features, as Harrison et al. (2013) suggest, this effect would be present for all the presented stimuli and not limited to the target. In other words, if visual features are no longer averaged, identification performance of all stimuli should increase. However, this is not supported by previous findings (Kowler et al., 1995). More support for our alternative hypothesis is provided by Deubel (2008), who investigated the time course of the attentional shift that precedes every eye movement. They found a linear increase of performance that became significant 50 ms before the onset of a saccade. Figure 2*A* in Harrison et al. (2013) shows a similar pattern.

In addition to the increase of performance resulting from directing attention to the saccade location, saccade unmasking might further result in an increase in performance. Harrison et al. (2013) presented white noise stimuli immediately preceding and following presentation of the target and flankers, in other words the targets were not only crowded, but also forward and backward masked. De Pisapia et al. (2010) showed that preparing a saccade in the direction of a backward masked stimulus improves performance. In their study, participants were asked to identify a target that was immediately backward masked. Performance increased when the stimulus was presented just before saccade onset. Similar to Harrison et al. (2013), the target was no longer visible when the eye movement was executed. Although both the target and the mask were presented in the same spatial position, subjects often perceived the target as being slightly displaced from the mask, i.e., the target became unmasked. These findings demonstrate that targets and masks can be perceptually separated during saccades, thereby increasing performance. More recently, Hunt and Cavanagh (2011) extended these findings by reporting unmasking before saccade onset using a different paradigm.

In their second experiment, Harrison et al. (2013) tested whether eye movement preparation interacts with the distance between flanker and target at which crowding starts to occur, i.e., whether the distance at which crowding starts to occur is reduced just before an eye movement is generated. The experimental design was similar to that of their first experiment, but this time only forward masking was applied and the target was presented at a 7° visual angle. To study the effect of the target-flanker separation on target discrimination, the separation between flankers and target was varied between blocks, being 1, 1.5, 2, 3.5, or 5°. According to Bouma's law, the critical distance for crowding to occur is ~0.5 times the target eccentricity when no saccade is generated, predicting no crowding for 3.5 and 5 degree target–flanker separation. This prediction was confirmed in the blocks in which subjects were required to maintain central fixation and no saccades were executed: crowding was reported only for critical distances of 1, 1.5, and 2°. As in the first experiment, when participants were instructed to make saccades toward the target, discrimination increased just before the saccade was initiated. However, this increase was only significant when target–flanker distance was 2°. There was no significant increase in performance when target–flanker distance was 1.5°, although this distance was comparable to that used in the first experiment (1.3°). The authors also investigated whether the size of the critical distance was reduced 50 ms before the saccade onset. It was found that the critical distance shrunk by 47% just before the onset of a saccade, supporting the authors' hypothesis that extraretinal signals interact with visual neurons from the peripheral visual field.

We would argue that the findings of the second experiment, can also be partially explained by saccadic unmasking (although targets were only forward masked), and the coupling of attention and eye movements. For example, the decrease of the critical distance could be the result of an attentional shift that accompanies every eye movement. Yeshurun and Rashal (2010) investigated the effects of exogenous attention on crowding while participants maintained central fixation. They presented a crowded stimulus 70 ms after the presentation of a peripheral cue, and found identification performance increased when the crowded target was presented at the cued location. Moreover, this attentional shift also reduced the critical distance.

In summary, the finding that preparing an eye movement increases behavioral performance at the saccade target location contributes to our understanding of how the brain creates a stable percept across separate fixations. Harrison et al. (2013) argue that just before a saccade is made, an active remapping mechanism interacts with peripheral visual neurons resulting in reduced crowding. However, this finding can also be (partially) explained by attentional allocation and saccadic unmasking. A future step would be to rule out these alternative explanations, and study both crowded and uncrowded targets, with and without masking.

References

Chakravarthi R, Cavanagh P (2009) Recovery of a crowded object by masking the flankers: determining the locus of feature integration. J Vis 9:1–9. CrossRef Medline

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

Deubel H (2008) The time course of presaccadic attention shifts. Psychol Res 72:630–640. CrossRef Medline

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

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. CrossRef Medline

Harrison WJ, Mattingley JB, Remington RW (2013) Eye movement targets are released from visual crowding. J Neurosci 33:2927–2933. CrossRef Medline

Hunt AR, Cavanagh P (2011) Remapped visual masking. J Vis 11(1):13 1–8. CrossRef Medline

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

Melcher D (2011) Visual stability. Philos Trans R Soc Lond B Biol Sci 366:468–475. CrossRef Medline

Whitney D, Levi DM (2011) Visual crowding: a fundamental limit on conscious perception and object recognition. Trends Cogn Sci 15:160–168. CrossRef Medline

Yeshurun Y, Rashal E (2010) Precueing attention to the target location diminishes crowding and reduces the critical distance. J Vis 10:1–12. CrossRef Medline