Influences of Voluntary Eye Movements on Object Perception In Peripheral Vision

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Abstract

A key question in visual neuroscience is how our subjective experience of the visual world remains largely uninterrupted by the many eye movements we make, each of which abruptly displaces the retinal image. It has long been hypothesized that extra-retinal signals, generated by voluntary movements of the eye, alter our vision in such a way that facilitates visual perception across eye movements. However, it is unclear how these extra-retinal signals influence the integration of form information, giving rise to our ability to identify visual objects in spite of the fact that eye movements shift those objects on the retina. Thus, I used eye tracking and psychophysics to test the influence of eye movements on object perception in peripheral vision. In this thesis I present studies in which I show for the first time substantial changes in object identification that result from eye movement preparation and execution. The results from these studies show that our visual experience is not just constructed from the different images that hit the retina, but is influenced by eye movement signals that facilitate the perception of objects from one glance to the next.

The studies presented in Chapters 2 and 3 examined the ways in which eye movements alter visual crowding. Visual crowding refers to the reduced ability to recognize an object in peripheral vision when other objects surround it. A widely held view posits that crowding is caused by compulsory interactions of visual signals throughout early visual brain areas. In Chapter 2, I compared the spatial extent of crowding when no eye movements were made with the spatial extent of crowding during saccade preparation. I found that, just prior to a saccadic eye movement, the spatial extent of crowding is reduced for the target of the saccade despite no change in the retinal position of stimuli. In contrast, results presented in Chapter 3 show that during smooth pursuit eye movements, the spatial extent of crowding increases for objects contraversive to the direction of the eye movement. These results suggest that crowding is not caused solely by the interaction of visual signals in early brain areas, but is also modulated by neural processes involved in the generation of eye movements. Furthermore, these findings suggest that crowding is modified according to an object’s relevance to a current action. In the case of saccades, crowding is reduced such that discriminability of the saccade target itself is enhanced. In the case of smooth pursuit, on the other hand, discriminability is degraded for objects that are no longer in the path of the eye movement.

In Chapters 4 and 5, I examined “predictive remapping”. Predictive remapping refers to pre-saccadic changes in visual processing that are thought to anticipate the
retinal position of objects following a saccade, and has been linked to phenomenological visual stability across eye movements. In Chapter 4, I used a task that combined a spatial cueing task with a saccadic eye movement paradigm. I found that visual processing is prioritized not only at the location of a visual cue, but also in the direction of an impending saccade. Interestingly, the direction of this shift in visual attention is opposite to what would be expected were the shift to compensate for the retinal displacement of visual objects across saccades. I therefore argue that this finding results from a general interaction between saccade programming and exogenous visual attention.

In Chapter 5, I exploited visual crowding to test whether predictive remapping preserves an object’s visual features. When presented just prior to a saccade, I found that a probe in one visual field is “crowded” by distractors that surround the probe’s predicted, post-saccadic location in the opposite visual field. Importantly, the degree of such “remapped crowding” depends on how similar the distractors’ features are to the probe. These findings reveal that the predictive remapping signal conveys featural information such that pre-saccadic visual processing is prioritized according to the expected position and identity of an object that will shift on the retina across saccades.

Overall, the results presented in this thesis suggest that eye movements reliably alter peripheral visual processing. Importantly, my studies show that changes in visual perception act to increase or decrease the discriminability of objects in peripheral vision according to the oculomotor demands of a given task. Moreover, my findings show that these changes in perception are independent of changes in the image on the retina, and must therefore result from extra-retinal signals that are generated during the preparation and execution of saccadic and pursuit eye movements. The modification of vision by these extra-retinal signals likely facilitates the subjective impression of visual stability when eye movements continuously alter the image that falls on the retina.
Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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William John Harrison
December 2012
Publications during candidature

*Peer-reviewed journal articles*


*Manuscripts in preparation*


*Conference abstracts*


Publications included in this thesis

Harrison, W. J., Mattingley, J. B., & Remington, R. W. (2013). Eye movement targets are released from visual crowding. Journal of Neuroscience, 33(7), 2927–2933. doi:10.1523/jneurosci.4172-12.2013 – A version of this paper is incorporated as Chapter 2. The full article is incorporated as Appendix A.

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Contributions by others to the thesis

My advisors, Roger Remington and Jason Mattingley, contributed to the conception and design of all studies presented in this thesis, and made comments and suggestions regarding the written work. James Retell contributed to the conception and design of some parts of the study presented in Chapter 5, and commented on the manuscript incorporated in that chapter.

Statement of parts of the thesis submitted to qualify for the award of another degree

None.
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saccades, eye movements, visual crowding, smooth pursuit, peripheral vision, remapping, predictive remapping, oculomotor selection, visual attention, covert attention

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List of Abbreviations Used In the Thesis

- ANOVA – analysis of variance
- BOLD – blood oxygen level dependent
- FEF – frontal eye fields
- FF – future field
- LIP – lateral intraparietal area
- MVPA – multi-voxel pattern analysis
- RF – classic receptive field
- SC – superior colliculus
- V1 – primary visual cortex
- V2 – visual area 2
- V3 – visual area 3
- V4 – visual area 4
Chapter 1 - Introduction and Overview
In humans, only the central retina – the fovea – is capable of the high-resolution acuity needed to process the visual environment in detail. The fovea represents about 1° of visual angle of external space, and so only a small portion of the world is sampled in high detail during a single fixation. Thus, eye movements are necessary to bring visual objects of interest to the fovea for detailed processing, and to allow us to determine which objects in the environment are behaviorally relevant. In particular, saccadic eye movements are used to quickly shift the fovea several times per second during inspection of a visual scene. Each saccade results in a change in the retinal position of objects throughout the visual field, yet we have the subjective experience that the visual world remains stable. This experience of visual stability may be achieved via interactions between neural systems involved in visual perception and neural systems involved in moving the eyes (“oculomotor” brain areas). It has long been hypothesized that the perceptual system utilizes oculomotor signals to update internal representations of the world across saccades. A simple demonstration makes apparent that such a mechanism exists to compensate for the retinal displacements induced by saccades. By closing one eye and gently pushing the open eye with a finger, we can experience visual instability resulting from the eye moving in its orbit. Saccades also shift the image on the retina, though more abruptly, but the changes in the image on the retina across saccades do not cause the same perceptual instability. Thus, changes in the retinal image across saccadic eye movements are likely to be accompanied by extra-retinal signals that facilitate the perception of a stable world.

In this thesis, I present studies in which I tested how eye movements interact with object perception in peripheral vision. In particular, I tested how extra-retinal information associated with eye movement preparation and execution affects processing and identification of visual objects. In Chapters 2 - 5, I present four empirical studies showing evidence for changes in object identification resulting from extra-retinal signals that arise around the time eye movements are made. Findings from these studies converge on the conclusion that the preparation and execution of eye movements alter peripheral visual processing in a way that facilitates visual stability across saccades. An overview of these chapters is presented toward the end of this Introduction. The purpose of this Introduction is to provide a concise summary of previous research most relevant to the studies presented in this thesis. In Chapters 2, 3 and 5, I examine how eye movements affect integration of visual form information in peripheral vision. I therefore begin this Introduction with a description of visual crowding. I then review relevant eye movement research
pertinent to all chapters, including Chapter 4. A General Discussion and Conclusion section are presented in Chapter 6.

**Visual crowding**

Coordinated shifts of covert visual attention and overt eye movements are used to selectively process those stimuli that are likely to be behaviorally relevant (Corbetta & Shulman, 2002). Eye movements are particularly important in cases where the identity of an object in peripheral vision cannot be resolved due to interference from nearby stimuli. For example, while fixating the black spot in Figure 1, the reader will find that identifying the central letter in the blue display is more difficult than identifying the central letter in the purple display. The difficulty in recognizing the blue letter cannot be accounted for by decreased visual acuity in peripheral vision because it is located the same distance from fixation as the purple letter. The greater difficulty in identifying the blue letter than the purple letter, therefore, must be related to the closer proximity of the flanking elements to the blue letter. In this example, it is necessary to shift fixation toward the blue display to recognize the central blue letter. The loss of discriminability of an object amongst such visual clutter, referred to as visual crowding, was first reported by Bouma (1970). He noted that an object in peripheral vision becomes difficult to recognize when a distractor appears within approximately half the object’s eccentricity (Bouma, 1970). Visual crowding has been studied extensively in recent years (for reviews, see Levi, 2008; Pelli & Tillman, 2008; Whitney & Levi, 2011). Simple demonstrations of crowding like the one shown in Figure 1 imply that crowding is a primary limit of object recognition under natural viewing conditions, where visual environments are densely cluttered with visual objects.
While fixating the black spot, the central letter in the blue configuration (left) is difficult to recognize. By contrast, the letter at the center of the purple configuration (right) should easily be recognized as the letter “J”. Both central elements are the same letter and the same distance from the black spot. Thus, the difficulty in recognizing the blue J must arise from interference from the surrounding flanking elements. The deleterious effects of crowding can usually only be minimized by reducing the eccentricity of the crowded object (Pelli & Tillman, 2008) by shifting gaze to bring the object closer to the fovea. Whether eye movements per se affect the identification of crowded objects has not been examined.

The spatial characteristics of crowding have been studied extensively, and several empirical generalities have been noted (see Figure 2). Flanking elements cause interference when they appear within a distance of the target object referred to as the ‘critical distance’ (e.g. Yeshurun & Rashal, 2010) or ‘critical spacing’ (e.g. Levi & Carney, 2009). Quantifying critical distance typically involves systematically varying the distance between a visual probe and its surrounding flankers, and finding the probe-flanker spacing at which observers’ ability to correctly identify the probe reaches a certain threshold (e.g. Kooi, Toet, Tripathy, & Levi, 1994). Critical distance scales linearly with an object’s retinal eccentricity, such that more eccentric targets have larger critical distances (Pelli & Tillman, 2008). As first observed by Bouma (1970), and as shown in Figure 2, critical distance can be expressed as a proportion of target eccentricity, φ, and typically has a scaling factor or “Bouma’s constant” (Pelli, 2008) of 0.1 - 0.5 depending on the measure of crowding and the observer (for examples of inter-subject variability, see Bouma, 1970; Toet & Levi, 1992; Wallis & Bex, 2012). Toet and Levi measured the two-dimensional shape of crowding by measuring probe interference caused by a single flanking element at varying positions around the probe. As shown in Figure 2, they found that crowding zones normally have an elliptical shape. This ellipse is elongated such that critical spacing in the radial direction is greater than critical spacing in the tangential direction, with a radial-tangential ratio of approximately 1.5 (see also, Bex, Dakin, & Simmers, 2003).
Figure 2. Critical distance of crowding.
This diagram shows the two-dimensional zones in which flankers will cause crowding of an object (Toet & Levi, 1992), and the scaling of critical distance at different retinal eccentricities for two visual objects, the letters J and K. These positions of these letters can each be described as a distance from the fixation point (the black spot), $\varphi_J$ and $\varphi_K$, respectively. The solid ellipses show hypothetical zones and the spatial extent of crowding for each object. For the letters to be identified, distractors must appear beyond a distance of $0.5\varphi$, as measured by Bouma (Bouma, 1970). Subsequent studies have shown this distance varies from observer to observer, ranging from approximately 0.1-0.5$\varphi$. Crowding zones are elliptical, such that critical distance is larger in the radial than tangential direction, with a radial-tangential ratio of approximately 1.5 (Toet & Levi, 1992). Flankers further from fixation than the probe will cause more crowding than those closer to fixation (Bex et al., 2003). These characteristics of crowding are relatively constant throughout the visual field, though there are asymmetries in the upper and lower visual fields when stimuli fall on the vertical meridian (Abrams, Nizam, & Carrasco, 2011; He, Cavanagh, & Intriligator, 1996).

Although the spatial profile of crowding is well understood, the cause remains unknown. One hypothesis posits that crowding arises from interactions within the "combining fields" of early visual neurons, such that features of multiple objects are averaged together when those objects fall within a single combining field (Pelli, 2008). This hypothesis is supported by the finding that the linear scaling of crowding zones corresponds to the organization of the visual cortex (Pelli, 2008). The size of crowding zones correlates well with the size of V2 receptive fields, suggesting that area V2 is a critical stage in the visual hierarchy in which information is averaged (Freeman & Simoncelli, 2011; Wallis & Bex, 2012). Contrary to an averaging account of crowding, however, He et al (1996) found that an oriented grating, crowded beyond recognition, produces strong orientation adaptation aftereffects (but see Blake, Tadin, Sobel, & al, 2006). They argue that because these aftereffects primarily occur in primary visual area V1, the visual signal is not averaged but filtered at a higher visual stage to reduce the amount of information that reaches conscious awareness. In this way, crowding may represent a limit in the resolution of visual attention (He et al., 1996; Intriligator &
Cavanagh, 2001). However, neither an averaging account of crowding, nor a visual attention account, explains the characteristic elliptical shape of crowding zones as shown in Figure 2.

Although the mechanisms that give rise to crowding are debated, studies have shown that the most reliable way to mitigate crowding is to reduce the retinal eccentricity of the crowded object (Pelli & Tillman, 2008). Under natural viewing conditions, the simplest way to reduce the retinal eccentricity of a visual object is to move the eyes such that the fovea is closer to the object of interest. However, crowding has been studied almost exclusively under conditions in which fixation is maintained, leaving open the question of whether eye movements affect form integration in peripheral vision. In the next section, I summarize studies of object identification with uncrewded targets that have shown improved discriminability at the goal of an intended eye movement. This raises a question: Does identification of a crowded object improve if the object is the target of an impending saccade? A potential answer to this question is provided in Chapter 2, and it has important implications for theories of crowding.

Enhanced perception of (uncrowded) saccade targets

Saccades quickly bring an object of interest in peripheral vision to the fovea for detailed processing. Several perceptual phenomena occur around the time of a saccade eye movement. For example, around the time of saccade onset, there are distortions in the perceived position of briefly flashed stimuli (Cai, Pouget, Schlag-Rey, & Schlag, 1997; Honda, 1999; Lappe, Awater, & Krekelberg, 2000; Ross, Morrone, & Burr, 1997) that may anticipate the changes in retinal positions of stimuli across the saccade (Ross, Morrone, Goldberg, & Burr, 2001). Time is also compressed (Morrone, Ross, & Burr, 2005) and visual motion resulting from the saccadic eye movement itself is suppressed (Burr, Morrone, & Ross, 1994; Thiele, Henning, Kubischik, & Hoffmann, 2002). Compression of time and space, and suppression of motion, may help to explain the apparent threshold elevation for object perception (e.g. Riggs, Merton, & Morton, 1974) during each saccade (Ross et al., 2001). In contrast to these perceptual distortions, other visual processes are facilitated around the time of an eye movement. In this section I will focus on findings from

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1 To the best of my knowledge, only two previous studies have investigated how saccadic eye movements affect crowding, but neither study has been published in a scientific journal. Results from one study were presented at the European Conference on Visual Perception (Morvan & Cavanagh, 2011). Results from the other study were presented in a doctoral thesis by Bjorn Vlaskamp, defended in 2006.
human psychophysical studies, and neurophysiological studies of single cells in the monkey brain, which that show visual perception is facilitated for targets of saccadic eye movements. Although they have expanded our knowledge of how eye movements affect peripheral vision, these studies have primarily probed peripheral vision using isolated targets, leaving open the question of how saccadic eye movements affect perception of crowded objects.

A focus of eye movement studies has been to examine the perceptual consequences resulting from oculomotor selection. For example, Kowler et al (1995) and Deubel and Schneider (1996) tested whether identification of an alphanumeric character improves when the object is also the target of a saccade. These studies employed paradigms in which human observers were required to saccade to a specific location and identify a briefly presented visual probe. Importantly, the probe was presented before the onset of the saccade, so any changes in performance could not be due to changes in the retinal position of stimuli. Observers’ probe identification accuracy was highest when the probe appeared at the same position as the saccade target, but was relatively poor when the probe appeared anywhere else in the display. Saccade endpoints often miss the intended saccade target (e.g. Lord & Wright, 1949), so Deubel and Schneider examined whether the pre-saccadic perceptual benefit applied to the intended saccade target, or to the location upon which the fovea actually landed. They found that objects at the intended location received the most facilitation, suggesting that any pre-saccadic perceptual benefit is somewhat independent of the saccade endpoint. Deubel (2008) further investigated the time course of this improved object identification. As shown in Figure 3, he found that discrimination accuracy increased as a function of time to saccade, such that an observer’s ability to identify the target object was greatest immediately prior to saccade onset. More recently, Rolfs and Carrasco (2012) showed that perceived contrast and visual sensitivity are enhanced at the goal of an eye movement, suggesting that visual signals are boosted for saccade targets. Furthermore, Deubel (2008) found that the improved performance for saccade targets was greater than the improved performance associated with a spatial cue used to draw visual attention to the probe without a change in gaze position (Posner, Snyder, & Davidson, 1980). Rolfs and Carrasco (2012) further showed that changes in perception at the saccade goal can occur on a shorter time scale than changes associated with covert attention alone. Taken together, these studies show that saccade preparation results in enhanced perception at the goal of the saccade. Such a pre-saccadic change in perception may serve to “pre-sample” the stimulus that is

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predicted to appear at the fovea following an eye movement, thus mitigating the negative consequences of the impending retinal displacement.

**Figure 3.** Improved identification of uncrowded saccade targets. Data show proportion of correct identifications of an alphanumeric character presented at the location of a planned saccade, plotted as a function of time to saccade. Accuracy rises sharply within 50 ms of saccade onset. Adapted from Fig. 5 in Deubel (Deubel, 2008).

Single-cell studies in monkeys have established a neurophysiological basis for the enhanced perception of saccade targets. Moore, Tolias, and Schiller (1998) found that oculomotor preparation modulates activity of neurons in visual cortex. Specifically, they were interested in how activity in area V4 is modulated during saccade preparation. Presaccadic changes in V4 are interesting because neurons in V4 are known to be sensitive to visual features such as orientation (Desimone & Schein, 1987) and color (Schein & Desimone, 1990), and project to brain areas that may be important for object identification (Desimone & Duncan, 1995; Distler, Boussaoud, Desimone, & Ungerleider, 1993). Moore et al measured the activity of V4 neurons in response to a visual probe presented during a delayed saccade task, in which the monkey was first shown the saccade target but was required to withhold any saccade until cued. The visual probe, an oriented bar, was presented within the receptive field of a sampled V4 neuron. After the probe’s appearance, the monkey was cued to saccade to one of two stimuli: the probe (positioned within the recorded neurons’ receptive field), or a small spot contralateral to the probe (positioned outside the receptive field). By introducing a time delay between the onset of the probe and the cue to saccade, Moore et al were able to measure V4 activity in response to the probe onset and, separately, activity resulting from saccade preparation. Following the onset of the probe, the cells’ activity increased selectively for a specific probe orientation, but adapted within a few hundred milliseconds. Within 100 ms of a saccade toward the
probe, the cells’ firing rate again increased selectively for the orientation of the probe. The cells’ firing rate did not increase if the monkey made a saccade away from the probe. Thus, saccade preparation resulted in an enhanced representation of the saccade target’s feature within V4. Moore et al suggested that pre-saccadic changes in V4 activity might serve to maintain a representation of the saccade target throughout the execution and completion of the eye movement, facilitating visual continuity despite the loss of coherent visual input during the saccade itself (Burr et al., 1994).

Moore and colleagues further demonstrated the link between oculomotor planning and visual perception by directly stimulating neurons within the frontal eye fields (FEF) while measuring corresponding changes in V4 (Armstrong, Fitzgerald, & Moore, 2006; Moore & Armstrong, 2003). FEF is known to be involved in the generation of eye movements (Bruce & Goldberg, 1985), and direct electrical stimulation of neurons in FEF elicits saccades, the vectors and amplitudes of which depend on the specific site of stimulation (Bruce, Goldberg, Bushnell, & Stanton, 1985). Thus, Moore and Armstrong (2003) were able to measure the response properties of V4 neurons with receptive fields that corresponded to the endpoints of the saccades elicited by FEF stimulation. Importantly, however, they stimulated FEF using currents below those required to evoke a saccade, such that any effect on V4 activity must result from oculomotor selection or preparation rather than execution. Results from this study showed that, following subthreshold stimulation of FEF neurons, V4 activity increased when the neurons’ preferred stimulus appeared within their receptive field.

More recently, Gregoriou, Gotts, and Desimone (2012) measured the correspondence between activity in FEF and V4 while a monkey performed a saccade task, and classified FEF neurons according to whether they responded to a visual stimulus only, the onset of the saccade only, or a combination of both. They showed that only activity in “visual” FEF neurons corresponded to activity in V4. This finding raises the possibility that it is not necessarily neurons directly involved in motor commands that modulate visual responses in area V4. However, the anatomical connections between different classes of FEF neurons and V4 neurons are yet to be determined. As discussed by Steinmetz and Moore (2012), if visual FEF neurons do not project to V4, it would be unlikely that they participate directly in modulating firing rates of V4 cells during saccade preparation. Furthermore, Armstrong and Moore (2006) found that modulation of V4 activity depended strongly on the accuracy of the saccades elicited by FEF stimulation.
This finding reveals that the spatial component of the motor command plays an important role in how visual signals are affected during saccade preparation.

In addition to measuring changes in the firing rates of V4 neurons just prior to a saccade, pre-saccadic changes of the area in external space to which the neurons respond – their receptive fields – have also been examined. Tolias et al (2001) mapped the receptive fields of V4 neurons while monkeys performed a simple saccade task. Monkeys were trained to maintain fixation on a spot until the onset of a saccade target, the position of which varied from trial to trial. Prior to the onset of the saccade target, a visual probe appeared and remained visible throughout the duration of the trial. By varying the position of the visual probe, Tolias et al were able to map out V4 receptive fields according to different saccade vectors. Because the visual probe appeared prior to the onset of the saccade target and remained visible following the saccade, they could also analyze the temporal dynamics of any changes in the receptive fields. They found that, regardless of the area to which they responded during fixation, neurons in V4 began firing in response to probes in close spatial proximity to the saccade target immediately prior to saccade onset. Thus, the receptive fields of V4 neurons effectively shrank and shifted toward the saccade target. Interestingly, these changes began approximately 50 ms prior to saccade onset, which corresponds closely to the time course of improved identification of saccade targets found in human studies (Deubel, 2008; Rolfs & Carrasco, 2012). The shift in receptive fields toward the goal of a saccade means that saccade targets are represented by a greater number of V4 neurons just prior to an eye movement, which may help to explain the changes in visual perception described above (e.g. Deubel & Schneider, 1996). Moreover, the reduction in size of receptive fields suggests that the resolution of peripheral vision may be enhanced for saccade targets, and thus visual crowding may be attenuated just prior to saccade onset.

To summarize, visual perception is enhanced at the goal of a planned eye movement. As measured psychophysically in humans, identification of a visual object improves when the object is the target of a saccade (e.g. Kowler et al., 1995). This improved identification occurs prior to the onset of the saccade (Deubel, 2008; Deubel & Schneider, 1996; Kowler et al., 1995), revealing that extra-retinal signals involved in saccade preparation alter visual perception (Rolfs & Carrasco, 2012). Single-cell recordings in the monkey reveal that these pre-saccadic changes in visual perception may be accounted for by the influence of oculomotor brain areas on the firing rate of V4 neurons that represent the saccade target (Armstrong et al., 2006; Moore et al., 1998;
Moore & Armstrong, 2003). Dynamic changes in the size and shape of V4 neurons during saccade preparation may also facilitate perception (Tolias et al., 2001). In Chapter 2, I test whether links between oculomotor preparation and visual processing can also modify the magnitude and spatial extent of visual crowding.

**Object identification during smooth pursuit eye movements**

Smooth pursuit eye movements are distinct from saccades, so comparing and contrasting the effects of each class of eye movement on peripheral vision may reveal important insights into the mechanisms underlying crowding. In contrast to saccades that rapidly bring an object in peripheral vision to the fovea, pursuit eye movements rotate the eyes relatively slowly and stabilize on the fovea an object that moves relative to the observer. Importantly, after initiation, the velocity of pursuit eye movements is corrected online to reduce retinal motion of the tracked object (Krauzlis, 2004). Some pursuit eye movements can be triggered automatically in response to large-field motion, as in the case of optokinetic nystagmus (Cohen, Matsuo, & Raphan, 1977), but voluntary pursuit of a single target requires that the observer explicitly intends to pursue the target (e.g. Collewijn & Tamminga, 1984). The neural networks involved in pursuit eye movements overlap extensively with those involved in saccade generation (Krauzlis, 2004), yet the number of studies that have investigated how smooth pursuit affects object identification in peripheral vision is substantially fewer than the number that have investigated the influence of saccades (for a review, see Schütz, Braun, & Gegenfurtner, 2011). The limited research on the interaction between pursuit eye movements and peripheral vision leaves open the question of whether smooth pursuit affects crowding.

When observers pursue a moving target, their ability to discriminate objects in peripheral vision is limited. Khurana and Kowler (1987) tested whether selecting one moving stimulus as the target of a pursuit eye movement impairs perceptibility of other moving stimuli. Specifically, they tested whether observers could identify letter probes at various locations in peripheral vision while they pursed a moving object. Observers pursued a string of letters that translated across a display, and then were asked to identify a letter probe presented in a second letter string elsewhere in the display. They found that observers' ability to discriminate a probe presented in the non-pursued stimulus was far poorer than their ability to discriminate the pursued stimulus, regardless of whether both letter strings were moving at the same or a different velocity.
Following a similar line of investigation, Lovejoy, Fowler, and Krauzlis (2009) tested whether observers’ ability to discriminate objects during pursuit depended on the position of the object relative to the direction of pursuit. In their experiments, observers foveated and pursued the center of a moving array of digits that spanned the horizontal meridian. Observers had to identify which of two probe digits was briefly presented at a random position within the array. Although discrimination accuracy was high when probes were presented within approximately 1° of the foveated region, accuracy was at chance for probe locations beyond this area. When observers had no information about the upcoming location of the probe, performance dropped systematically as a function of the distance from the pursuit target to the probe, regardless of whether probes were presented in the same or opposite direction to smooth pursuit. When the likely position of an upcoming probe was indicated with a visual cue, there was a small but reliable improvement in performance for probes presented ahead of the pursuit target. These findings suggest that visual processing during pursuit is somewhat limited to the fovea, but, under some conditions, can be selectively biased according to the direction of pursuit.

The studies by Khurana and Kowler (1987) and Lovejoy et al (2009) suggest that object discrimination during smooth pursuit is generally poor for stimuli beyond the fovea. Whether the loss of discriminability for peripheral objects during pursuit is due to a general impairment in visual processing or to changes in visual crowding remains an open question. That an observer’s ability to identify an object is improved at the goal of a saccade but is made worse during smooth pursuit suggests the function of these different classes of eye movement may affect crowding in distinct ways. In Chapter 3, I present the first study of visual crowding during voluntary smooth pursuit eye movements. I measured the spatial extent of crowding for objects at different retinal eccentricities and positioned either contraversive or ipsiversive to the direction of pursuit. The results of this study show that pursuit eye movements cause a change in crowding that is markedly different from changes in crowding observed around the time of saccades (Chapter 2), and suggest that visual crowding is flexibly altered depending on the behavioral goals of the observer.

**Remapping visual attention**

In the preceding sections, I reviewed studies that found systematic changes in peripheral visual processing around the time of an eye movement. The functional purpose of these changes in peripheral vision remains less clear than the empirical observations. For example, changes in perception are strongest immediately prior to the onset of an eye
movement (Deubel & Schneider, 1996; Rolfs & Carrasco, 2012; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011), and the duration of any changes in perception is typically very brief (e.g. < 50 ms, see Figure 3). Immediately following these changes in perception, movement of the eyes displaces on the retina the visual objects that benefit from enhanced processing. Given that the human visual cortex contains a topographic map of external space based on retinal locations ("retinotopic" mapping; Engel et al., 1994), each shift of an object on the retina requires that the object is re-encoded by a new population of visual neurons. What might be the functional purpose of such short-lived changes in perception? As discussed above, changes in visual perception prior to a saccade might boost the neural representations of relevant visual objects so they are sustained for the duration of the eye movement and until they can be re-encoded following the saccade (Moore et al., 1998). In this way, pre-saccadic activity anticipates the impending retinal displacement. Because the fovea only represents a small portion of the visual field, the majority of visual objects are displaced from one part of peripheral vision to another. In this section, I summarize studies that suggest that changes in visual processing before and after an eye movement facilitate perception of peripheral objects that shift on the retina across saccades. Critically, some of these processes begin prior to each saccade, and are thus predictive of the outcome of the eye movement.

One of the principal riddles of visual neuroscience is how the apparently uninterrupted perception of visual objects is maintained across saccades (Krauzlis & Nummela, 2011). Recently, researchers have argued that such trans-saccadic perceptual stability is achieved at least in part via spatiotopic maps, in which low-level visual information, such as orientation, shape and motion, is encoded in world-centered coordinates independently of retinotopic position (Melcher, 2005; Melcher & Morrone, 2003; Zimmerman, Burr, & Morrone, 2011). Spatiotopy provides an appealing solution to how object perception is preserved across saccades, and single cells within ventral intraparietal area have been found to encode stimuli in external coordinates (Duhamel, Bremmer, Ben Hamed, & Graf, 1997). However, currently there is no evidence that these cells converge to provide a spatiotopic map (Wurtz, 2008). Moreover, behavioral evidence for spatiotopy is either absent (Irwin, Yantis, & Jonides, 1983; Rayner & Pollatsek, 1983) or hotly debated (Knapen, Rolfs, Wexler, & Cavanagh, 2010; Morris et al., 2010). Other models of perceptual stability (Cavanagh, Hunt, Afraz, & Rolfs, 2010a; Wurtz, 2008) propose that trans-saccadic object continuity is achieved simply by “remapping” the spatial positions of objects of interest, negating the need for spatiotopic feature maps. Here, I
focus on studies that have addressed this possibility by measuring changes in visual attention before and after a saccadic eye movement.

“Visual attention” is used to describe a range of cognitive, perceptual, and neurophysiological effects, and has been a major focus of psychological research (for a review, see Carrasco, 2011). For the majority of this section, I use the term “visual attention” to mean covert spatial attention. Covert spatial attention involves prioritizing visual processing at a specific location in peripheral vision while the eyes remain still or move elsewhere. Covert spatial attention can be attracted involuntarily by certain visual events, such as an abrupt visual onset (Remington, Johnston, & Yantis, 1992), or can be shifted intentionally (Posner et al., 1980). Response times and accuracy are affected by visual attention, such that observers respond faster and more accurately to targets that are spatially congruent with the focus of attention than those that are spatially incongruent (e.g. Folk, Remington, & Johnston, 1992). Likewise, visual attention can alter spatial resolution (Yeshurun & Carrasco, 1998), contrast sensitivity (Carrasco, Penpeci-Talgar, & Eckstein, 2000), and perceived contrast (Carrasco, Ling, & Read, 2004). Directing visual attention to an object in peripheral vision facilitates processing of that object (e.g. Posner et al., 1980), but if observers direct their visual attention to a world-referenced location and then execute an eye movement, the attended location will shift on the retina. This raises a question: How are covert shifts of visual attention coordinated with overt shifts of the eyes?

In a series of studies, Golomb and colleagues (Golomb, Chun, & Mazer, 2008; Golomb, Marino, Chun, & Mazer, 2011; Golomb, Nguyen-Phuc, Mazer, McCarthy, & Chun, 2010a; Golomb, Pulido, Albrecht, Chun, & Mazer, 2010b) tested how visual attention directed to the position of a cue is updated following an eye movement, so that the focus of attention corresponds to the pre-saccadic position of the cue. In particular, they were interested in the time course and neural correlates of shifts of visual attention from pre-saccadic to post-saccadic coordinates. The basic design of their experiments is shown in Figure 4. Observers were cued to attend to a specific screen location. They then executed a saccadic eye movement to a specified location and respond to the orientation of a visual probe (a bar oriented left or right) presented at varying delays following the saccade (Golomb et al., 2008). They measured trans-saccadic changes in the focus of visual attention by presenting the probe at locations that corresponded either to the pre-saccadic retinal position of the cue (“retinotopic” location) or to the post-saccadic, world-referenced (“spatiotopic”) location of the cue. When the probe was presented within approximately 75
ms of the end of the saccade, observers’ responded faster and more accurately if the probe appeared at the cue’s retinotopic position than if it appeared at its spatiotopic position. When the probe was presented approximately 400 ms after the offset of the saccade, observers’ performance was better for spatiotopic probes than retinotopic probes. These findings suggest that visual attention takes a short amount of time following a saccade to remap from pre- to post-saccadic coordinates.

In a subsequent study, Golomb, Pulido, Albrecht, Chun, and Mazer (2010b) tested whether faster remapping of visual attention was possible if the spatiotopic frame of reference was strengthened using a visually structured display background. They used the same paradigm as that shown in Figure 4, but gridlines were presented in the background of the displays throughout the duration of each trial. Within 75 ms of saccade offset, observers responded faster to probes presented at the spatiotopic location of the cue than probes at the control location. Thus, visual structure led to a shift of visual attention from retinotopic to spatiotopic coordinates that was measurable immediately after a saccade. However, this shift was not complete: responses to retinotopic probes were also faster than to controls. Using functional magnetic resonance imaging, Golomb, Nguyen-Phuc et al (2010a) recorded neural correlates of visual attention in both retinotopic and spatiotopic coordinates in area V4 immediately following the saccade. Golomb and colleagues interpreted these effects as showing that visual attention takes time to decay from retinotopic coordinates following an eye movement. Perhaps more interesting, however, was their finding that in some cases the processing benefits associated with visual attention were observed in spatiotopic coordinates immediately following the saccade. This finding suggests that some remapping from retinotopic to spatiotopic coordinates occurs prior to the saccade.
Figure 4. Testing remapping of visual attention following a saccade. The panels schematize the experimental displays employed by Golomb and colleagues (e.g. Golomb et al., 2008). A) Observers were required to first fixate a gray spot and attend to the screen location corresponding to a visual cue (left panel), and then (B) execute a saccade. C) Following the saccade, a probe could appear either at the screen location of the cue (spatiotopic probe), or the retinotopic location of the cue. Compared with probes presented at a control location (e.g. blue bar in C), response times were facilitated when the probe appeared at either the retinotopic or spatiotopic location of the probe (Golomb, Pulido, Albrecht, Chun, & Mazer, 2010b). These results suggest that visual attention “lingers” in retinotopic coordinates, but is partially remapped to spatiotopic coordinates by the end of the saccade. Note that only one of the three probe locations was tested per trial.

Mathôt and Theeuwes (2010) modified the paradigm of Golomb et al (2008) to probe shifts of visual attention immediately prior to a saccade. Their basic design was similar to that shown in Figure 4, except they used briefly presented cues to reflexively summon visual attention (e.g. Yantis & Jonides, 1984). Critically, probes were presented immediately prior to the onset of the saccade. Thus, probes presented at the same location as the cue (red bar in Figure 4C) corresponded to both the spatiotopic and retinotopic cue location. The position corresponding to the “retinotopic probes” shown in Figure 4C (orange bar) were referred to by Mathôt and Theeuwes as the “future-retinotopic” location of the cue. As expected (Theeuwes, 1991), Mathôt and Theeuwes found that, compared with probes presented at a non-cued control location, responses were facilitated when probes appeared at the retinotopic/spatiotopic location of the cue. Interestingly, they also found facilitation of responses to probes presented at the “future-retinotopic” location of the cue. Could such a change in visual attention anticipate the shift of visual objects on the retina following a saccade?

Despite Mathôt and Theeuwes’ terminology, this probe position does not correspond to the future-retinotopic location of the cue. I discuss this issue below and in Chapter 4.
The notion that visual attention is remapped prior to a saccade is in line with the model of visual stability based on changes in activity of neurons within visual and attention areas, as recently proposed by Cavanagh and colleagues (2010a). Throughout oculomotor areas, populations of neurons begin to respond to stimuli outside their receptive field if an impending saccade will bring the stimulus into the receptive field (Duhamel, Colby, & Goldberg, 1992; Nakamura & Colby, 2002; Sommer & Wurtz, 2006; Umeno & Goldberg, 1997). An example of this anticipatory response, referred to as “predictive remapping”, is shown in Figure 5A. Duhamel et al measured the activity of cells in the lateral intraparietal area (LIP) of the monkey brain during steady fixation and just prior to a saccade. During initial fixation, neurons in LIP responded to stimuli presented only at one location, the neurons’ classical receptive field (red circle, top panel of Figure 5A). Just prior to a saccade, however, Duhamel et al found that these same neurons increased their firing rate if a stimulus appeared at their “future-field”, i.e. the location corresponding to where the classic receptive field would fall following the saccade (see orange dotted circle in the middle panel of Figure 5A). Cavanagh et al suggest that this pre-saccadic neural activity serves to remap relevant stimuli on a salience map to compensate for the changing retinal positions of visual objects with each saccade. The correspondence between predictive remapping and shifts of visual attention as reported by Mathôt and Theeuwes (2010) is made apparent by comparing Figure 5A and B. Indeed, Mathôt and Theeuwes interpreted their findings as evidence that visual attention is remapped via neurons found in areas such as LIP (Mathôt & Theeuwes, 2011).
**Figure 5.** Examples of predictive remapping. 
A) During steady fixation, neurons in LIP respond to stimuli that appear within a specific area, the neurons’ classical receptive field (red circle, top panel). However, when the monkey is cued to make a saccade, the same neurons begin to respond to stimuli presented at the location the classical receptive field would represent following the eye movement, the “future-field” (dashed orange circle, middle panel; Duhamel et al., 1992). B) The pre-saccadic shift of visual attention as found by Mathôt and Theeuwes (2010) maps closely onto the activity of neurons shown in (A). Just prior to a saccade, a visual cue facilitated responses to probes presented either at the classical receptive field or future-field of the cue. If visual attention were remapped in this way, however, it would be allocated to an irrelevant (non-cued) location following the eye movement (bottom panel). C) As shown by Rolfs et al. (2011), visual attention must be remapped opposite to the direction of the saccade for it to correspond to spatiotopic coordinates following the saccade. The changes shown in (C) can result from the same mechanistic changes as in (A), but are subserved by a population of neurons whose classical receptive field is to the left of fixation. Reproduced from Harrison, Mattingley and Remington (2012).

However, in contrast to the findings and interpretations of Mathôt and Theeuwes (2010), to anticipate the retinal displacement of visual objects, visual attention must shift in the **opposite** direction to the saccade. Evidence for the predictive remapping of visual attention opposite to the direction of a planned saccade comes from a recent behavioural study by Rolfs et al (2011). In their study, observers were required to execute two saccades in quick succession, and then report the orientation of a Gabor presented briefly at various intervals prior to the onset of the first saccade. The key finding was that observers reported the orientation of the Gabor more accurately if it appeared at the retinotopic location corresponding to where the second saccade target would fall following the first saccade. This facilitation for the perceptual target only occurred if it appeared within approximately 50 ms of the onset of the first saccade, and no facilitation was found for targets at a control site matched for retinal eccentricity. That is, visual attention was drawn to the retinotopic location that corresponded to the future location of a task relevant
stimulus. These results are consistent with the notion that the second saccade target location was remapped predictively of the first saccade via pre-saccadic transfer of activation throughout oculomotor areas (Cavanagh, Hunt, Afraz, & Rolfs, 2010a; Rolfs et al., 2011). Rolfs et al termed this effect “functional remapping”. If location information is remapped just prior to a saccade, visual processing can begin with the expectation of relevant information appearing at these locations following the saccade. The difference in logic between Mathôt and Theeuwes’ interpretation and the interpretation of Rolfs et al can be seen by comparing Figure 5B and C.

To summarize, Mathôt and Theeuwes (2010) claim that visual attention shifts in the direction of a saccade, whereas Rolfs et al (2011) suggest that visual attention shifts in the opposite direction. Both groups of researchers interpret their findings as evidence of predictive remapping. I address this issue in Chapter 4 by examining further the effects described by Mathôt and Theeuwes, and conclude that their results probably reflect changes in visual attention that are independent of predictive remapping.

**Remapping visual features**

Whether shifts of visual attention alone (e.g. Rolfs et al., 2011) can account for the impression of object continuity across saccades, or whether pre-saccadic activity conveys featural information, has been the subject of much recent debate (Cavanagh, Hunt, Afraz, & Rolfs, 2010b; Mayo & Sommer, 2010). Although recent studies have claimed to provide evidence for featural remapping via the transfer of low-level tuning properties of early visual neurons (Melcher, 2005; 2007; Melcher & Morrone, 2003), these data have been challenged (Afraz & Cavanagh, 2009; Knapen et al., 2010; Knapen, Rolfs, & Cavanagh, 2009; Morris et al., 2010). It is well established that activity in brain areas that possess neurons with remapping properties, such as FEF (Sommer & Wurtz, 2006), can modulate responses in early visual areas with featural preferences like V4 (Moore & Armstrong, 2003; Moore & Fallah, 2004). Thus, a relationship between neurons that remap spatial information and visual areas that code featural information might negate the need for featural information to be remapped: an object’s remapped location can signal where processing is required in corresponding areas in retinotopic visual cortex (Cavanagh, Hunt, Afraz, & Rolfs, 2010a).

In a recent psychophysical experiment, Hunt and Cavanagh (2011) found evidence that spatial information is linked with featural information during predictive remapping. They combined a saccade task with an adapted backward-masking paradigm. In their
experiment, observers were required to identify the orientation of a visual probe (a Landoldt C) followed by a pattern mask, both of which were presented during steady fixation, or just prior to a saccade. Critically, the position of the mask relative to the probe was varied. On a subset of trials the mask appeared at the same screen location as the probe, and, on another subset of trials, the mask appeared at a retinal location that corresponded to where the probe would fall following the saccade (the “remapped” location). When observers withheld an eye movement, their probe identification accuracy was poorer when the probe and mask were spatially congruent than when there was a spatial offset (a standard backward masking effect). However, when the probe and a spatially congruent mask were presented within 100 ms of saccade onset, masking was reduced; observers’ probe identification accuracy improved relative to the no saccade condition. Furthermore, within 100 ms of a saccade, observers’ identification accuracy dropped when the mask appeared at the probe’s remapped location, compared with accuracy for the same stimulus condition when no eye movement was made. According to the authors’ account, this “remapped masking” effect occurred because predictive remapping processes shifted the spatial focus of visual attention from the probe location to the probe’s remapped location, and thus the position of the mask. This account lends support to the suggestion that visual attention is predictively remapped to track the spatial position of stimuli across saccades (Cavanagh, Hunt, Afraz, & Rolfs, 2010a; Rolfs et al., 2011).

It remains unclear, however, whether visual processing at remapped locations is specific to the features that comprise the remapped object’s identity. That is, did the visual similarity of the probe and mask matter in Hunt and Cavanagh’s (2011) experiment? It seems unlikely that the transient shifts of visual attention that precede eye movements would be devoid of any top-down control settings that accompany similar shifts of visual attention (Folk et al., 1992; Folk & Remington, 1998; White & Carrasco, 2011). Thus, I developed a novel visual crowding paradigm in which I could test whether pre-saccadic visual processing at an object’s remapped location is sensitive to the features of that object. In Chapter 5, I provide a direct demonstration that predictive remapping preserves an object’s features across saccades by linking remapped spatial information with the object’s featural information. These results have important implications for how the subjective experience of trans-saccadic perceptual continuity is achieved.
Overview of contribution

In this section I provide summaries of the four empirical investigations and findings presented in this thesis. Each study was distinct in its specific aim, but all studies addressed the general question of how eye movements affect visual processing.

In Chapter 2, I tested whether targets of saccades are released from crowding. This study was based on the work of Deubel and Schneider (1996) and Kowler et al (1995), which found that identification of uncrowded saccade targets improves just prior to the execution of an eye movement. I found that perception of a crowded saccade target is also facilitated. Relative to when no saccade was made, observers’ accuracy at reporting the identity of a crowded object improved within 50 ms of the onset of a saccade toward the object. Moreover, the spatial extent of crowding was almost halved within the same presaccadic time period. These results show that eye movement preparation can alleviate the deleterious effects of visual crowding. The reduction of crowding for saccade targets could facilitate visual search in cluttered natural environments.

In Chapter 3, I examined whether smooth pursuit eye movements modify visual crowding. Observers were required to overtly track a pursuit target and identify a crowded letter probe presented at positions either contraversive or ipsiversive to the direction of pursuit. Compared with a condition in which no eye movements were made, the spatial extent of crowding was greater for probes positioned contraversive to the direction of pursuit. No change in crowding was observed for probes ipsiversive to the direction of pursuit. This apparent asymmetry in crowding during pursuit occurred when the probe was 3° from the pursuit target, but not 7°. The results reveal that smooth pursuit selectively modifies visual crowding for nearby objects that trail the fovea. This may facilitate the eye movement itself by reducing distraction by visual elements in the background relative to the pursuit target.

In Chapter 4, I replicate and extend Mathôt and Theeuwes’ (2010) study of pre-saccadic shifts of visual attention. They found that an exogenous cue presented just prior to a saccade draws attention to the location of the cue, and, simultaneously, toward the direction of the impending saccade. Although they interpreted this as evidence for predictive remapping of visual attention, I found that the effects they described are not unique to the locations tested in their paradigm. I argue that these pre-saccadic changes in visual attention probably do not reflect a remapping mechanism that predicts trans-
saccadic changes in retinal input. Instead, I suggest that in this paradigm visual attention is widely spread in the direction of the impending eye movement.

In Chapter 5, I exploited visual crowding to test whether pre-saccade changes in visual processing can preserve the featural elements of objects. Visual distractors typically cause crowding only when they are close to a probe object. However, I found that during a brief period prior to saccade onset, distractors that flanked a probe’s predicted, post-saccadic location disrupted identification of the probe, even though the probe and distractors appeared in opposite visual hemifields. Critically, this “remapped crowding” was stronger when the distractors shared elementary visual features with the probe than when they were featurally distinct. These results suggest that predictive remapping conveys information about which features should be prioritized at remapped locations, thus preserving visual features across saccades without the need for spatiotopic feature maps.

These chapters reveal several ways in which object discrimination in peripheral vision is altered by extra-retinal signals generated during the preparation and execution of voluntary oculomotor actions. In Chapter 6 I provide a General Discussion and Conclusions that bring together the theoretical implications these studies. Importantly, these studies show that eye movements not only serve to shift the image on the retina, but also change the way in which visual signals are processed throughout the visual system.
Chapter 2 - Eye movement targets are released from visual crowding
The published version of this chapter appears as Appendix A.


Abstract

Our ability to recognize objects in peripheral vision is impaired when other objects are nearby (Bouma, 1970). This phenomenon, known as crowding, is often linked to interactions in early visual processing that depend primarily on the retinal position of visual stimuli (Pelli, 2008; Pelli and Tillman, 2008). Here we tested a new account that suggests crowding is influenced by spatial information derived from an extra-retinal signal involved in eye movement preparation. We had human observers execute eye movements to crowded targets and measured their ability to identify those targets just before the eyes began to move. Beginning around 50 ms prior to a saccade towards a crowded object, we found that not only was there a dramatic reduction in the magnitude of crowding, but the spatial area within which crowding occurred was almost halved. These changes in crowding occurred despite no change in the retinal position of target or flanking stimuli. Contrary to the notion that crowding depends on retinal signals alone, our findings reveal an important role for eye movement signals. Eye movement preparation effectively enhances object discrimination in peripheral vision at the goal of the intended saccade. These pre-saccadic changes may enable enhanced recognition of visual objects in the periphery during active search of visually cluttered environments.
Introduction

Voluntary eye movements are crucial for efficient sampling of the visual environment. During fixation, objects at the fovea receive enhanced processing and are easily recognized, whereas those in the periphery are more difficult to identify, particularly when closely adjacent objects surround them, a phenomenon referred to as visual “crowding” (Bouma, 1970; Pelli and Tillman, 2008). This effect can be experienced by fixating first on the red cross and then on the blue cross in Figure 1A. Note that the letter “Y” is much harder to discern when fixating the red cross than the blue one, even though it is located an equal distance from fixation in the two situations.
Figure 1. Demonstration of visual crowding and method used to test crowding prior to eye movements.

(A) Visual crowding for letter stimuli. In the upper row, the Y in the word “EYES” is virtually impossible to identify while fixating the red cross. In the lower row, the Y on its own is relatively easy to identify while fixating the blue cross, even though it is located at the same eccentricity as the Y in “EYES” above. (B) Sequence of displays used to quantify the magnitude of crowding prior to a saccade. At the offset of a blue fixation spot observers executed a saccade to the target and then reported the orientation of the central Gabor. If the fixation spot was red observers maintained fixation and performed the same task on the central Gabor. (C) Schematic showing the timing of target displays relative to saccade onset. The saccade commences at time zero, and negative times on the x-axis reflect the pre-saccade intervals over which target stimuli were presented. Saccadic latencies were re-calculated continuously online. These latencies were used to determine target-saccade onset asynchronies, such that targets were presented with close to equal probability in each of three intervals prior to the saccade (-149 to -100 ms, -99 to -50 ms and -49 to 0 ms) (Hunt and Cavanagh, 2011). Dimensions of stimuli in (B) are not to scale.
Crowding has been assumed to reflect obligatory integration of visual features in early visual areas that represent a region of space that includes both target and non-target stimuli (Parkes et al., 2001). The extent of this region – the “critical distance” – scales with eccentricity, so that the zone of crowding becomes progressively larger as target stimuli are moved further into the periphery. Critical distance is approximated by Bouma’s law as \(0.5 \phi\), where \(\phi\) is the eccentricity of the target (Bouma, 1970; Pelli and Tillman, 2008). The spatial extent of crowding can be used to approximate the minimum cortical distance between two objects necessary for accurate object recognition (Pelli, 2008).

Attempts to reduce crowding using spatial cues to indicate the location of the crowded target have yielded mixed findings, and only modest improvements in target discriminability at best (Felisberti et al., 2005; Strasburger, 2005; Scolari et al., 2007; Yeshurun and Rashal, 2010). Thus, it has been suggested that crowding imposes a fundamental limit on conscious vision (Levi, 2008; Whitney and Levi, 2011).

It is well established that responses of visual neurons and perception of uncrowded targets can be modulated by extra-retinal signals generated prior to an eye movement. For example, Moore and colleagues showed that activity related to an eye movement command in the frontal eye fields (FEF) alters the gain of V4 responses to stimuli presented at the goal of the intended eye movement (Moore and Armstrong, 2003; Moore et al., 2003; Moore and Fallah, 2004). Moreover, Tolias et al. (2001) showed that the receptive fields of V4 neurons shrink in size and shift toward the saccade goal just prior to a saccadic eye movement. Human psychophysical studies have shown that enhanced identification of uncrowded targets at the goal of a saccade (Remington, 1980) is substantially greater than that arising from visual cues alone (Deubel, 2008). Critically, these neural and perceptual effects are evident before the eyes begin to move, prior to any change in the retinal location of the target stimulus (Kowler et al., 1995; Deubel and Schneider, 1996; Moore and Fallah, 2004; Deubel, 2008).

The evidence reviewed here suggests that an extra-retinal signal involved in saccade preparation (Wurtz, 2008) can enhance perception at the goal of an eye movement. Whether similar perceptual improvements prior to a saccade occur for crowded targets remains an open question. We therefore tested whether visual crowding is reduced when a crowded stimulus is the target of an intended saccade.
Materials and Methods

**Overview of experiments.** In two experiments, we quantified changes in the magnitude and spatial extent of visual crowding during steady fixation and before a saccade toward a crowded target. Observers’ basic task was to report the orientation of a peripheral target Gabor surrounded by four vertically oriented Gabors (Fig. 1B). Blocks in which central fixation was maintained (“no-saccade” trials) were intermingled with blocks in which observers executed a saccade to the target placeholder (“saccade” trials). Target presentation durations were brief (< 24 ms) and, in saccade trials, were presented at varying times prior to the eye movement (Fig. 1C and Fig. 2B). Critically, because all orientation judgments were made before the eyes moved, the retinal locations of target and flanking stimuli were identical for the saccade and no-saccade conditions.

**Observers.** Five experienced psychophysical observers (one female) participated in each experiment. Two observers, including one author (W.J.H.), participated in both experiments. All observers had normal or corrected-to-normal vision and gave informed consent. The study was approved by The University of Queensland’s School of Psychology Ethical Review Committee.

**Materials.** Participants sat with their head in a head and chin rest positioned 57 cm from a 20-inch Dell CRT monitor (1600 x 1200 pixels, 85 Hz) in Experiment 1 or 61 cm from a 17-inch Samsung CRT monitor (1280 x 1024 pixels, 85 Hz) in Experiment 2. Stimulus presentation, eye movement recording and response collection were programmed using the Psychophysics Toolbox Version 3 (Brainard, 1997; Pelli, 1997) and Eyelink Toolbox extensions (Cornelissen et al., 2002) for MATLAB (MathWorks). Eye movements were recorded at 500 Hz with an EyeLink 1000 (SR Research) infrared eye tracker, calibrated using a 9-point calibration procedure.

**Stimuli and procedure.** Each trial began with a fixation spot (width = 0.2°) in the center of a uniformly gray display. As shown in Figure 1B, the target and four flanker positions in Experiment 1 were indicated with black placeholders (1°x1°). The target in Experiment 1 was 7.7° to the right of the fixation spot, and the center-to-center distance between target and flankers was 1.3°. In Experiment 2, only the target position (7° from central fixation) was indicated with a placeholder, and this placeholder was offset at target onset such that
no borders were visible during target presentations. Target and flanking stimuli were Gabors (width = 1°, 2 cpd, 100% contrast) presented for 23.5 ms. Immediately prior to target presentation, patches of white noise randomized with each screen refresh (85 Hz) were presented at positions corresponding to targets and flankers. In Experiment 1 only, the same dynamic white noise followed target and flanker presentation. Randomly from trial to trial, the combined target and flanker configuration was jittered vertically by ± 1° to ensure that observers could not pre-program eye movements throughout each testing session.

A trial began after gaze was detected continuously for 500 ms within a 2° x 2° region centered on the fixation spot. The fixation spot offset after a variable delay of 750 – 1250 ms (randomly drawn from a uniform distribution), cueing the observer either to make a saccade to the target (blue spot), or to remain fixated (red spot). Runs of saccade and no-saccade trials were alternated in blocks of 12, and testing always began with a saccade block to estimate target presentation times, as described below. In Experiment 1, observers completed 360 trials (180 saccade, 180 no-saccade) in a single testing session. In Experiment 2, each target-flanker separation was tested in a different session, and each observer completed a minimum of two sessions per target-flanker separation. The minimum number of trials completed by each observer in Experiment 2 was 3600.

Using a method similar to that described by Hunt and Cavanagh (2011), the interval between the offset of the fixation spot and target onset was manipulated to maximize the number of trials presented in three time bins prior to saccade onset (see Fig. 1C and Fig. 2B). We estimated the median saccadic latency of a saccade block after each saccade trial, and from this value subtracted 25, 75, or 125 ms to adjust the delay between fixation offset and target onset. During testing only, saccade latencies were taken as the time between fixation spot offset and the time at which the point of gaze shifted beyond 2° to the right of screen center. Median saccade latencies were calculated separately for each saccade block. For the first trial of a block we used the median saccade latency from the previous block. For the first trial of the experiment, median saccade latency was manually set to 200 ms. These time adjustments were pseudo-randomized across a block of trials, such that there were 4 of each (-25, -75, -125 ms) per block of 12. We then used these time adjustments in the next block of no-saccade trials to ensure stimulus timing was closely matched across saccade and no-saccade blocks. Saccade trial data were sorted into bins offline according to the recorded target-saccade onset asynchrony, using a velocity of 30°/s and acceleration of 8000°/s2 as criteria for saccade onset. Following
target presentation, there was a delay of 500 ms before observers were able to indicate the orientation of the target Gabor (rotated left or right off vertical; unspeeded, two-alternative forced-choice judgment).

Prior to testing, each observer completed a threshold procedure in which we established the minimum orientation to yield 75% correct identification of an unflanked target Gabor. We took the average orientation yielded by two interleaved QUEST procedures (40 trials each) (Watson and Pelli, 1983). The target was presented after a delay of between 12 and 200 ms (randomly drawn from a uniform distribution) following the offset of the fixation spot. Observers were required to maintain steady fixation throughout threshold trials and gaze was monitored online. All other trial details during this threshold procedure were as described above.

**Statistical analyses.** To quantify changes in performance over time and across different target-flanker separations (Experiment 2), we used a permutation analysis described by Rolfs and colleagues (Rolfs et al., 2005; 2011). Expected performance under the null hypothesis (i.e., that data within each target-flanker condition are temporally invariant) can be estimated by randomly permuting the observed data across time. These permutations were achieved by randomly reassigning each response to a time bin (without replacement), creating a surrogate time course of data for each individual, from which we derived an average surrogate time course. This procedure was repeated 1000 times to yield a distribution of surrogate means for each time bin, representing an estimate of null performance across time. Using the distributions of permuted data, we calculated 95% confidence intervals around estimated null performance, such that actual data falling beyond these intervals represent significant changes in performance across time. To verify this analysis, we bootstrapped data from each condition to estimate the distribution of the means (Efron and Tibshirani, 1993). In this case, for the number of observations in a given condition for each observer, we randomly sampled data from that condition (with replacement) to create bootstrapped means. By repeating this procedure 1000 times we created a distribution of means from bootstrapped data. From these distributions, we derived confidence intervals around the observed means, where two means falling outside each other’s confidence intervals represents a significant change in performance. This analysis yielded the same significant changes over time as the permutation method.

Curve fitting and critical distance calculations followed previously described
analyses (Scolari et al., 2007; Yeshurun and Rashal, 2010). Proportion correct data were modeled using a function with the following equation: \( pc = a(1 - e^{-s(d-i)}) \), \( d > i \), where \( pc \) is proportion correct, \( a \) is the asymptote, \( s \) is the scaling factor, \( d \) is the target-flanker separation, and \( i \) is the x-intercept. We repeated this procedure for each set of bootstrapped data (see above) to derive the confidence intervals. Critical distance, \( c \), was calculated by: \( c = i - \ln(0.1)/s \).

We quantified oculomotor precision by fitting an ellipse to saccade endpoints using custom code in MATLAB. We first found the x-y coordinate of the center of all saccade endpoints, then, unconstrained, found the points in 2D space that created the center-to-edge distances of an ellipse comprising 95% of all points. The axes of the ellipse were calculated by finding the two most extreme pairs of x-y coordinates on the circumference of the ellipse in horizontal and vertical space.

**Eye trace filtering.** Trials were excluded if: 1) fixation drifted more than 2° in any direction from the fixation spot; 2) a saccade greater than 2° in amplitude was executed on a no-saccade trial; 3) probe onset occurred earlier than 150 ms or later than 24 ms prior to a saccade (with the exception of the analysis presented in Fig. 5, see text); 4) the target was presented during an eye-blink; 5) a saccade endpoint was greater than 2° from the target in Experiment 1, or 4° in Experiment 2. In total, 1373 trials (76%) were included in Experiment 1, and 15353 trials (79%) were included in Experiment 2.

**Results**

**Experiment 1.** We first compared discrimination accuracy for a crowded target to which observers made a saccade to discrimination accuracy for the same target when observers instead maintained fixation centrally. The orientation of the target Gabor was adjusted for each observer using a staircase procedure (Watson and Pelli, 1983) to yield 75% correct responses for targets presented in isolation (i.e., unflanked) when no saccade was planned (see Methods). As expected, when no saccade was planned the flanking stimuli impaired orientation judgments for the target Gabor, such that observers’ discrimination accuracy fell significantly to 60% ± 2% (mean ± s.e.m.; two-tailed single sample t-test against 75%: \( t(4) = 5.93, P = 0.004 \); Fig. 2A).
When observers prepared a saccade to the crowded target, orientation judgments improved markedly in the interval between the signal to saccade to the crowded target and the initiation of the saccade (Fig. 2A). When the target and flankers appeared during the 50 ms immediately prior to saccade onset, orientation judgments were just as accurate as when the target was presented alone (unflanked) with no planned saccade. During this same 50 ms epoch prior to saccade onset, orientation judgments were also significantly improved compared to the no-saccade condition, as shown in Figure 2B. The horizontal red line in the graph indicates performance without flanking Gabors.

Figure 2. Influence of saccade preparation on visual crowding. (A) Mean percentage correct orientation judgments for a crowded Gabor target during central fixation (black symbol) and at 50 ms intervals prior to saccade execution (colored symbols). The horizontal red line indicates performance without flanking Gabors. (B) Frequency distributions of trials as a function of target-saccade onset asynchrony. Target onset was timed to yield an approximately equal number of observations across three epochs (colored frequency distributions), and trials were screened and divided into 50 ms time bins (individual points). Only trials in which the target-saccade latency was greater than 24 ms were included (i.e., included trials were exclusively those in which the target disappeared before the eyes moved). (C) Graph showing mean gaze deviation from screen center during target presentation. Overlapping symbols show that observers maintained fixation close to the screen center in both no-saccade (black symbol) and saccade (colored symbols) trials. (D) Mean saccade endpoints corresponded to each of the three jittered target locations (see Methods). Observers executed eye movements towards the crowded targets with high accuracy, but saccadic errors were generally radially dispersed. Error bars in all panels represent 1 s.e.m. n = 5.
more accurate than in no-saccade trials [two-tailed paired samples t-test, t (4) = 4.29, P = 0.013]. We screened data from the saccade condition to include only those trials in which the target was offset before the eyes moved (Fig. 2B). Thus, throughout the pre-saccadic interval, target and flanker stimuli always appeared at exactly the same retinal locations as in the no-saccade trials (Fig. 2C). As shown in Figure 2D, saccades were accurate despite the presence of flanking elements, and saccade endpoints were radially dispersed. The proportion of trials excluded due to saccade error was 5.2%, 5.0% and 5.3% for the 0 – 49 ms, 50 – 99 ms, and 100 – 149 ms pre-saccade conditions, respectively. These values were statistically indistinguishable (pairwise comparisons, all P’s > 0.69, uncorrected), ruling out the possibility that improved performance in the final time bin was artificially inflated by our saccade accuracy exclusion criterion.

To summarize the results of Experiment 1, immediately prior to a saccade, orientation discrimination accuracy is significantly improved for a crowded stimulus that is the target of an impending saccade. This release from crowding prior to a saccade yielded target judgments that were just as accurate as those made for unflanked targets at the same peripheral location in the no-saccade condition.

**Experiment 2.** Having established that visual crowding is significantly reduced when a peripheral stimulus is the target of a saccade, we next tested whether the critical distance of crowding around a target is also reduced just prior to an eye movement. A reduction in critical distance would suggest eye movement signals interact with the compulsory averaging of visual features (Pelli, 2008; Pelli and Tillman, 2008), effectively enhancing object discrimination in peripheral vision at the goal of the intended saccade. There are conflicting reports as to whether advance information reduces the critical distance of crowding in the absence of eye movements, despite improvements in target identification accuracy (Felisberti et al., 2005; Strasburger, 2005; Scolari et al., 2007; Yeshurun and Rashal, 2010). In a second experiment, therefore, we tested orientation discrimination for a peripheral target located at 7° eccentricity, and surrounded by non-target stimuli across a range of target-flanker separations. As in Experiment 1, observers either made a saccade to the target, or remained fixated at the center of the display.

Figure 3 shows the accuracy of target orientation judgments as a function of the time to saccade onset, plotted separately for each target-flanker separation. As expected, orientation judgments became progressively more accurate with increases in target-flanker
separation (Bouma, 1970). When target and flankers were separated by less than 1°, 1.5° or 2°, accuracy peaked in the final 50 ms prior to the saccade (blue, purple and green plots, respectively). By contrast, accuracy remained unchanged at target-flanker separations of 3.5° and 5° (orange and red plots, respectively).

To quantify these changes in target identification accuracy across time, we used a permutation analysis to simulate expected performance under the null hypothesis of no change in accuracy across time (Rolfs et al., 2011) (see Methods). In each plot in Figure 3, the dark lines show chance performance across time at each target-flanker separation, and the shaded regions the 95% confidence intervals around these simulated means. Points falling beyond the shaded regions indicate significant changes in accuracy. Improved performance just prior to a saccade was significant when target and flankers were separated by 2°, and fell just short of being significant when target and flankers were separated by 1° or 1.5°. We verified these analyses using conventional bootstrapping methods to estimate confidence intervals (Efron and Tibshirani, 1993) (see Methods), which yielded the same significant changes over time as described for the permutation tests. Taken together, the results reveal that pre-saccadic perceptual benefits for the 7° target were not equal across all flanker separations, but were limited to the smallest separations, with marked improvement when flankers were separated from the target by 2°.
Figure 3. Pre-saccadic changes in accuracy of orientation judgements as a function of saccade-onset latency, displayed individually for a range of target-flanker separations. The dark horizontal line in each plot shows expected null performance for each target-flanker separation, based on permutations of actual data (see Results and Methods). Shading represents 95% confidence intervals, where observed data falling beyond this area are significant changes in performance across time. n = 5 observers.

To estimate the critical distance of crowding we computed exponential fits to the accuracy data across target-flanker separations, separately for no-saccade trials and for saccade trials in which the target was presented within 50 ms prior to saccade execution (see Methods). Figure 4 shows the resulting functions plotted separately for no-saccade trials (gray) and saccade trials (maroon). By convention (Scolari et al., 2007; Yeshurun and Rashal, 2010) the critical distance of crowding is defined as 90% of the asymptotic value for each function (see Methods). The critical distance for no-saccade trials was estimated at 3.7°. Expressed as a ratio of target eccentricity, this yields a critical distance of 0.53φ, conforming well to Bouma’s law (Bouma, 1970; Pelli and Tillman, 2008). In contrast, critical distance during the final 50 ms prior to a saccade was estimated at 2.0°, or 0.28φ, a 47% decrease in the critical distance observed during fixation.

In absolute terms, the critical distance for saccade trials indicates that flankers interfered with identification when they appeared within 2° of the target stimulus. This critical distance estimate is consistent with the accuracy data presented in Figure 3: while accuracy improved when flankers were 2° from the target, no reliable improvements in orientation judgments were observed when target-flanker separations were less than 2°. The influence of saccade preparation on the critical distance of crowding cannot be attributed to differences in the retinal positions of target and flanker stimuli in saccade versus no-saccade trials. Horizontal and vertical gaze position during target presentation were matched across no-saccade trials and trials in which the target was presented in the final 50 ms prior to the saccade (Fig. 4B).
Figure 4. Change in the critical distance of crowding just prior to a saccade. (A) Critical distance of crowding when no saccade is planned (gray fitted curve and vertical line) and in the final 50 ms prior to a saccade (maroon fitted curve and vertical line). The upper x-axis shows target-flanker separation as a proportion of the target eccentricity, $\phi$. Error bars show 95% confidence intervals of the curves, derived from standard bootstrapping procedures (see Methods) (Efron and Tibshirani, 1993). (B) Horizontal and vertical gaze position during target presentation, shown as separate colored disks for the no-saccade condition (open symbols) and the 0 – 49 ms pre-saccade condition. Colors denote target-flanker separations as in Figure 3. Error bars have been omitted for clarity.

In line with studies showing eye movement centers influence visual processing of uncrowded stimuli (Corbetta et al., 1998; Moore and Armstrong, 2003), we propose that oculomotor programming interacts with early visual processes to alleviate crowding. If the reduction in the critical distance of crowding is due to spatially precise selection of the
target location immediately before a saccade, then there should be a tight relationship between critical distance and the precision of oculomotor selection. To test this hypothesis, we plotted the accuracy of saccade landing points relative to the target position for all observers (Fig. 5A). The red and purple points show mean saccadic deviation from the target center when flankers were separated from the target by 1° or 5°, respectively. These points fell the same distance from target center, revealing that oculomotor accuracy was unaffected by target-flanker separation. Each black spot in Figure 5A represents the endpoint of a saccade included in the critical distance estimates for Experiment 2. We fitted an ellipse that encompassed 95% of all saccade endpoints (see Methods). The horizontal extent of the ellipse corresponds to the radial precision of the saccades and the vertical extent denotes the tangential precision. The axes of the fitted ellipse reveal that saccadic precision is poorer in the radial plane than in the tangential plane, with a radial-to-tangential ratio of 1.6. This asymmetry in saccadic precision corresponds closely to the classical radial-tangential asymmetry of critical distance measured using pairs of flankers arranged either radially or tangentially with respect to the target (Toet and Levi, 1992). Moreover, as shown in Figure 5B, the absolute, edge-to-edge spatial extent of crowding when no saccade was planned (gray line) is roughly twice that observed for trials in the 50 ms just prior to a saccade (maroon line). Note that oculomotor precision (pink line) closely approximates the spatial extent of crowding just prior to a saccade.
Figure 5. Relationship between oculomotor precision and the critical distance of crowding. 
(A) The horizontal and vertical deviations of 8153 saccade endpoints obtained from 5 observers are plotted on the x- and y-axes, respectively. Position 0°, 0° represents the target center, and the target Gabor extended from -0.5° to +0.5° on both axes. Saccades with negative x-values fell short of the saccade target center, and saccades with positive x-values overshot the target center. An ellipse was adjusted to fit 95% of the saccade endpoints. As shown by the ellipse and its axes, saccadic precision was radially biased. The purple and red points show average deviations of saccade endpoints to targets with flankers at distances of 1° and 5°, respectively. There was no difference between these points; the proximity of flankers to the target did not interfere with oculomotor selection. (B) The spatial extent of observers’ oculomotor radial precision closely matches the edge-to-edge spatial extent of crowding within 50 ms prior to a saccade, and both are approximately half the spatial extent of crowding when no saccade is planned.

We further tested the extent to which saccade endpoints are related to identification of a crowded target by comparing performance for trials in which saccades deviated from the target center by more than one degree with those in which the saccade fell within one
degree of the target center. We performed this analysis separately for three conditions that represent the full range of perceptual performance. We chose: (1) the condition in which performance was poorest (100 – 149 ms time bin, 1° target-flanker separation); (2) the condition in which performance improved the most (0 – 49 ms time bin, 2° target-flanker separation); and (3) the condition in which performance was best (0 – 49 ms time bin, 5° target-flanker separation; see Fig. 3). We chose these three conditions to maximize the likelihood of uncovering any effect of saccade accuracy, while limiting the risk of type 1 error due to multiple post-hoc comparisons. There was no difference in target discrimination according to saccade accuracy in any of these conditions (P's > 0.81, uncorrected), and the differences in performance were less than 1.5% within each condition. Thus, performance corresponds best to the overall precision of eye movements (Fig. 5a) rather than the accuracy of saccade endpoints.

Discussion

We have shown that improvements in perception immediately prior to saccade onset, previously demonstrated with isolated stimuli in sparse displays (Remington, 1980; Kowler et al., 1995; Deubel and Schneider, 1996; Moore and Armstrong, 2003; Deubel, 2008; Rolfs and Carrasco, 2012), can also operate to release peripheral targets from visual crowding. By systematically varying target-flanker separations, we also found that the critical distance of crowding established during passive fixation shrinks by roughly half in the 50 ms immediately prior to saccade onset. The changes in crowding we observed during saccade trials relative to no-saccade trials cannot be attributed to differences in the retinal locations of target and flanker stimuli, as the critical visual events were offset prior to any eye movements. Moreover, in both saccade and no-saccade conditions observers always knew the precise location of the upcoming target, indicating that the saccade-related mitigation of crowding cannot be ascribed to differences in advance positional information.

The fact that crowding of a target at a fixed retinal eccentricity is significantly attenuated prior to a saccade implies that extra-retinal signals that arise just before the eyes move (Wurtz, 2008) play a key role in modifying the spatial extent of visual crowding, and extend a recent computational modeling report linking crowding and eye movements (Nandy and Tjan, 2012). Enhancement in perceived contrast at the saccade goal (e.g., Rolfs and Carrasco, 2012) might have contributed to the improved discriminability of the
crowded targets in our experiments, but our finding that performance improvements varied across target-flanker separations (Fig. 3) suggests that changes in perceived contrast alone cannot account for the results. The change in critical distance just before a saccade (Fig. 4A) reflects the fact that target identification improved most for the smallest target-flanker separations, but did not change for the larger separations. If the pre-saccadic benefit we have shown were attributable solely to contrast enhancement of the target, this effect should have been equivalent across all target-flanker separations. Moreover, attempts to mitigate crowding by cueing attention to the target, which has also been linked to increased contrast sensitivity (Carrasco et al., 2000), have not always yielded reliable reductions in visual crowding (Felisberti et al., 2005; Strasburger, 2005; Scolari et al., 2007; Yeshurun and Rashal, 2010).

Changes in the spatial extent of crowding prior to a saccade suggest that oculomotor signals required for accurate localization of a saccade target can influence responses of visual neurons involved in integrating form information from the peripheral visual field. Such an influence is consistent with evidence for a close functional relationship between oculomotor and visual sensory areas in the primate brain (Wurtz and Mohler, 1976; Umeno and Goldberg, 1997; Moore et al., 1998; Tolias et al., 2001; Moore and Armstrong, 2003; Moore and Fallah, 2004; Gregoriou et al., 2012). In particular, Tolias et al. (2001) found that just prior to a saccade there is a reduction in the size of the receptive fields of neurons throughout V4, an area thought to be important in crowding (Anderson et al., 2012), as well as a shift of these receptive fields toward the saccade goal. Such a reduction in the size of receptive fields of V4 neurons could result in a corresponding reduction in the critical distance of crowding. Indeed, the mean reduction in receptive field size reported by Tolias et al. (2001) was $2.1^\circ$, similar to the $1.7^\circ$ reduction in critical distance we observed just prior to a saccade (Fig. 4A). Critically, the changes in receptive field sizes observed by Tolias et al. were greatest in the final 50 ms prior to saccade onset, consistent with our findings in human observers.

The observation that crowding is reduced prior to a saccade is consistent with recent accounts that suggest that crowding arises from imprecise position information for peripheral stimuli. Greenwood, Bex, and Dakin (Greenwood et al., 2009) found that the perceived position of target elements can be accounted for by a weighted average of noisy representations of target- and flanker-feature positions. Following from this finding, our results can be explained by assuming that operations involved in preparing and executing an eye movement to a crowded target effectively change the weights of target- and
flanker-position noise. For example, weightings for flanker stimuli might be reduced just prior to oculomotor target selection, via suppression of neural activity in FEF associated with distractor stimuli (Schall et al., 1995). In line with this, saccadic accuracy in Experiment 2 was unaffected by the separation between target and flanking stimuli (Fig. 5A). Alternatively, an impending saccade to a crowded target could simply reduce the position noise of the target via a reduction in the size of the receptive fields of V4 neurons that represent the target (Tolias et al., 2001). Performance for crowded targets is well modeled using values for position and identity uncertainty of unflanked targets (van den Berg et al., 2012), suggesting that sharpening of target position estimates could form the basis for reduced crowding prior to saccades.

Previous studies have linked perceptual enhancements during saccade and non-saccade conditions to common neural activity in such areas as FEF and posterior parietal cortex, both of which are known to play an active role in saccade generation (Corbetta and Shulman, 2002). Indeed, changes in the gain of V4 neurons occur even when FEF activity is below that required to trigger a saccade (Moore and Armstrong, 2003; Moore and Fallah, 2004). In line with these accounts, both the elliptical shape and radial-tangential asymmetry of saccadic precision we observed in Experiment 2 (see Fig. 5) correspond to the classic spatial characteristics of crowding zones measured previously (Toet and Levi, 1992). These observations suggest a functional interaction between oculomotor control systems and visual neurons whose responses are susceptible to crowding in the absence of eye movements. Crucially, our data also reveal that the substantial gains in target discriminability and reductions in critical distance for saccade targets arise exclusively in the last 50 milliseconds prior to a saccade, consistent with recent psychophysical reports for uncrowded stimuli (Deubel, 2008; Rolfs et al., 2011; Rolfs and Carrasco, 2012). The time course of these perceptual changes raises the possibility that, in addition to the benefits associated with target selection alone, visual centers involved in oculomotor preparation and execution can modulate visual sensitivity during the immediate pre-saccadic period (but see Gregoriou et al., 2012).

An interesting finding in Experiment 2 was that the spatial extent of crowding observed just prior to a saccade corresponded closely with the overall precision of saccades (Fig. 5). Yet, observers’ ability to identify the target did not vary according to the accuracy of saccade endpoints. This finding suggests that changes in crowding during saccade preparation do not simply depend on the specific outcome of the saccade motor command. In our experiment, pre-saccadic changes in the identification of a target at 7° in
peripheral vision were relatively uniform when saccades landed within 2° of the target. These data show that the benefits from saccade preparation accrue to a region around the intended endpoint and are not determined by the precision of the executed saccade.

In summary, the current findings are consistent with the idea that oculomotor signals associated with intended eye movements can alter the resolution of object identification within a spatial zone immediately surrounding a peripheral saccade target. This hypothesized link between oculomotor control and visual perception is further supported by the finding that the distribution of saccade errors closely matches the characteristic, radially-biased spatial region within which crowding occurs. By using oculomotor signals to release saccade targets from crowding, the visual system may effectively “pre-sample” an object that will soon be foveated for detailed processing. Such a preview of the saccade target may help to explain the subjective experience of visual continuity across eye movements in natural environments where peripheral vision is densely cluttered.
References


Chapter 3 - Visual crowding is anisotropic along the horizontal meridian during smooth pursuit
Chapter 3 - Visual crowding is anisotropic along the horizontal meridian during smooth pursuit

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Abstract

An object in peripheral vision is increasingly difficult to recognize when the distance between it and flanking stimuli decreases (1). Such visual crowding has been widely investigated, but rarely in the context of voluntary eye movements (2–4). We recently showed that the area within which crowding occurs is greatly reduced during preparation of a saccadic eye movement, revealing a contribution of the oculomotor system to crowding (Harrison, Mattingley, Remington, Under Review). Here, we tested whether the involvement of the oculomotor system in crowding was unique to saccades, or whether crowding is also modified during voluntary smooth pursuit. Approximately 3° from the fovea, we found that crowding was anisotropic according to the direction of pursuit. Relative to when no eye movement was made, the spatial extent of crowding increased for objects located contraversive to the direction of smooth pursuit. By contrast, crowding for objects locatedipsiversive to the direction of pursuit remained unchanged. This anisotropy in crowding was independent of retinal motion (5), the perceived position of the crowded stimuli (6-8), and asymmetry in the distribution of visual attention during pursuit (9-11); nor was there a change crowding during pursuit for objects located approximately 7° from the fovea. Thus, the spatial extent of crowding depends on the direction of smooth pursuit and the distance of the crowded object from the pursuit target. The increase in the size of crowding zones trailing the fovea may compensate for the systematic lag of the fovea behind the pursuit target during smooth eye movements (12).
Introduction

Our ability to recognize an object in peripheral vision is largely determined by the spacing between it and any surrounding objects (1). As shown in Figure 1, for example, while fixating the black spot it is more difficult to identify the central letter in the blue display than the central letter in the purple display, despite both letters having the same retinal eccentricity. The loss of discriminability of objects in visual clutter is known as crowding. Crowding is thought to occur because visual features of nearby objects are integrated in early visual cortex (13), or because the resolution of visual attention is too coarse to resolve crowded objects (14). However, crowding has been studied almost exclusively under conditions in which fixation is maintained, leaving open the possibility that eye movement signals contribute to form integration in peripheral vision. Indeed, we recently found that, during saccadic eye movement preparation, the area around an object in which other objects cause crowding is almost halved (Harrison, Mattingley & Remington, Under Review). In that study, we proposed a new account of crowding: Oculomotor brain areas play a role in determining the spatial extent of crowding. This proposal raises the question of whether any movement of the eye attenuates crowding, or whether different classes of eye movements affect crowding in distinct ways. In the present study, we tested whether visual crowding is modified during smooth pursuit eye movements.

**Figure 1.** Demonstration of visual crowding. The reader can experience the deleterious effect of crowding by fixating the black spot and trying to identify the central letter in the blue configuration and the central letter in the purple configuration. Whereas the purple T should readily be identified, the blue T is not easily identified. Because the blue and purple Ts are the same distance from the fixation spot, the difficulty in recognizing the blue T cannot be attributed to its eccentricity alone, but must arise instead from interactions with the surrounding letters.

Extra-retinal signals generated during smooth pursuit eye movements are known to cause perceptual phenomena such as increased sensitivity to color (15), suppression of motion streaks (16-18), and distortions of space (e.g. 6), but how they interact with form integration in peripheral vision is yet to be determined. The few studies that have
investigated recognition of uncrowded objects during smooth pursuit suggest object perception is poorer during pursuit than during steady fixation (for a review, see 19). In one such study, Khurana and Kowler (20) tested whether perceptual processing and pursuit eye movements share a common selective mechanism. In their experiments, observers pursued a string of letters that translated across a display, and reported the identity of a letter probe presented in the pursued string of letters or a second letter string elsewhere on the display. They found that observers' ability to discriminate the probe presented in the non-pursued stimulus was far poorer than the pursued stimulus regardless of whether both letter strings had the same or different velocities. They concluded that smooth pursuit eye movements and perception share a common selective mechanism such that selecting an object for pursuit reduces discriminability of unselected objects in peripheral vision. Following a similar line of investigation, Lovejoy, Fowler, and Krauzlis (21) had observers foveate and pursue the center of a moving array of digits that spanned the horizontal visual meridian. Observers had to identify which of two probe digits was briefly presented at a random position within the array. Although discrimination accuracy was high when probes were presented within approximately 1° of the foveated region, accuracy was at chance for probe locations beyond this area. The relatively poor recognition of objects in peripheral vision found in both studies suggests that pursuit eye movements degrade object identification in peripheral vision. These results may further suggest that smooth pursuit exacerbates crowding, the opposite of the modification of crowding resulting from saccadic eye movements (Harrison, Mattingley, & Remington, Under Review).

In the present study, we tested how smooth pursuit eye movements affect the spatial area over which distractors will cause crowding of a probe object. An observer’s ability to identify an object is degraded when the distance between the object and any flanking elements is less than the “critical spacing” of crowding (2). Thus, critical spacing quantifies the spatial extent of crowding (13). Critical spacing scales linearly with an object's retinal eccentricity such that it is greater for more eccentric targets (1). When expressed as a proportion of target eccentricity, $\phi$, critical spacing is approximately invariant throughout the visual field (3) ranging from approximately $0.1 \phi$ – $0.5 \phi$ across observers (22).

However, along the vertical meridian, crowding is anisotropic, such that the spatial extent is greater for objects in the upper visual field than lower visual field (14). The results of the
present study reveal a similar anisotropy of the size of crowding zones along the horizontal meridian that is dependent on the direction of smooth pursuit eye movements. We found that the spatial extent of crowding is greater for objects located contraversive to the direction of pursuit than for objects located ipsiversive to the direction of the pursuit, but only for objects within approximately 3° of the fovea.

Results and Discussion

We compared the spatial extent of crowding during smooth pursuit with the spatial extent of crowding when no eye movement was made. Because object recognition during pursuit may be altered differentially according to the position of the object relative to the direction of pursuit (21), we further compared the spatial extent of crowding on the side of the fovea ipsiversive to the direction of the eye movement, with the extent of crowding on the side of the fovea contraversive to the direction of the eye movement. During smooth pursuit trials, observers were required to pursue a spot that translated across the display at 10°/sec, and report the orientation of a probe letter “T” presented briefly in peripheral vision and oriented in one of the four cardinal directions (north, south, east, west). We systematically varied the spacing between the probe and flanking distractors, and measured observers’ ability to discriminate the probe as a function of probe-flanker spacing. To reduce noise associated with confusability between probes and flankers (24), distractor letters were drawn from a set of letters that excluded the probe letter (see Materials and Methods). To mitigate retinal motion of the probe and flankers during pursuit, which may exacerbate crowding (5), all stimuli translated across the display at the same speed as the pursuit target. Thus, for a hypothetical trial in which an observer’s eye velocity matched the velocity of the pursuit target, there would be no retinal motion of probe and flankers. For no eye movement trials, observers performed the same orientation discrimination task, but all stimuli remained stationary in the display.

In a first experiment, we measured the spatial extent of crowding when the screen distance between the pursuit target and probe letter was 7° of visual angle. However, because the fovea typically trails the pursuit target (e.g. 12, 21, 25, 26), we used observers’ eye position during probe presentation to calculate the actual retinal eccentricity of the probe, $\phi$, and quantified each tested probe-flanker spacing as a
proportion of $\phi$ (13). Because the direction of smooth pursuit was held constant within testing blocks (see Materials and Methods), no eye movement and pursuit trials were divided according to whether the probe letter appeared contraversive or ipsiversive to the direction of pursuit for that block. By classifying no eye movement trials in this way, we were able to analyze directional differences in crowding during pursuit while controlling for directional biases in crowding in the absence of eye movements (27). Moreover, we could control for changes in crowding during no eye movement trials due to observers distributing visual attention differentially based on the anticipation of the pursuit target shifting on the screen (11).

Figure 2A shows observers’ orientation discrimination accuracy as a function of probe-flanker spacing. As expected (1), the proportion of correct orientation discriminations increased with larger probe-flanker distances, and this was true for both the no eye movement and pursuit conditions. We calculated critical spacing by modeling performance for each condition with a two-parameter log function. For each function, we took critical spacing to be the probe-flanker spacing at which performance reached 0.625 proportion correct (midway between chance and perfect performance (27, 28); see Materials and Methods). Critical spacing values are shown as vertical lines in Figure 2A and are described in detail below.
Visual crowding is anisotropic along the horizontal meridian during smooth pursuit.

Figure 2. Orientation discrimination accuracy as a function of probe-flanker spacing for two experiments.

A) Orientation discrimination accuracy for probes 7° from the pursuit target. Filled symbols show proportion correct for no eye movement conditions, and open symbols show proportion correct for pursuit conditions. Blue and purple represent contraversive and ipsiversive probe presentations, respectively. The probe-flanker spacing corresponding to 0.625 proportion correct represents the spatial extent of crowding. Critical spacing for each condition is shown as a vertical line. B) Orientation discrimination accuracy for probes 3° from the pursuit target. Figure conventions are as described for (A).

To determine whether smooth pursuit modified critical spacing for objects 7° from the pursuit target, we performed a resampling analysis to simulate distributions of critical spacing for each condition and for each observer (see Materials and Methods) (29). Results from this analysis are shown in Figure 3A, with no eye movement data shown as solid distributions and pursuit data as dotted distributions. Data are presented as though the direction of pursuit is rightwards, such that crowding contraversive to the direction of pursuit is plotted leftwards (blue), and ipsiversive crowding is plotted rightwards (purple). Across observers there were no reliable changes in crowding during pursuit relative to when no eye movements were made.
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Figure 3. Critical spacing of crowding during smooth pursuit and in the absence of eye movements.
The graphs show resampled distributions of critical distance for no eye movement (solid distributions) and pursuit (dotted distributions) conditions for each observer and the group. Data are shown according to the probe position relative to the direction of pursuit, with contraversive critical spacing shown in blue on the left axis, and ipsiversive critical spacing shown in purple on the right axis. Shaded background regions show differences between the observed critical spacing for no eye movement and pursuit conditions derived from the log functions described above (vertical lines in Figure 2A). A) Results from Experiment 1 in which the probe was 7° from the fixation point. B) Results from Experiment 2 in which the probe was 3° from the fixation point.

We next compared the difference in critical spacing according to the position of the probe object relative to smooth pursuit direction. Using the values derived from the log functions plotted in Figure 2A, we computed difference scores for contraversive minus ipsiversive critical spacing after controlling for directional differences in the no eye movement condition. This analysis was also performed on the slope parameter of the log function (see Materials and Methods), which indicates the precision of responses. These values, critical spacing, and precision, are plotted against each other in Figure 4A. A difference
from zero on the x- or y-axis represents a contraversive-ipsiversive difference in either critical spacing or precision, respectively. In the top panel, data for each observer are superimposed over data from the resampling analysis described above. Horizontal and vertical error bars show the 95% confidence intervals for each observer’s critical distance and precision difference scores, respectively. For all observers, there was no change in critical distance or precision according to the position of the probe relative to pursuit. The absence of any difference according to probe position is reflected in the distribution of the group data, which cluster around 0,0 (red cloud in lower panel of Figure 4A). These data show that the extent of crowding during smooth pursuit is symmetrical contraversive and ipsiversive to the direction of pursuit for objects at 7° from the pursuit target.

We repeated the probe discrimination task with the same observers in a second experiment, but reduced the distance between the pursuit target and the letter probe to 3° of visual angle. Accuracy data as a function of probe-flanker spacing are shown in Figure 2B, and are presented as in the first experiment. We again calculated probe-flanker spacing according to the actual retinal eccentricity of the probe, \( \phi \). Consistent with the first experiment and with previous studies (25, 26, 30), the fovea systematically trailed the pursuit target during smooth pursuit and thus each probe-flanker separation was greater for contraversive (blue) than ipsiversive (purple) trials. Therefore, the observers' fovea was closer to contraversive probes than to ipsiversive probes.

Reducing the retinal eccentricity of the probe while holding the physical probe-flanker spacing constant reliably improves performance (e.g. 1, 5, 9, 22, 27, 31). However, as shown in Figure 2B, orientation discrimination at a given probe-flanker spacing was actually worse for contraversive than for ipsiversive probes for all observers, despite contraversive probes being closer to the fovea. As shown in Figure 2B, for pursuit trials critical spacing for contraversive probes was greater than for ipsiversive probes for all observers.

Figure 3B shows the results from the resampling analysis of critical spacing when the probe was 3° from the pursuit target. A very clear pattern of results is apparent: for all observers, critical spacing contraversive to the direction of eye movement was greater for
pursuit trials than for no eye movement trials; by contrast, critical spacing ipsiversive to the direction of pursuit did not change relative to no eye movement trials. Figure 4B shows the difference in critical spacing for contraversive and ipsiversive crowding during pursuit, after controlling for directional differences in the absence of eye movements. Changes in critical spacing are plotted against changes in precision for each observer in the top panel. All observers had a positive critical spacing difference score, indicating there was an increase in critical spacing for objects presented contraversive to pursuit relative to objects presented ipsiversive to pursuit. This larger critical spacing for contraversive crowding than ipsiversive crowding was highly significant for observers KS (P < 0.001) and WH (P < 0.0001), and marginally significant for JR (P = 0.061).

The bottom panel of Figure 4B shows results for the group, where the expansion of crowding for probes positioned contraversive to the direction of smooth pursuit was highly significant (P < 0.0001). As shown by the negative precision difference score, precision was also worse for contraversive probe discriminations compared with ipsiversive probe discriminations. This difference was marginally significant (P = 0.054), but as shown in the top panel of Figure 4B, was driven by the variability in precision estimates for observer KS. In summary, when probes were 3° from the pursuit target, the spatial extent of crowding increased only for probes contraversive to the direction of smooth pursuit.
Figure 4. Critical spacing for contraversive versus ipsiversive probes. The contraversive-ipsiversive difference in critical spacing is plotted against the contraversive-ipsiversive difference in precision of responses for individual observers (top panels) and the group (bottom panels). Both measures are calculated for pursuit after controlling for contraversive-ipsiversive differences in the absence of eye movements. A difference from zero represents a change in critical spacing or precision according to probe position relative to pursuit direction. Clouds of colored points show bootstrapped distributions. Error bars in the top panels show 95% confidence intervals. Distributions plotted along the axes in the bottom panels show bootstrapped distributions for the group. A) Results from Experiment 1 in which the probe was 7° from the fixation point. B) Results from Experiment 2 in which the probe was 3° from the fixation point. Symbols in (B) are as presented in (A).
Because retinal motion affects crowding (5), we tested whether differences in retinal motion across conditions may have contributed to the asymmetry of crowding during pursuit, as shown in Figure 3B. Probes and flankers translated across the screen at the same speed and in the same direction as the pursuit target, and so retinal motion could arise only from differences between the velocity of the stimuli and the velocity of observers’ eye movements. We therefore calculated pursuit gain (eye velocity as a proportion of stimulus velocity) separately for contraversive and ipsiversive pursuit trials, and according to whether observers correctly discriminated the orientation of the probe or made an error. Gain was calculated for a period of 100 ms leading up to probe onset. The brief duration of the probe and flankers (47 ms) ensured that there was no perturbation of pursuit gain in response to the stimulus presentation during probe presentation (32, 33).

Figure 5 shows the gain results as stacked density plots and box-and-whisker plots. As expected (12), median gain (box plot bands) was just less than 1 for all observers and all conditions. Thus, smooth pursuit velocity was consistently just below the velocity of the pursuit target for all conditions. Importantly, there were no differences in gain across any conditions, indicating that retinal motion of stimuli was equivalent across contraversive and ipsiversive probe presentations, and thus that discrimination accuracy was independent of retinal motion.
Figure 5. Pursuit gain for each observer in Experiment 2. Stacked density plots show pursuit gain at the time of probe onset as a function of probe direction and accuracy. There were no differences in the gain of eye movements across conditions. Box-and-whisker plots summarize the data, where the length of each box shows the interquartile range, the box band shows the median, the length of the whiskers shows the range, and the whisker cross-hatches show 95% of the range.

The increase in critical spacing contraversive to the direction of pursuit might imply that contraversive probes were systematically misperceived as appearing further from the pursuit target than ipsiversive probes. Indeed, it is known that briefly flashed stimuli can be mislocalized during pursuit (6, 34-38). Crowding is tuned to perceived rather than physical location (7, 8), so shifts in perceived position during pursuit trials may have affected our estimates of crowding. On the other hand, mislocalizations during pursuit shift perceived position in the direction of pursuit and occur for stimuli presented both contraversive and ipsiversive to the direction of the eye movement (e.g. 6). It is unclear, therefore, why mislocalizations might uniquely affect crowding contraversive to the eye movement. Nonetheless, to rule out the possibility that critical spacing differences were due to contraversive probes being perceived as more distant from the pursuit target than ipsiversive probes, a control experiment was conducted in which we tested for asymmetries in the perceived position of the crowded probe. While observers tracked the
pursuit target, probe and flanker stimuli were presented contraversive and ipsiversive to pursuit direction simultaneously. The ipsiversive probe was at a fixed distance of 3° from the pursuit target. By contrast, the distance of the contraversive probe was varied pseudorandomly in steps of 0.25° from trial to trial. Observers reported whether the contraversive probe and flanker stimuli were closer to or further from the pursuit target than the ipsiversive stimuli.

Figure 6 shows the proportion of trials in which contraversive stimuli were reported as being further from the pursuit target than the ipsiversive stimuli, plotted as a function of physical difference. We fitted cumulative Gaussian functions to these data to derive the physical offset at which the contraversive stimuli were judged to be of equal distance from the pursuit target as the ipsiversive stimuli (point of subjective equivalence; PSE). The PSEs for observers KS and WH were -0.019° and -0.017°, respectively (see dashed lines in Figure 6), indicating that contraversive stimuli were indeed perceived as being further away from the pursuit target than ipsiversive stimuli. However, such small shifts in PSE are negligible and an order of magnitude below our conservative estimates of the minimum PSE required to nullify the critical distance differences for each observer (-0.53° for KS, and -0.27° for WH; see Materials and Methods).

Figure 6. Position judgments of stimuli presented during pursuit. Cumulative Gaussian fits of the proportion of times stimuli contraversive to pursuit were reported as appearing further from the pursuit target than ipsiversive stimuli, plotted as a function of physical offset. Positive values on the x-axis (plotted leftward, in purple) indicate that the contraversive stimuli were physically further from the pursuit target than ipsiversive stimuli. Dashed lines indicate the physical offset at which observers perceived contraversive and ipsiversive stimuli as equidistant from the pursuit target.
To summarize, results from the control experiment indicate that differences in the perceived position of contraversive and ipsiversive stimuli cannot account for the asymmetrical changes in crowding observed during pursuit.

We conducted a second control experiment in which we tested whether the asymmetry of crowding during pursuit is due to directional differences in visual attention during smooth eye movements. Directing visual attention away from a crowded probe can increase critical spacing (11). Previous studies of smooth pursuit have suggested that visual attention is directed ahead of the pursuit target (21, 39-41). In our experiments, there were no explicit task-constraints on observers’ visual attention and the probe appeared to the left or right of the pursuit target with equal probability (see Materials and Methods). The increase in critical spacing for probes positioned contraversive to the direction of pursuit might therefore be due to observers directing attention away from contraversive probes. To test this possibility, we again measured observers’ ability to discriminate the orientation of crowded probes contraversive and ipsiversive to the direction of pursuit, but made the probe position 100% predictable by holding it constant within each testing block. By making the probe location entirely predictable, we reasoned that observers would be free to allocate their attention covertly to just one side of the pursuit target in anticipation of the probe and flanker stimuli appearing there on every trial within each block (42).

Probe discrimination accuracy was tested at the probe-flanker spacing corresponding to each observer’s critical spacing for crowding contraversive to pursuit direction (see Materials and Methods). This probe-flanker spacing should be sensitive to manipulations of visual attention (11). Moreover, by using the contraversive critical spacing for both contraversive and ipsiversive probe presentations, we were able to use the model fits shown in Figure 2B to derive clear predictions about expected performance. If knowledge of the probe location has no effect on probe discrimination, performance for ipsiversive and contraversive probes should be equivalent to that found in Experiment 2. Specifically, if voluntary shifts of attention play no role then performance should correspond to the values on the ipsiversive and contraversive log functions that correspond to the contraversive critical spacing distance when visual attention was unconstrained in Experiment 2. Because we used the contraversive critical spacing distance, predicted
Predicted performance for observers KS and WH is shown on the gray background of Figure 7. Visual crowding again depended on pursuit direction, such that discrimination accuracy for contraversive probes was significantly poorer than accuracy for ipsiversive probes (P’s < 0.0001). This result replicates the findings from Experiment 2. Furthermore, both observers’ performance was statistically indistinguishable from predicted performance under the null hypothesis that voluntary shifts of visual attention have no effect on the directional asymmetry of crowding during pursuit. The lack of an effect of visual attention on probe identification is consistent with a recent study which showed that visual attention is tightly locked on the tracked target during pursuit (21).

![Figure 7](image_url)

**Figure 7.** Testing the contribution of covert attention to the directional asymmetry in crowding by comparing predicted and observed accuracy scores. Blue and purple symbols show contraversive and ipsiversive probe discrimination accuracy, respectively. Data for KS are shown as stars, data for WH are shown as triangles. Each point of observed data represents a minimum of 150 trials for KS and a minimum of 200 trials for WH. Error bars show 95% confidence intervals.

To summarize the findings across all experiments, we found that during smooth pursuit eye movements the spatial extent of crowding is increased selectively for visual probes positioned contraversive to the direction of pursuit, whereas crowding for probes positioned in the ipsiversive direction remained unchanged relative to trials in which no eye movement was made. This anisotropy in the extent of crowding occurred for objects 3° from the pursuit target, but not for objects 7° from the pursuit target. Control experiments revealed that differences in retinal motion, perceived position, and visual...
attention cannot account for the asymmetry. The expansion of the spatial extent of crowding contraversive to pursuit is especially surprising given that the observers' eye position consistently lagged the pursuit target, effectively reducing the retinal eccentricity of contraversive probes. In the absence of eye movements, reducing the eccentricity of a crowded probe results in better identification (1, 3, 22, 27, 43), contrary to what we observed during pursuit trials. Thus, it appears that smooth pursuit eye movement signals alter object recognition in a way that compensates for foveal error during pursuit: visual resolution is degraded for objects close to the fovea but that are unlikely to be the behaviorally relevant stimulus (i.e. the pursuit target). This selective exacerbation of crowding may facilitate perception of the pursuit target, and therefore the pursuit eye movement itself, possibly by reducing the distraction by background objects.

A potentially important aspect of the change in crowding we observed is how it relates to motion streak suppression. Recent studies have shown that there is active suppression of motion-induced streaking during pursuit eye movements (16-18). For example, Bedell and Lott demonstrated that a physically stationary probe presented during smooth pursuit is perceived as less smeared than a probe with the same retinal motion but presented in the absence of eye movements. Interestingly, Tong et al. (18) further showed that streak suppression is greatest when probe position and retinal motion are contraversive to the direction of the eye movement. Although it is unclear how such streak suppression may interact with crowding, streak suppression for probes and flankers contraversive to the direction of pursuit may imply an attenuation of crowding relative to the ipsiversive direction in which streaks are less suppressed (18). Clearly, this is the opposite of what we found. This raises the possibility that it is the selective expansion of the spatial extent of crowding contraversive to the direction of pursuit that nullifies visual streaking. By integrating visual form over a larger area during pursuit than during steady fixation, visual streaks would effectively be masked. This potential relationship between suppression of streaking and visual crowding during pursuit will be an important avenue for future research.

Modification of crowding during pursuit could be achieved via reciprocal connections between oculomotor and visual brain areas. Activity in the frontal eye fields, for example, can modify activity in visual brain areas in response to the presentation of visual objects.
Furthermore, saccade preparation has been shown to alter the receptive field sizes of neurons in V4 (45), and to reduce critical spacing at the goal of an intended saccade (Harrison, Mattingley, Remington, Under Review). Given the saccadic system and smooth pursuit system have a common neural circuitry (46), similar changes may occur during pursuit eye movements. The spatial profile of crowding during saccade preparation is markedly different than that during pursuit, however, so whether a common neural mechanism is involved remains an open question. Regardless of the specific neural circuitry involved, that smooth pursuit alters the spatial extent of crowding according to the direction of the eye movement reveals that the brain areas involved in crowding are dynamically influenced by oculomotor actions.

In conclusion, the current findings suggest that extra-retinal signals involved in the generation of smooth pursuit eye movements modulate the spatial extent of crowding. During smooth pursuit, form information is integrated over a larger area for objects close to the fovea and positioned opposite to the direction of pursuit. This anisotropic change in crowding may be related to streak suppression contraversive to the direction of pursuit, and reflect the operation of processes that help to compensate for the fact that the fovea systematically typically trails the pursuit target.
Materials and Methods

Observers

One author (W.H.) and two experienced psychophysical observers (K.S. and J.R.) participated in the experiments. Observers K.S. and J.R. were naïve to the purpose of all experiments. All observers had normal or corrected-to-normal vision and gave informed consent. The University of Queensland’s School of Psychology Ethical Review Committee approved the study.

Setup

Observers sat 57 cm from a 17-inch Samsung CRT monitor (1280 x 1024 pixels, 85 Hz) with their head in a head and chin rest. Experiments were programmed using the Psychophysics Toolbox Version 3 (47, 48) and Eyelink ToolBox (49) in MATLAB (MathWorks). Eye movements were recorded at 500Hz with an EyeLink 1000 (SR Research), calibrated using a 9-point calibration procedure every 40 trials or as otherwise required (see below).

Stimuli and procedure

Each trial began with the onset of a blue fixation spot (0.2° in diameter) in the center of the display for no eye movement trials. For pursuit trials, the spot appeared 10° to the left or right of the center of the display for rightward and leftward pursuit trials, respectively. In order for the trial to continue, observers were required to maintain their gaze within a 2° x 2° region of the fixation spot for 500 ms or else the eye tracker would be recalibrated and the trial would restart. Following the 500 ms fixation interval on pursuit trials, the spot immediately began translating horizontally across the screen at 10° per second. After a normally distributed time interval ($\mu = 1000$ ms, $\sigma = 250$ ms), the probe and flankers were presented for 47 ms. Probe and flanker stimuli were Sloan letters with widths and heights adjusted to appear within a 0.5° x 0.5° region, and, for Experiments 1 and 2, could appear to the left or right of the fixation point with equal probability. On each trial, flankers were randomly drawn without replacement from a set of 16 letters (A, B, D, E, F, H, I, J, L, K, M, N, P, R, S, and V). Flanker contrast was set to 50% in all experiments. Based on pilot data, probe contrast was set to 50% for Experiment 1 for all observers, and 5% for
W.H. and 10% for K.S. and J.R. for Experiment 2 and control experiments. Following the offset of the probe and flankers, observers pressed the up, down, right, or left arrow key of a standard keyboard to indicate that the probe was oriented north, south, east, or west, respectively. No feedback was given. Blocks of pursuit and no eye movement trials each consisted of 72 trials (2 probe positions relative to fixation spot x 4 probe orientations x 9 probe-flanker separations). Within a testing session there were three blocks each of no eye movement trials and pursuit trials in which the direction of pursuit was held constant. Each no eye movement block followed a pursuit block. Thus, each testing session for the main experiments consisted of 432 trials (216 no eye movement trials and 216 pursuit trials) and took approximately 30 minutes to complete. W.H. completed 8 testing sessions for Experiments 1 and 2 (3456 trials per experiment). K.S. and J.R. each completed 4 testing sessions for Experiment 1 (1728 trials) and 8 testing sessions for Experiment 2 (3456 trials).

**Eye movement analyses**

Trials were discarded if the observer blinked or if the observer's gaze deviated by more than 2° from the fixation spot during probe presentation. Pursuit gain was computed offline by calculating the change in gaze position over a 100 ms interval immediately prior to probe onset, and dividing the result by the distance the pursuit target travelled in the same interval (1°). To ensure the number of observations per observer was sufficient for the bootstrapping analyses, all trials were initially included regardless of pursuit gain and regardless of whether a saccade was executed during a trial. We repeated the analyses from the main experiments using a strict pursuit gain criterion of 0.7 < pursuit gain < 1.3, which would detect all but small saccades, and the results were unchanged.

Figure 8 shows example data of probe timing relative to gaze deviation from the center of the screen for no-eye movement trials (left panel) and pursuit trials (right panel). Probes were timed such that probe onset occurred after the open-loop component of the pursuit eye movement (> ~100 ms). The normal distribution of probe onset timing (see Stimuli and Procedure section, above) meant that temporal uncertainty was matched across no eye movement and pursuit trials. However, this necessarily meant that gaze position varied across no-eye movement and pursuit trials, as well as across eye movement directions.
Therefore, we timed probe onset such that the probe appeared, on average, when gaze was close to the center of the screen regardless of condition (see Figure 8).

**Figure 8.** Probe timing relative to gaze position for a representative observer. Individual points show gaze deviation from the center of the display (x-axis) and the timing of the probe (y-axis) for no-eye movement trials (left panel) and pursuit trials (right panel). Distributions along each axis show frequencies (in arbitrary units) of observations along each dimension. These distributions are summarized by box and whisker plots. The central band of a box represents the median, the upper and lower bands represent the interquartile range, the extent of the whiskers shows the range, and the lower and upper whisker crosshatches show 2.5th and 97.5th percentiles, respectively.

**Statistical analyses**

We modeled accuracy data from the main experiments with log functions described as:

\[ y = \frac{1}{1 + e^{-a(x-b)}} \]

where \( y \) is proportion correct responses, \( a \) is the slope (precision) and \( b \) is the mid-point of the function (i.e. 0.5 proportion correct). We used the model’s parameters in the following equation to find critical spacing, \( c \), for each condition:

\[ c = -\ln \left( \frac{-1 + y}{y} \right)^\frac{1}{a} + b \]

where \( y \) was set to 0.625.

To test whether pursuit eye movements affected the spatial extent of crowding, we performed bootstrapping analyses (29) to simulate distributions of critical spacing. For the number of trials in each point shown in Figure 2, raw data for that point were re-sampled.
with replacement to create a bootstrapped mean proportion correct. All points were resampled in this way. We fitted log functions to these bootstrapped points to calculate a bootstrapped critical spacing and precision value using the equations above. We repeated this procedure 2000 times to create distributions of critical spacing and 95% confidence intervals. Two observed means that fell beyond each other’s bootstrapped confidence intervals were significantly different. We further calculated bootstrapped distributions of the difference in critical spacing between contraversive and ipsiversive probes during pursuit, after controlling for differences in the no eye movement conditions. This was done by first subtracting the contraversive critical spacing bootstrapped values from the ipsiversive values, and, from the resulting values, subtracting the difference between contraversive and ipsiversive values from no eye movement conditions. The same procedure was performed for precision scores to create the 2-dimensional distributions shown in Figure 4.

Control experiments

Only observers W.H. and K.S. participated in the control experiments. We tested whether there was a contraversive-ipsiversive difference in the perceived distance of the probe from the pursuit target. Experimental procedures were as described for Experiment 2, and in the Results and Discussion, with the following differences. The probe-flanker spacing was at a fixed distance that corresponded to each observer’s critical spacing for contraversive crowding. The inner flankers – the contraversive flanker and ipsiversive flanker closest to the pursuit target – were removed to prevent them from overlapping the pursuit target during trials with a large physical offset of the contraversive probe. Only pursuit trials were run in this experiment. The direction of pursuit was alternated every 36 trials, and each observer completed 324 trials. Observers pressed the left arrow key to indicate they perceived the contraversive stimuli further from the pursuit target than the ipsiversive stimuli, and the right arrow key for the reverse situation. To estimate the minimum perceived displacement required to nullify the relative expansion of crowding for contraversive probes, we calculated the minimum physical probe eccentricity that, given the probe-flanker spacings and accuracy data, would have reduced the contraversive-ipsiversive critical spacing difference to zero. Because we did not take into account the foveal lag during pursuit for this calculation, the estimated perceived offset slightly underestimates the offset that would actually be required. Thus, this calculation provides a
conservative estimate of the minimum perceived offset required to attribute changes in crowding to mislocalizations of probe and flanker stimuli.

We tested whether making the probe position predictable affected crowding contraversive or ipsiversive to pursuit direction using similar experimental procedures as those described for Experiment 2, but with the following changes. Only pursuit trials were included, and the direction of pursuit alternated every 36 trials. The position of the probe relative to the direction of pursuit was held constant within a testing block of 216 trials, and observers completed a single block for each probe position. The probe-flanker spacing was adjusted to the contraversive critical spacing during pursuit. We calculated the required physical spacing by converting critical spacing as a proportion of $\phi$ into absolute degrees of visual angle. This distance was then adjusted for the systematic foveal lag by adding the average error in eye position during pursuit (relative to the position of the pursuit target).

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Chapter 3 - Visual crowding is anisotropic along the horizontal meridian during smooth pursuit

References


Chapter 3 - Visual crowding is anisotropic along the horizontal meridian during smooth pursuit


Chapter 3 - Visual crowding is anisotropic along the horizontal meridian during smooth pursuit
Chapter 4 - Pre-saccadic shifts of visual attention
Abstract

The locations of visual objects to which we attend are initially mapped in a retinotopic frame of reference. Because each saccade results in a shift of images on the retina, however, the retinotopic mapping of spatial attention must be updated around the time of each eye movement. Mathôt and Theeuwes [1] recently demonstrated that a visual cue draws attention not only to the cue’s current retinotopic location, but also to a location shifted in the direction of the saccade, the “future-field”. Here we asked whether retinotopic and future-field locations have special status, or whether cue-related attention benefits exist between these locations. We measured responses to targets that appeared either at the retinotopic or future-field location of a brief, non-predictive visual cue, or at various intermediate locations between them. Attentional cues facilitated performance at both the retinotopic and future-field locations for cued relative to uncued targets, as expected. Critically, this cueing effect also occurred at intermediate locations. Our results, and those reported previously [1], imply a systematic bias of attention in the direction of the saccade, independent of any predictive remapping of attention that compensates for retinal displacements of objects across saccades [2].

Introduction

We process detail in our visual environment through a combination of shifts of spatial attention and saccadic eye movements. For spatial attention to be coordinated successfully with eye movements, the attention system must take into account the changing retinal positions of visual objects brought about by each saccade. Rolls, Jonikaitis, Deubel, and Cavanagh [2] recently demonstrated that, just prior to a saccade, perceptual sensitivity is enhanced at a location in the opposite direction to the saccade that corresponds to the retinal location that will subserve task-relevant stimuli following the saccade. They, and others [3], have suggested these pre-saccadic changes in visual sensitivity represent the remapping of visual attention to compensate for the impending retinal displacement caused by the saccade. By contrast, a study by Mathôt and Theeuwes [1] found increases in perceptual sensitivity in the same direction as an impending eye movement, and argued that predictive remapping shifts the focus of attention in the direction of the saccade. In the present study, we examine further the effects described by Mathôt and Theeuwes, and conclude that shifts of attention in the direction of the saccade are probably independent of remapping mechanisms, thus explaining this apparent empirical discrepancy.

The behaviour of single cells throughout the visual attention system has provided an insight into how retinotopically mapped visual attention may be maintained across saccades. Brain activity in areas associated with saccade generation and spatial attention suggests that neurons in these regions predict the retinal consequences of eye movements. For example, as shown in Figure 1a, Duhamel, Colby, and Goldberg [4] found that cells in the macaque lateral intraparietal area (LIP) begin to respond to a stimulus outside the cells’ receptive field when an impending saccade brings the stimulus into the receptive field. That is, these cells begin to respond to the predicted post-saccadic location of the receptive field, hereafter called the “future-field”. This change in activity around the time of a saccade is referred to as remapping [4]. Cells showing a remapping response have been found in other regions also involved in attentional control, including the frontal eye fields [5] and superior colliculus [6]. These changes in neural activity may represent the updating of a target’s location on a retinotopic salience map, guiding the deployment of spatial attention to task relevant information across saccades [3]. Importantly, just prior to a saccade, the responses of remapping cells anticipate a stimulus appearing within the receptive field following the saccade.

Recently, Mathôt and Theeuwes [1] examined how shifts of spatial attention are coordinated with eye movements, and argued that pre-saccadic shifts of spatial attention are similar to the change in responsiveness of remapping neurons (see Figures 1a and 1b). Mathôt and Theeuwes combined a standard spatial cueing paradigm (e.g. [7]) with an eye movement task. They had participants make a saccade either horizontally or vertically to the location of a visual marker. Just prior to the saccade, a non-predictive cue briefly appeared midway between the initial fixation point and the saccade goal, offset 45° above or below the required saccade trajectory. After the cue disappeared, but prior to the saccade, a target (a tilted bar) was presented at one of four locations: the retinotopic location of the cue; the “future-field” location (the display location corresponding to where the cued region of the retina would fall following the eye movement); or one of two uncued, “control” locations. Control locations were distant from the retinotopic or future-field locations, but matched for...
Figure 1. Examples of remapping and shifting attention across saccades. (A) Responsiveness of single cells prior to a saccade (e.g. [4]). During initial fixation (the cross), the retinotopic location of the receptive field of a population of cells is shown in red; these cells would initially respond to the onset of the square. When there is an impending saccade, however, these cells should begin to respond to a stimulus presented within their future-field (dotted orange circle). (B) Mathôt and Theeuwes [1] suggested attention is predictively remapped in the direction of the saccade. According to their account, if attention at the dotted circle is subserved by the same cells as in (A), attending to a cue (the square) should increase the firing rate of these cells during fixation. Because of predictive remapping, these cells should begin to respond to stimuli at the cells’ future-field just prior to the saccade. As suggested by Mathôt and Theeuwes [1,8], the cued cells’ increased firing rate might enhance processing of targets within the future-field. Such a change in attention, however, could also result in attention being allocated to a non-cued location following the saccade, which would be functionally irrelevant. (C) “Functional remapping”, as demonstrated by Rolfs et al [2]. Remapping attention in this case is subserved by a population of neurons similar to those shown in (A), but whose classic receptive field is to the left of fixation. Because the position of the cue will shift from the right visual field during fixation to the left visual field following a rightward saccade, functional remapping of attention would require a shift of attention in the opposite direction to the saccade. This attention shift compensates for the retinal shift of visual objects following the saccade.

Figure 2. The basic arrangement of stimuli employed in the current experiments, adapted from Mathôt and Theeuwes [1]. Participants made a saccade from a grey spot to a green spot, as indicated by the arrow. Prior to the saccade, a cue (the black square) was briefly flashed. Shortly following the offset of the cue and still prior to the saccade, a target was shown at locations represented by the tilted bars. In Mathôt and Theeuwes’ study, the target appeared at the retinotopic or future-field location of the cue, or one of their relative control locations (the broken tilted bars). In the present study, we also probed several intermediate locations.

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retinal eccentricity (see Figures 1 and 2). After executing the saccade, participants made speeded responses to the orientation of the target.

Relative to the uncued locations, participants responded faster to targets presented at the retinotopic location of the cue and at the future-field location of the cue. Mathôt and Theeuwes [1] interpreted their results as showing that visual attention, captured at the retinotopic location of the cue, was partially remapped to the future-field of the cued location, thus facilitating responses to targets at both these locations. They further speculated on the underlying neurophysiology of their results, arguing that the cue excited a population of remapping neurons during the pre-saccadic interval, so that processing of targets presented in the neurons’ future-field was facilitated due to an increase in their baseline firing rate (see also [8]).

Although Mathôt and Theeuwes’ [1] interpretation of their data appears consistent with the neurophysiological remapping findings (compare panels a and b in Figure 1), their interpretation raises a concern: a shift of attention in the direction of the saccade, in the manner outlined in Figure 1b, seemingly serves no functional purpose [2]. That is, a pre-saccadic shift of the focus of attention from the cued location to a location that is in the direction of the saccade results in attention being deployed to a location that was important neither prior to nor following the saccade. As argued by Rolfs et al., and as shown in Figure 1c, for attention to be allocated to the cued location following an eye movement, it must shift in the opposite direction to the saccade. Rolfs et al. refer to this shift of attention as “functional remapping”. In this hypothesis, a population of remapping neurons whose receptive fields fall at the predicted post-saccadic location of the cue would show the classic anticipatory remapping response [2,4]. Furthermore, Mathôt and Theeuwes’ suggestion that the focus of attention is shifted in the direction of the saccade via predictive remapping is inconsistent with the notion that remapping neurons anticipate a stimulus falling within their receptive field following the saccade [3,4].

These issues raise the question of whether Mathôt and Theeuwes’ [1] findings do in fact represent remapping of spatial
information to compensate for retinal displacements of visual objects following a saccade. For example, although Mathôt and Theeuwes ruled out the possibility that their result could be accounted for by the cue and target appearing in the same visual quadrant (see [9]), they did not rule out the possibility that attention spreads more generally in parallel to the saccade vector across visual quadrants. Hughes and Zimba [10] demonstrated that, when cued along an oblique visual meridian, visual attention does indeed spread across the visual quadrants during fixation. If attentional benefits occurred between the retinotopic and future-field locations of the cue in Mathôt and Theeuwes’ paradigm, spreading of attention [10] could account for their data without invoking predictive remapping.

In the current study, we asked whether the shifts of attention observed by Mathôt and Theeuwes [1] are unique to the retinotopic and future-field locations of an attended cue, or whether the cue also affects the perception of stimuli between these locations. We followed Mathôt and Theeuwes’ experimental design by presenting cues and targets during the pre-saccadic interval. In addition to probing the retinotopic and future-field locations of the cue, however, we also probed intervening locations (the “intermediate” area in Figure 2). As discussed in a recent review [9], if attention is remapped predictively as a consequence of relevant cells discretely shifting the spatial location to which they respond, we might expect the focus of attention also to shift discretely from the retinotopic coordinates of an attended location to that location’s future-field prior to the saccade. Alternatively, however, if attention spreads more generally, intermediate locations should also receive some attentional benefit. In two experiments we found evidence for a cueing effect at both the retinotopic and future-field locations, replicating Mathôt and Theeuwes [1]. Crucially, however, we also found significant effects of attention at intermediate locations.

In an initial experiment, we probed for attentional facilitation at intermediate locations between the retinotopic and future-field locations of a brief cue flashed just prior to a saccade. If attention to the cue location shifts directly from the retinotopic coordinates of the cue to future-field coordinates, then perception should be facilitated at these locations, but not at intermediate target locations (see Figure 2). By contrast, if attentional benefits of the cue apply more generally across space, targets presented at intermediate locations should be responded to faster than (uncued) control locations.

Methods

Ethics statement

Prior to testing, each participant was given an information sheet outlining what was required of him or her during the experiment. Participants were informed via the information sheet and verbally by the experimenter that they were free to withdraw from the experiment at any time without penalty. Before testing began, informed consent was obtained verbally from all those who participated in the study. Verbal consent was deemed sufficient due to the experiment not involving any foreseeable risk beyond that of everyday living. The study and consent procedure were approved by The University of Queensland’s School of Psychology Ethical Review Committee (code: 09-PSYCH-PhD-38-CVH).

Participants

Twenty-nine (29) individuals from The University of Queensland participated in Experiment 1 for a monetary reward (A$10) or course credit. Participants were aged from 18–42 years (M = 23.15, SD = 3.70; 12 females), and all were naive to the purpose of the experiment with the exception of one of the authors (WJH). All participants reported normal or corrected to normal vision.

Materials

Participants sat with their head in a head and chin rest positioned 57 cm from an LCD monitor (60 Hz). Stimuli were generated using Presentation (Neurobehavorial Systems). Eye movements were recorded at 500 Hz with an EyeLink 1000 (SR Research, Canada).

Stimuli and procedure

The display and procedure were the same as those described by Mathôt and Theeuwes [1], except that extra target locations were included. Figure 3 shows the displays in a typical trial sequence. In each trial, participants were required to make a saccade and then to respond to the orientation of a tilted bar. Each trial began when participants fixated a single grey spot (1.5°) presented at one of four possible locations. After 500 ms, three more grey spots were presented, forming a square of 9° x 9°. After a further 500 ms, a single grey spot, aligned horizontally or vertically with fixation, turned green to signal the saccade target. At the same time, the fixation spot reduced in size, and the visual cue (a square frame of 1.8° x 1.8°) was flashed for 50 ms. The cue could appear at one of two possible locations that deviated from the required saccade trajectory by −45° or 45°, and was located 6.4° of visual angle from the fixation and saccade target spots. Participants were instructed to make an eye movement to the green spot as quickly and as accurately as possible.

The target was a 2.5° bar with a width of 0.25° presented 125 ms after the onset of the cue, for a duration of 75 ms. The bar was tilted 45° left or right off vertical. There were 10 possible target locations relative to the direction of the required eye movement (see Figure 2 and Figure 3). The tilted bar could appear at the retinotopic location of the cue, or at the future-field location of the cue. In addition, targets could appear at any of three locations between the retinotopic and future-field locations (intermediate locations). The distance between adjacent target locations was 1.8°. We refer to the retinotopic, future-field and intermediate target locations as “test” locations. Targets could also appear at five “control” locations that were directly opposite the test locations (see Figure 3). The target appeared at each location with equal probability irrespective of the cue location (i.e., the cues were not predictive of target location). Participants were instructed to report the orientation of the bar as quickly as possible (tilted left or right) by pressing a left or right arrow key. Auditory feedback signalling a correct or incorrect response was provided, and the screen then went blank for 1500 ms before the next trial began. Participants completed two practice blocks, the first consisting of 10 trials of just the saccade task, and the second consisting of 20 full trials. There were 32 trials for each target location, resulting in 320 experimental trials per participant.

Results

Data filtering

We excluded trials using the same screening criteria as Mathôt and Theeuwes [1]. Data from three participants who had more than 30% of their trials excluded were omitted from analyses. Data from a further two participants who had error rates higher than 20% in a single condition, and from a single participant for whom the eye-tracker could not be calibrated reliably, were also omitted from analyses. For the remaining participants, trials were removed if gaze deviated by more than 2° from the initial fixation point.
(0.5% of trials), if the saccade trajectory deviated more than 22.5° from the saccade target (6.2% of trials), if saccade latency was below 100 ms or above 600 ms (1.1% of trials), if response time was below 200 ms or above 1000 ms (3.4% of trials), or if a participant’s gaze arrived at the saccade target before the offset of the target (1.8% of trials). In total, 86.9% of trials from 23 participants were included in the statistical analyses.

Response times
As shown in Figure 3, response times were faster to targets presented at the retinotopic, future-field, and at two of the three intermediate locations than their relative controls. We conducted a repeated measures ANOVA with the factors condition (test and control) and location (retinotopic, close-intermediate, center-intermediate, far-intermediate, and future-field; see Figure 3). There were significant main effects of both condition, $F(1, 22) = 12.96, p = .002$, and location, $F(4, 88) = 3.99, p = .005$, but no significant interaction, $F(4, 88) < 1$.

To assess whether the cue facilitated responses to targets at different locations, we conducted planned comparisons on mean response times to targets at test versus control positions at each of the five spatial locations. Response times were significantly faster to targets at both the retinotopic and the future-field locations than their control locations, $t(22) = 2.09, p = .049$, and $t(22) = 2.34, p = .029$, respectively, thus replicating the findings of Mathôt and Theeuwes [1]. Response times were also significantly faster when the target was presented at the far-intermediate location compared with its control location, $t(22) = 2.25, p = .033$, and marginally faster when the target was presented at the center-intermediate location compared with its control location, $t(22) = 1.97, p = .062$. There was no difference in response times to targets at the close-intermediate target location and its control location, $t(22) = 0.44, p = .662$.

In summary, we found a significant cueing effect at both the retinotopic and the future-field locations, as expected. Crucially, we also found evidence for a cueing effect at two out of three intermediate locations (see Figure 4).

There is a possibility that our exclusion criteria, based on Mathôt and Theeuwes [1], failed to eliminate inaccurate saccades. Because the intended saccade goal determines which screen positions correspond to the future-field of the cue, “intermediate” targets may have been processed preferentially when saccades were inaccurate. If this had occurred, it might have generated a spurious cueing effect at one or more of the intermediate locations. We therefore re-analysed the data including only saccades that fell within 2° of the saccade target. This resulted in the exclusion of a further 0.3% of trials only, demonstrating that participants were generally highly accurate in the saccade task. As for the response time data, this more stringent analysis again yielded significant differences in response times at all test locations compared with their control locations (all $p$'s < .05), with the exception of the close-intermediate location.

Figure 3. Example trial sequence from Experiment 1 (top) and all tested target locations (bottom). In this example, the participant first fixates the top left spot for the first two frames and is then required to make a saccade towards the green spot at the same time as the onset of the cue (square frame). In this example, the target (the tilted bar) appears at the retinotopic location of the cue, but can actually appear at any target location shown in the bottom panel. Note there was only one target presented per trial, all targets and cues were grey, and the background of the display was black.
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Errors and saccadic latencies

Planned comparisons revealed no differences in the frequency of target errors between the test and control locations (all $p's > 0.15$). Nor was there any such difference for saccadic latencies (all $p's > 0.20$; Table 1).

Discussion

The aim of Experiment 1 was to determine whether, just prior to a saccade, attention is allocated exclusively to the retinotopic and future-field locations of an exogenous cue. Participants responded faster to targets at the retinotopic and future-field locations of the cue, and at the far-intermediate location. Responses to targets at the center-intermediate location fell just short of being significantly different from responses to targets at a control location, but when we restricted analyses to trials showing high-precision saccades, this difference became significant.

We offer two explanations for finding a cueing effect at only two out of the three intermediate locations. First, in support of the notion of a pre-saccadic spread of attention, the lack of a cueing effect at the close-intermediate location could be due to attentional suppression around the cue [11,12]. Previous studies have demonstrated a “suppressive annulus” surrounding an attended location that spans approximately $2^\circ$ [11,12]. Only the close-intermediate probe location fell within this region. Second, in support of the notion that attention shifts discretely from retinotopic to future-field locations, the influence of the cue at two out of the three intermediate locations could be due to the locations’ proximity to the saccade endpoint. It is well established that during saccade planning attention shifts to the goal of the saccade (e.g. [13,14]). An interaction between attention shifting towards the saccade goal and towards the future-field location could account for our finding at the close- and far-intermediate target locations. Therefore, in Experiment 2, we changed the design of the experiment and probed a single, intermediate location that should be free from both of these issues.

Experiment 2

In Experiment 2 we replicated the cueing effects observed at intermediate locations in Experiment 1 using a design that was free from the two potential spatial limitations mentioned above. We aimed to probe an intermediate location that should be unaffected by any attentional suppression around the cue, and that should not be preferentially processed based on its proximity to the saccade goal. The changed design can be seen in Figure 5. To prevent attentional suppression around the cue location from affecting responses to targets adjacent to the cue [11,12], we chose a single intermediate target location beyond the region expected to be

Table 1. Experiment 1 error rates and saccadic latencies (ms).

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Figure 4. Experiment 1 response-time results. The left panel depicts absolute response times for all conditions. The right panel shows the response time differences between test and control locations, with positive values indicating faster responses to targets at test than control locations. Error bars represent standard error. Asterisks indicate that differences are different from 0. *$p<0.10$; **$p<0.05$. doi:10.1371/journal.pone.0045670.g004

doi:10.1371/journal.pone.0045670.t001
suppressed, and equidistant from the retinotopic and future-field locations. We also changed the display configuration so that the saccade goal could not influence target processing at the intermediate location. If attention shifts directly from retinotopic to future-field coordinates, there should be no facilitation of responses to targets presented at the intermediate target location. Alternatively, if attention spreads between these locations, any cueing effect should be equivalent across retinotopic, future-field, and intermediate target locations.

Method

Participants. Nine individuals from The University of Queensland participated in Experiment 2. They ranged in age from 17–27 years (\(M=21.22, \ SD=4.24; 4\) females), and received a monetary reward (AU$10) or course credit. All were naive to the purpose of the experiment with the exception of WJH, and all had normal or corrected to normal vision.

Materials. These were the same as in Experiment 1.

Stimuli and procedure. Figure 5 shows an example trial sequence from Experiment 2. Equipment and testing conditions were the same as in Experiment 1. Each trial began with a fixation spot at the center of the screen for 500 ms. Two additional spots were then presented for 500 ms along the horizontal meridian, at 9° to the left and right of fixation. One of the two peripheral spots then turned green to signal the saccade target, and the fixation spot reduced in size. At the onset of the saccade target, the cue appeared for 50 ms at 3.8° above or below the fixation spot.

The target was presented for 75 ms, 125 ms after the onset of the cue, at one of six locations for each possible eye movement (leftward or rightward). As in Experiment 1, the target appeared either at the retinotopic location of the cue, or at the future-field location of the cue. Due to the change of location of the cue in Experiment 2, the retinotopic and future-field target locations were now adjacent to the start- and end-point of the saccade, respectively. Targets were also presented at a location equidistant (2.8°) from the retinotopic and future-field target locations (the intermediate location). This intermediate location was not only distant from the saccade goal, but also distant from the cue location, reducing the possibility that targets at this location could be affected by any attentional suppression around the cue [11]. There were also three control locations, matched for the retinal eccentricities of the retinotopic, future-field, and intermediate locations. Targets were presented at each location with equal probability, making the cue location non-predictive of target location, as in Experiment 1. Responses, auditory feedback and intertrial intervals were also the same as described in Experiment 1. Participants completed 20 practice trials before commencing 480 experimental trials, yielding 80 trials per target location.

Results

Data filtering. Using the same criteria as in Experiment 1, trials were excluded on the basis of gaze deviation (<0.1%), saccade deviation (2.4%), saccade latency (0.6%), response time (1.0%), and when participants’ eyes arrived at the saccade target before the offset of the probe target (1.0%). In total, 94.9% of trials from nine participants were included in the analysis.

Response Times. As shown in Figure 6, participants responded faster to targets presented at the retinotopic, future-field, and intermediate locations compared with their control locations. We conducted a repeated-measures ANOVA with the factors condition (test and control) and location (retinotopic, intermediate, and future-field). We found a significant main effect of condition, \(F(1, 8) = 22.13, p = .002\), but no main effect of location, \(F(2, 16) = 1.05\), and no interaction, \(F(2, 16) < .1\). Planned comparisons revealed that response times were significantly faster for targets presented at both the retinotopic and the future-field locations of the cue, compared with their respective control locations, \(\hat{\epsilon}(8) = 3.31, p = .011\), and \(\hat{\epsilon}(8) = 2.83, p = .022\), respectively. These cueing effects replicate those from Experiment 1, and are also consistent with the findings of Mathôt and Theeuwes [1]. Crucially, there was also a significant cueing effect when the target was presented at the intermediate target location, equidistant from the retinotopic and future-field locations, \(\hat{\epsilon}(8) = 4.09, p = .003\).

Errors and saccadic latencies. Error rates for Experiment 2 are shown in Table 2. Planned comparisons conducted on error rates revealed no differences between any of the test locations and their control locations (all \(p > .091\)).

Saccadic latency distributions and their means are plotted in Figure 7. Generally, saccadic latencies were shorter when targets appeared at the test locations than when they appeared at the control locations (see Figure 7). Planned comparisons confirmed that saccadic latencies were shorter when targets were presented at the retinotopic and intermediate locations compared with their controls, \(\hat{\epsilon}(8) = 2.79, p = .024\), and \(\hat{\epsilon}(8) = 2.50, p = .033\), respectively. Latencies were marginally shorter when targets were presented at the future-field location compared with its control, \(\hat{\epsilon}(8) = 2.23, p = .056\).

Response time analysis according to probe-saccade onset asynchrony. Predictive remapping alters responses of single neurons within approximately 100 ms of saccade onset, without significantly affecting neuronal activity at longer intervals prior to the saccade [4–6,15]. To examine whether our results conform to this established pattern we binned trials according to the onset time of the probe relative to saccade onset on a trial-by-trial basis. We classified probe onsets as occurring either within 100 ms of saccade onset, or between 100 and 200 ms before saccade onset.
One participant was omitted from this analysis because there was only a single trial in which the probe appeared within 100 ms of saccade onset and other trial parameters met the inclusion criteria listed above. In Figure 8, we show the cueing effect (response time difference between test and control locations) for each probe location according to relative probe timing. For each probe location, there were only small changes in the cueing effect across time. Importantly, at the future-field location, there was less than 2 ms difference in the cueing effect across time bins (all $p's > 0.58$, uncorrected). We conducted a similar analysis comparing data from the final 100 ms prior to a saccade against trials in which the probe was presented earlier than 200 ms prior to saccade, which revealed similar non-significant changes across time. These results argue against a predictive remapping account of our results, which should have shown greater modulation of response times when probes were presented within 100 ms prior to a saccade [2].

Saccade trajectories. We analyzed saccade trajectories to determine whether the cue had any effect on saccadic programming [16]. Across conditions, we found no significant deviations from a straight line. Individual traces of saccades from a single observer (author WJH) whose response times were representative of the group are shown in Figure 9A. Average trajectory data from the group are shown in Figure 9B. All deviations were small, and were not statistically different from zero (all $p's > 0.05$, uncorrected).

Discussion

In Experiment 2 we again found that, prior to the saccade, a non-predictive cue facilitated response times to targets presented not only at the retinotopic and future-field locations, but also at an intermediate location between them. Furthermore, an examination of response times according to when the probe was presented relative to saccade onset showed there was no change in the cueing effect at the future-field in the final 100 ms prior to a saccade, contrary to what would be expected from predictive remapping [2,4–6,15].

General Discussion

The aim of the present study was to examine how visual processing is affected by an attentional cue presented just prior to a saccade. Mathôt & Theeuwes [1] recently demonstrated that a cue presented just prior to a saccade attracts attention not only to the cue’s retinotopic location, but also to the future-field of that retinotopic location. We examined cueing effects at intermediate spatial locations, and found significant cueing effects for them as well as for retinotopic and future-field positions. The overall pattern of results suggests that response time facilitation at retinotopic and future-field locations is not unique but occurs at locations within the interval from the cue to the future-field. Mathôt and Theeuwes [1,8] have suggested that their results are consistent with neurophysiological data showing that neurons in several regions of the visual attention system begin to respond to stimuli in their future-field just prior to a saccade (e.g. [4]). Early findings suggested that remapping neurons in FEF respond only to stimuli within their future-field and not at intermediate locations [15], but more recent data suggest some neurons in FEF respond to stimuli at intermediate locations [17,18]. The pre-saccadic shifts of attention we observed appear broadly consistent with these more recent findings, though this hypothesis will need to be tested in future studies.

Regardless of the apparent parallels with the relevant neurophysiological findings, we suggest that these results – and those of Mathôt and Theeuwes [1] – reflect more general changes in attention allocation during the pre-saccadic interval, and that these changes are probably independent of saccadic remapping neurons. As argued by Rolls, et al. [2], changes in activity of remapping neurons appears to anticipate a stimulus appearing in the cells’ receptive-field following an eye movement, and this anticipatory change affects a location that is in the opposite direction.
to the saccade. In contrast, the probed locations in the present study (as that of Mathôt and Theeuwes) were in the same direction as the saccade. We therefore assume that the reliable attention effects we have observed must arise from the operation of mechanisms other than those evoked during predictive remapping.

As outlined in the Introduction, remapping attention in the direction of the saccade does not preserve attention in world-centered coordinates [2]. Why, then, might attention be redistributed in the manner revealed in the present study? One possibility is that, rather than serving a role in remapping per se, these effects represent disruption of the normal allocation of attention to the saccade goal (e.g. [13]). Attentional capture at the location of the cue requires that attention be subsequently reoriented toward the saccade goal before a saccade can be executed [14], thus facilitating processing of stimuli across a region of space as attention shifts from one location to another [19]. Alternatively, the response time differences observed between the retinotopic and future-field locations compared with control locations could have been due to participants responding more quickly to apparent motion [20]; faster responses might have arisen from apparent motion perception, rather than through changes in attention prior to the saccade. Such a finding would also contradict the predictive remapping account.

In replicating Mathôt and Theeuwes’ [1] work, we felt it important to replicate their response-time measure. However, seminal studies examining pre-saccadic attention shifts have used masked, force-choice discrimination measures that limit the potential of post-saccadic decisions to affect responses (e.g. [13,14]). Response time measures leave open the possibility that some facilitation of targets at the future-field location could arise from a post-saccade retinotopic trace of the cue [21–24]. But this account also requires an interaction with memory for the target, because the target was extinguished before the end of the saccade. We think this is unlikely. Moreover, a post-saccade memory trace of the cue cannot account for the cueing effects we observed at “intermediate” locations.

Figure 7. Experiment 2 saccadic latency distributions. Frequencies are plotted on the y-axis, and mean saccadic latencies are plotted on the x-axis (vertical lines). Color codes correspond to those used in Figure 6, with solid lines representing test conditions and dotted lines representing control conditions. Asterisks indicate significant differences between means. *p<0.10; **p<0.05.

doi:10.1371/journal.pone.0045670.g007

Figure 8. Experiment 2 response-time analyses according to probe-saccade onset asynchrony. According to probe-saccade onset asynchrony, trials were sorted into 100 ms time bins. Response time differences between test and control locations were then calculated for each condition at each time interval, with positive values indicating faster responses to targets at test than control locations. No changes in response times across time bins were found.

doi:10.1371/journal.pone.0045670.g008
On first inspection, our findings appear inconsistent with those of Golomb et al. [23], who failed to find facilitation for intermediate cues following a saccade. However, there is at least one critical difference between the studies: Golomb et al. were interested in how, following an eye movement, visual attention is re-deployed to a world-referenced location defined prior to the saccade. Relative to the retinotopic location, therefore, the spatiotopic and intermediate locations they examined were in the opposite direction to the executed saccade, similar to those locations required for “functional remapping” as argued by Rolfs et al. [2] and outlined in Figure 1C. In contrast to this, we probed for pre-saccadic attention shifts in the same direction as the saccade (see Figure 1B and Figure 2). Since our intermediate positions did not correspond to those of Golomb et al., the results of the two studies are not directly comparable.

In two experiments we observed facilitation of target processing at locations between the retinotopic and future-field locations of the cue. In this regard the findings of the present experiments do not support a special status for the future-field location and, hence, question whether the results from this paradigm reflect remapping. Instead, these data suggest that an attentional cue presented in the pre-saccadic interval may affect processing of visual information across a broad region of space on the side of the saccade trajectory. The broad facilitation of response time for locations in the direction of the impending saccade may represent transitory changes in the allocation of attention when a briefly flashed cue competes for attention with the saccade target.
Author Contributions
Conceived and designed the experiments: WJH JBM RWR. Performed the experiments: WJH. Analyzed the data: WJH. Contributed reagents/materials/analysis tools: RWR. Wrote the paper: WJH JBM RWR.

References
Chapter 5 - Remapped crowding of visual features reveals an oculomotor contribution to object stability across saccades
The published version of this chapter appears as Appendix B.

ABSTRACT

When we move our eyes, images of objects in the world are displaced on the retina. Oculomotor activity just prior to an eye movement is used to predict where a stimulus will be on the retina immediately after a saccade, but it remains unclear whether an object’s features are also remapped. Here we used a visual crowding paradigm to show that presaccadic remapping preserves the elementary features of objects at their predicted postsaccadic locations. Observers identified a probe displayed briefly before a voluntary saccade. Flankers surrounding the probe’s predicted retinotopic location disrupted identification, despite being positioned in the opposite visual field. Crucially, this “remapped crowding” effect was stronger when the flankers shared elementary features with the probe than when the flanker and probe stimuli were distinct. Our findings reveal that featural information is preserved during predictive remapping, providing a mechanism for achieving perceptual continuity of objects across saccades.
Each time we make an eye movement the retinal image is displaced, yet our perception of the visual world remains stable. It has long been known that the visual system achieves perceptual stability by using the magnitude and direction of the impending saccade to predictively update an internal representation of the visual world. Single-unit recordings from primate oculomotor areas, including the lateral intraparietal area (LIP), frontal eye fields (FEF) and superior colliculus (SC), have shown that neurons in these regions begin to respond to visual stimuli outside their receptive fields if an impending saccade will bring the stimulus into the receptive field\textsuperscript{1-4}. Such anticipatory activity might provide a neural mechanism for predictive remapping of stimuli to facilitate trans-saccadic perception\textsuperscript{5}.

Whether pre-saccadic activity of remapping neurons conveys information about an object’s identity, such as its orientation and shape, has been the subject of intense debate\textsuperscript{6-17}. There is some evidence that early visual neurons integrate form information across eye movements\textsuperscript{6,7}, and that the remapping of such featural information begins just prior to the saccade\textsuperscript{8}. Others have argued against the transfer of visual features in early visual areas\textsuperscript{9-12}, and have shown instead that focal attention shifts toward the predicted location of task-relevant visual objects\textsuperscript{18,19}. These more recent studies provide a potential mechanism by which the positions of important stimuli might be tracked across saccades without the need for featural remapping\textsuperscript{13}. Thus, it remains unclear whether visual processing at updated locations is sensitive to the elementary \textit{features} of visual objects. Here, we demonstrate that an object’s features are preserved during predictive remapping.

We exploited the phenomenon of visual crowding\textsuperscript{20,21} to determine whether predictive remapping is sensitive to the visual features of an object whose retinotopic location shifts across saccades. Visual crowding is the reduced ability to recognize an object in peripheral vision when other objects surround it\textsuperscript{20} (see Fig. 1a). A crowded object is difficult to identify because its features are integrated with those of the flanking elements prior to object recognition\textsuperscript{22}. Flankers that share features with a crowded object impair identification of the target more than flankers with non-shared features\textsuperscript{23}, and the magnitude of crowding decreases as the flankers are moved further away from the target object\textsuperscript{20,21}. Crucially, in the current study we presented stimuli just \textit{prior} to a saccade, with a probe stimulus in one visual hemifield and distractors in the \textit{opposite} visual hemifield flanking the predicted, post-saccadic location of the probe (Fig. 1b). Thus, we measured...
probe identification interference caused by distractors at the probe’s future retinotopic location during the period of predictive remapping. By manipulating the featural similarity of flankers and probes and measuring any corresponding change in performance, we were able to test the featural specificity of this pre-saccadic visual processing.

**Figure 1.** Schematic of standard and “remapped” visual crowding. (a) Standard crowding. While fixating the blue spot in the top row, recognizing the letter H in the right visual field is made difficult because of crowding, whereas recognizing the letter H in (b) is relatively simple. (b) Hypothesized “remapped crowding”. If an impending saccade (orange arrow) will displace the retinal position of the H to a predicted location (dashed red line), the focus of visual processing will be remapped (red arrow) during the pre-saccadic interval. If predictive remapping preserves an object’s features, the visual system will begin processing features matching those of the H at the remapped location in anticipation of those features appearing there after the saccade. Thus, during predictive remapping, the identity of a letter probe in the right hemifield should be degraded by flankers at the predicted post-saccadic location in the left hemifield. Gaussian distributions represent hypothetical neural activity at positions in visual cortex supporting object recognition.

**RESULTS**

**Experiment 1: Remapped crowding**

We first established a standard crowding effect by having observers report the identity of a probe letter in the visual periphery. The probe letter was either presented alone or was directly flanked by distractor letters. Figure 2a shows the standard crowding effect when no saccade was required. When the probe was presented alone, observers’ probe identification accuracy was 0.74 ± 0.08 (mean ± s.e.m.). By contrast, when flankers directly surrounded the probe, observers’ accuracy fell significantly to 0.46 ± 0.05 (pairwise, two-tailed comparison, \( P = 0.004 \)).
Figure 2. Using crowding to test featural processing during predictive remapping.
(a) Standard crowding effect. Data from an initial pilot experiment ($N = 10$) show that while observers remained fixated in the center of the display, identification of a probe flanked by letters (red bar) was significantly poorer than identification a probe presented alone (blue bar). Error bars represent one s.e.m. *** $P = 0.001$. (b) Display sequence from a critical trial in Experiment 1, in which we tested for “remapped crowding”. Probes and flankers were presented around the period of saccadic remapping. At the offset of a central fixation point (white spot), observers were required to execute a horizontal saccade to the saccade target (outlined in green on every trial), and to report the orientation of the Gabor at this location. Observers reported which letter (L, T, or H) had appeared in the placeholder located mid-way between fixation and the saccade target (in the diagram, the third placeholder from the right). (c) Overview of the timing of probe onset relative to fixation offset, aligned to saccade onset (time zero) on the x-axis. (d) Saccade data from a representative observer in Experiment 1. Frequency of saccadic latency is plotted in orange. Onset asynchrony between probes and saccades is shown in pink. Probe onset latencies were normally distributed around 100 ms prior to the saccade. This method yielded an approximately equal number of observations across 100 ms time bins (see Methods).

We compared observers’ accuracy for displays in which probe and flanker items shared visual features, with their accuracy for displays in which probe and flanker features were different. As expected, letter probes were released from crowding when nonshared-feature flankers surrounded the probe. Specifically, probe identification accuracy was 0.50 ± 0.03 (mean ± s.e.m.) with shared-feature flankers, and 0.74 ± 0.02 with nonshared-features.
feature flankers (dark red and dark blue dashed lines in Fig. 3a, respectively; \( t(4) = 11.56, P = 3.18 \times 10^{-4} \)).

To measure visual processing during remapping, observers were required to identify a letter probe flashed briefly in the interval immediately prior to executing a goal-directed saccade to a predictable location. Probe letters were presented at an intermediate location between fixation and the intended saccade endpoint. The probe appeared within the context of one of four possible flanker conditions: (1) Directly flanked by distractors that shared features with the probe (“shared-feature” distractors); (2) Directly flanked by distractors that were featurally distinct from the probe (“nonshared-feature” distractors); (3) Alone in one hemifield, with shared-feature distractors presented in the opposite hemifield; or (4) Alone in one hemifield, with nonshared-feature distractors presented in the opposite hemifield.

An example of a typical trial from the combined saccade and letter identification task is shown in Figure 2b. Predictive remapping is highly dependent on the time course of stimulus presentation relative to saccade onset \(^{1,18,19}\). To motivate observers to execute saccades with predictable latencies, therefore, we presented a brief, masked saccade target which observers were also required to report (see Methods). The saccade target, a Gabor oriented 22.5° left or right from vertical, was always located at the extreme left or right end of an array of eight, evenly spaced placeholders arranged along the horizontal meridian. Participants practiced until they could execute the required eye movement and judge the orientation of the saccade target while performing above chance on the letter probe task (see Methods). To control for any effects of flankers on probe identification that were not specific to an impending saccade, we included blocks of trials in which observers undertook the same task but were required to maintain their gaze centrally at the offset of the fixation point (see Methods).

Observers’ accuracy in judging the orientation of the Gabor was high (mean accuracy = 92%), and did not differ across conditions. Saccadic latencies also did not differ across conditions. Thus, the Gabor was equally attended across saccade and fixation trials. Only
trials in which observers correctly identified the orientation of the Gabor were included in further analyses.

In “remapped crowding” trials, the probe was presented in isolation in one hemifield and the flankers at locations within the opposite hemifield that corresponded to the remapped locations of flankers in the standard crowding paradigm (see Fig. 2b). For these critical trials, we compared the accuracy of probe identification when no saccade was planned with accuracy during a brief period just prior to a saccade. If, during predictive remapping, the focus of visual processing shifts to the flanker locations, probe performance should fall when stimuli are presented just before the eyes begin to move. Furthermore, if activity during predictive remapping conveys information about the remapped object’s visual features, then flanker interference on critical trials should be greater for probe and flanker displays that share elementary features than for displays in which these features differ.

As shown in Figure 3a, relative to no saccade trials, probe performance was significantly reduced during the pre-saccade interval when both shared-feature flankers ($t(4) = 6.24, P = 0.003$) and nonshared-feature flankers ($t(4) = 3.13, P = 0.035$) surrounded the remapped location of the probe. These results indicate that an object’s identity can be degraded by flankers in the contralateral visual field due to predictive remapping. We refer to this pre-saccadic perceptual effect as “remapped crowding”.
Figure 3. Feature processing during predictive remapping.
(a) The two critical displays used to test whether featural information is remapped across saccades. (b) The proportion of letters correctly identified when probes and flankers appeared in no-saccade trials and in the pre-saccade interval of saccade trials. Red and blue bars represent accuracy for shared-feature and nonshared-feature conditions, respectively. Dark red and dark blue dashed lines represent accuracy for standard crowding conditions with shared-feature or nonshared-feature flankers, respectively. (c) Pre-saccade probe identification, plotted as a function of time prior to saccade onset (shown in separate 100 ms time bins). Error bars represent one s.e.m. N = 5; * P < 0.05, ** P < 0.01.

A second important finding shown in Figure 3a is that probe-flanker feature similarity effects observed under conventional crowding were also apparent in the remapped crowding conditions. Specifically, remapped crowding was significantly stronger in the shared-feature condition than in the nonshared-feature condition, suggesting that feature information is predictively remapped just prior to a saccade. This difference was confirmed by a significant interaction between flanker features (nonshared vs shared) and saccadic condition (no saccade vs pre-saccade; \( F(1,4) = 30.51, P = 0.005 \)). Whereas in the no-saccade condition probe performance was equivalent across flanker features \( (t(4) = 0.8, P = 0.471) \), in the pre-saccade condition performance deteriorated more when flankers shared features with the probe than when they were featurally distinct \( (t(4) = 6.01, P = 0.004) \).

In addition to analysing overall accuracy for probe identification across conditions, we examined the time-course of interference caused by flankers surrounding the remapped location of the probe. We divided the pre-saccade interval in saccade trials according to the time of probe presentation relative to saccade onset (Fig. 3b). This procedure yielded
an approximately equal number of observations across each of two bins of 100 ms duration (see Fig. 2 and Methods). The difference in probe identification accuracy for shared-feature and nonshared-feature conditions emerged 100-200 ms prior to saccade onset ($t(4) = 3.82, P = 0.019$), and was greatest 0-100 ms before the saccade ($t(4) = 3.75, P = 0.020$). Interestingly, the remapped crowding effect measured here closely matches the time-course of activity of remapping neurons in LIP $^1$, area V3 $^2$, FEF $^{3,4}$, and superior colliculus $^{24}$, as well as predictive remapping of spatial attention $^{18,19}$.

Taken together, the results of Experiment 1 demonstrate that just prior to a goal-directed eye movement, the identity of a letter probe is degraded when flankers surround the remapped location of the probe. This effect is greater when flankers share features with the probe than when they are featurally distinct. Thus, visual processing during predictive remapping depends on the visual features of the task-relevant object.

**Experiment 2: The extent of feature-specificity in remapped crowding**

In Experiment 1 the probe and shared-feature flankers were drawn from the same set of letters (L, T or H) from trial to trial. It is possible, therefore, that at least some of the errors in probe identification might have arisen from decision noise associated with selecting between these possible letter identities $^{25,26}$. We ruled out this potential contribution in Experiment 2 by employing flanking stimuli that were never letter probes. In this new experiment we used square Landoldt Cs as flankers in all trials of the shared-feature condition. These distractors were composed of the same vertical and horizontal line segments as the letter probes from Experiment 1, but were never used as probes. In the nonshared-feature condition, the distractors were Os whose circular contours meant that they were featurally distinct from the letter probes (see Fig. 4a, left panel). If featural information is indeed remapped across saccades, as we have suggested, then feature-specific remapped crowding should again be evident with these better-matched stimulus sets.
Chapter 5 - Remapped crowding of visual features reveals an oculomotor contribution to object stability across saccades

Figure 4. Remapped crowding depends on the features of flankers, not their identities.
(a) The shared-feature (red frame) and nonshared-feature (blue frame) displays were matched such that flankers could never be probes. (b) The drop in probe identification accuracy during the pre-saccade interval was significant only when flankers shared features with the probe. (c) There was a significant difference in remapped crowding between shared-feature and nonshared-feature conditions, arising 0 – 100 ms prior to the onset of the saccade. This difference is similar in size to the difference in standard crowding shared-feature [dark red dashed line in (b)] and nonshared-feature conditions [dark blue dashed line in (b)]. Error bars represent one s.e.m. N = 5; * P < 0.05.

As expected, when probes were directly flanked by distractors, the crowding effect was significantly stronger in the shared-feature condition than the nonshared-feature condition \((t(4) = 5.49, P = 0.005\); dashed lines in Fig. 4a). These findings confirm the importance of feature similarity for low-level visual interactions. Importantly, these results also demonstrate standard crowding effects in the presence of flankers with distinct identities from the probe, thus ruling out decision noise as the sole determinant of observers’ difficulty in selecting between probe and flanker identities. As in Experiment 1, observers’ accuracy at identifying the orientation of the Gabor was uniform across conditions (mean accuracy = 93%) and there were no differences in saccadic latencies.

As shown in Figure 4a, when the probe and flankers appeared in opposite visual hemifields, probe performance was lower during the pre-saccade interval of saccade trials than during fixation trials. Crucially, however, this decrement in accuracy for saccade trials was significant in the shared-feature condition \((t(4) = 4.29, P = 0.013)\), but not in the nonshared-feature condition \((t(4) = 2.02, P = 0.114)\). Moreover, during the critical period of remapping (0-100 ms prior to the saccade) accuracy was significantly lower when flankers surrounding the remapped location shared features with the probe than when the flankers
were featurally distinct \((t(4) = 2.82, P = 0.048)\). Note that the size of this decrement was 9%, comparable with the 10% difference observed between shared and nonshared-feature conditions when no saccade was executed and flankers appeared within the same hemifield as the probe (i.e., standard crowding).

**Experiment 3: The spatial extent of remapped crowding**

Flankers degrade object recognition most strongly when they fall within an area approximately half the eccentricity of the probe\(^{20}\), a region referred to as the *critical distance of crowding*\(^{21}\). To examine the spatial extent of feature processing at remapped locations, in Experiment 3 we varied the distance of the flankers from the remapped location of the probe (see Fig. 5a, left panel). The probe’s remapped location was 3.9° from fixation, and the flankers were either 1.3° or 2.6° from the probe, i.e., within or outside of the critical distance of the probe’s remapped location, respectively. If crowding depends on the remapped location of the probe, observers’ performance should be worse when flankers are 1.3° from the probe’s remapped location than when they are 2.6° from the probe’s remapped location.

**Figure 5.** Remapped crowding depends on the distance of flankers from the probe’s remapped location. (a) Flankers appeared beyond the critical distance of the remapped location of the probe (blue frame) or within the critical distance of the remapped location of the probe (red frame). (b) Probe identification accuracy diminished during the pre-saccade interval at both flanker eccentricities. (c) Within 100 ms of a saccade, performance was significantly worse in the 1.3° flanker condition than in the 2.6° flanker condition. This difference is similar in size to the difference in standard crowding with flankers at 1.3° from the probe [dark red dashed line in (b)] versus 2.6° from the probe [dark blue dashed line in (b)]. Error bars represent one s.e.m. \(N = 10\); * \(P < 0.05\), ** \(P < 0.01\).
During fixation and when flankers and probe appeared in the same hemifield, observers tended to be less accurate in identifying the probe in the 1.3° flanker condition than in the 2.6° flanker condition \( (t(9) = 2.11, P = 0.064) \); see dashed lines in Fig. 5a). A similar trend was observed during the pre-saccade interval \( (t(9) = 2.03, P = 0.073) \). These trends accord well with studies that have demonstrated the importance of probe-flanker distance in crowding (for a review, see ref. 21). As in Experiments 1 and 2, observers completed the saccade task with high accuracy (mean accuracy = 88%). For the critical remapping conditions, there was no difference in the accuracy of Gabor judgments between the 1.3° and 2.6° flanker conditions. Furthermore, there were no differences in saccadic latencies across flanker conditions.

As can be seen in Figure 5a, when flankers surrounded the probe’s remapped location, probe identification accuracy was lower during the pre-saccade interval than during fixation. This decrement in performance was significant when flankers were 2.6° \( (t(9) = 2.47, P = 0.032) \) and 1.3° \( (t(9) = 4.48, P = 0.002) \) from the probe’s remapped location. Critically, however, as shown in Figure 5b, the time-course of the decrement was markedly different across the two spatial arrangements. At 0-100 ms prior to the saccade, probe identification was significantly poorer for the 1.3° flanker condition than for the 2.6° flanker condition \( (t(9) = 2.78, P = 0.021) \).

By manipulating the distance of the flankers from the probe’s remapped location, we were able to test the spatial extent of visual processing around the probe’s remapped location just prior to a saccade. During remapping, the presence of flankers within the critical distance (1.3°) of the remapped location of the probe reduced probe performance compared with their presence beyond this region (2.6°). Just as recognition of a visual object in the periphery depends on the proximity of surrounding objects, remapped crowding depends on the proximity of visual information around the remapped location of the probe.
DISCUSSION

Just prior to a saccade, visual processing shifts to the predicted, post-saccadic location of a task-relevant visual object $^{1,5,18,19}$. In the present study, we found that the appearance of visual distractors surrounding a probe letter’s predicted, post-saccadic location interfered with observers’ ability to identify the probe. Importantly, we demonstrated that this interference is modulated by the visual similarity of the distractors to the probe: flankers that share features with a probe impair performance relative to flankers that are featurally dissimilar from the probe. Thus, our results reveal that visual features are preserved during remapping. Previous studies have linked pre-saccadic shifts of visual processing with perceptual stability across eye movements $^{13,28}$. Our experiments show for the first time that these predictive shifts result in the selective processing of a remapped object’s visual features, and can therefore support object continuity across saccade-induced retinal displacements.

The temporal profile of remapped crowding closely matches the time-course of activity of remapping neurons that fire in anticipation of a visual stimulus arriving in their receptive field following an eye movement $^{1,3}$. In addition to being temporally specific, the spatial area within which distractors cause the most interference is restricted to an area immediately surrounding the probe’s future retinotopic location. The dependence of remapped crowding on the features of the flankers also allows us to rule out the possibility that remapped crowding is due to a general impairment of performance during saccade preparation, and makes remapped crowding distinct from trans-saccadic backward masking $^{19,29}$. In a Supplemental Experiment (N = 10), we also found remapped crowding for vertical saccades, revealing the effect is not unique to the horizontal meridian (see Supplementary Fig. 1).

The featural sensitivity of remapped crowding reveals that visual features are preserved during predictive remapping. Just prior to saccade initiation, visual processing at the future retinotopic location of a visual object is tuned to the features that most closely match the object. Thus, not only is the location of a potentially relevant visual object updated just prior to a saccade $^2$, but visual sensitivity to the object’s features is also increased in anticipation of those features appearing at the remapped location. Such preservation of an
object’s features via remapping could facilitate the subjective impression of object continuity despite substantial changes in retinal inputs across saccadic eye movements.

We propose that the preservation of featural information across saccades is mediated in a top-down fashion by brain areas involved in both remapping and visual selection. The frontal eye fields (FEF), for example, contain remapping neurons and specify the locations of visual objects with task-relevant features. Just prior to a saccade, neurons in such remapping areas can signal both the position and featural information of an object that will shift on the retina. Reciprocal links between FEF and area V4 allow dynamic, spatiotemporal changes in featural processing at remapped locations. Top-down mediation of featural remapping provides a mechanism by which the subjective impression of trans-saccadic object continuity can be achieved via purely retinotopic representations, without the need to transfer feature gain settings of low-level visual neurons as previously suggested. Our account is in line with recent studies showing that the degree of post-saccadic remapping can be modulated by instructing observers to attend to the remapped location of objects (but see ), as well as a recent brain imaging study showing that a world-referenced representation of motion depends on the allocation of spatial attention to the motion stimulus.

The spatial characteristics of remapped crowding are markedly different from those of standard crowding. In standard crowding the probe and flankers appear in close spatial proximity, but in remapped crowding the flankers appear in the opposite visual hemifield to the probe. Given this difference in the physical arrangement of stimuli, the similar loss of object recognition can be attributed to the importance of spatiotemporal integration in visual crowding (see Supplemental Material of Ref 14). During predictive remapping, there is a brief window of time in which visual processing is prioritised at the location of the probe and, simultaneously, at its predicted location. Thus, remapped crowding arises because visual information is drawn from both the probe and the flankers, resulting in visual interference. This is in line with recent evidence from our lab showing that oculomotor signals play an important role in visual crowding (Harrison, Mattingley, Remington, Under Review).
In summary, we have shown that during eye movement preparation visual processing is altered to anticipate the appearance of task-relevant features at the predicted, post-saccadic location of a visual object. Under natural conditions, top-down featural remapping allows an uninterrupted and stable representation of visual objects across shifts of gaze, as relevant object features are primed at remapped locations in expectation of these features arriving there following the eye movement.
AUTHOR CONTRIBUTIONS

W.J.H., J.D.R., R.W.R, and J.B.M designed the experiments. W.J.H. conducted the experiments and analysed all data. W.J.H., R.W.R. and J.B.M. wrote the manuscript. All authors discussed the results and commented on the manuscript.

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COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.
METHODS

Observers

Twelve observers (4 females, 2 authors) participated in the experiments (five observers in Experiments 1 and 2, and 12 observers in Experiment 3). All observers had normal or corrected-to-normal vision. The study was approved by The University of Queensland’s School of Psychology Ethical Review Committee.

Materials

Participants sat with their head in a head and chin rest positioned 57 cm from a 22-inch widescreen Dell LCD monitor (1920 x 1200 pixels, 60 Hz) in Experiments 1 and 2, and a 20-inch Dell CRT monitor (1600 x 1200 pixels, 60 Hz) in Experiment 3. Stimulus presentation, eye movement recording and response collection were programmed using the Psychophysics Toolbox Version 3 and EyeLink Toolbox for MATLAB (MathWorks). Eye movements were recorded at 500 Hz with an EyeLink 1000 (SR Research) infrared eye tracker, calibrated using a 5-point calibration procedure.

Stimuli and procedure

Each trial began with the presentation of a fixation dot (width = 0.2°) at the center of a uniform gray display (31.2 cd/m²). Four placeholders (0.9° x 0.9°) in Experiments 1 and 2, and six placeholders in Experiment 3, were positioned to the left and right of the fixation spot, along the horizontal meridian. The distance from the fixation dot to the center of the nearest placeholder, and between the centers of adjacent placeholders, was 1.3°. There was a gap of 0.4° between adjacent placeholders. All placeholders were outlined in black with the exception of either the far left or far right placeholder, which was outlined in green to indicate the saccade goal and the location of the Gabor. The side of the saccade goal was selected with equal probability across trials and presented in a pseudorandom order. The distance from the fixation dot to the center of the saccade goal was 5.2° in Experiments 1 and 2, and 7.8° in Experiment 3. To reduce perceptual distortions of space around the time of the saccade, and to eliminate transients associated with the onset and offset of the probe and any flankers, all placeholders were filled continuously with animated white noise, except during the target frame (Fig. 2b). White noise was
randomised on each screen refresh (each pixel value was pseudorandomly and independently drawn from a normal distribution, $M = 128$, s.d. = 50).

Each trial began only if gaze was maintained within a $2^\circ \times 2^\circ$ area centered around the fixation spot for 500 ms. The fixation spot disappeared after a uniformly variable delay (750-1250 ms), cueing participants to execute the saccade. The saccade target (a Gabor oriented 22.5° left or right from vertical), letter probe, and any distractors were presented in a single frame during the pre-saccade interval (see below), and were immediately followed by dynamic white noise inside each placeholder. After 500 ms of white noise, participants reported the Gabor orientation with a button press (left or right arrow). If the orientation of the Gabor was reported correctly, the text, “T L or H?” was presented; participants then made a three-alternative forced-choice judgment on the identity of the letter probe via button press (left, down, or right arrow, for T, L and H, respectively). Observers were instructed that the letter probe to be identified would always appear in the placeholder located mid-way between fixation and the saccade target (i.e., the third placeholder from the end of the array). During testing, no feedback was given about letter probe performance. If participants reported the orientation of the Gabor incorrectly, they were provided with on-screen feedback and informed that the trial would be repeated at the end of the block. After responses were made and any feedback given, the next trial commenced immediately. Saccade and fixation blocks of at least 16 trials were alternated, giving a minimum of 480 trials per participant. The colour of the fixation spot changed to indicate whether the observer was required to execute a saccade (indicated in blue) or remain fixated (indicated in red).

The target frame, including the letter probe, Gabor, and any distractors, was presented for 17 ms. Letter probes, distractor letters (Experiment 1) and square Landoldt Cs (Experiments 2 and 3) were constructed from rectangles ($0.9^\circ \times 0.3^\circ$) arranged to form each symbol (T, H, L, C). Oval distractors in Experiments 1 and 2 had a diameter of 0.9°, and a line width of 0.3°. In Experiment 2, Landoldt Cs were always oriented with the gap on the right to ensure their identities were as consistent over trials as the dissimilar feature distractor identities (Os). In Experiment 3, the direction of each Landoldt C was randomised from trial to trial. In all experiments, probes and distractors were white (100% contrast). Based on data from a pilot study, the Gabor (1.4 cpd, 100% contrast) was
oriented 22.5° left or right off vertical. Correct identification of the saccade target required close allocation of spatial attention toward the saccade goal, and away from the letter stimuli in the remapped crowding condition.

The interval between the saccade cue (the offset of the fixation spot) and the target frame was adjusted so the target frame was presented during the pre-saccade interval on the majority of trials (see Fig. 2). This interval was calculated by subtracting 100 ms from the median saccadic latency. To time the target frame, saccadic latencies were calculated online as the time between the offset of the fixation spot and the time gaze deviated from this fixation point by more than 2°. Each experiment began with a block of saccade trials, and the median saccadic latency of the first trial of the first saccade block was estimated at 200 ms. Median saccadic latencies were calculated from all preceding saccades in the current block only. Reported saccadic latencies, and those used for all analyses, were recalculated offline using the native EyeLink saccade detection criteria. This method of timing target presentations worked well and yielded close to 50% of trials in each time bin (see below and Fig. 2). The interval between the saccade cue and target frame from the most recent saccade trial was used for the following block of no-saccade trials.

Observers completed a minimum of 60 trials per distractor condition in all experiments, collapsed across probe side (left or right). The same number of trials was completed for each condition during fixation. All participants completed at least one block of 20 trials in which all stimuli were displayed as described above, but the task was to execute a saccade and report the orientation of the Gabor only. This practice block was repeated until accuracy at the Gabor orientation task exceeded 75%. Observers also completed at least one practice block of saccade and letter identification tasks, and then an entire run of trials as practice. Data from practice blocks were discarded.

Data pre-processing and statistical analyses
Trials were discarded for the following reasons: (1) no saccade was executed or the saccade endpoint was greater than 2° from the center of the saccade target in saccade trials; (2) saccadic latency was shorter than 100 ms; (3) a saccade greater than 2° was executed within 500 ms of the removal of the fixation spot on fixation trials; (4) the target...
frame was presented during an eye-blink. Of the remaining trials, “pre-saccade” trials were those in which the onset of the target frame preceded the saccade by more than 17 ms, and by less than 200 ms. Trials in which the target frame onset occurred outside of these periods were excluded. For Experiment 3, data were excluded for one observer due to their poor performance at identifying the orientation of the Gabor (mean accuracy = 67%), and for one observer for whom there were less than 10 observations for each of two conditions. In total, 86.3% of trials were included in Experiment 1, 88.8% in Experiment 2, and 89.3% in Experiment 3. Pre-saccade trials were binned according to their onset time relative to the saccade (see Fig. 2). Of all included pre-saccade trials meeting the above criteria, 48.1% occurred 0-100 ms prior to the saccade in Experiment 1, 51.7% occurred 0-100 ms prior to the saccade in Experiment 2, and 49.4% occurred 0-100 ms prior to the saccade in Experiment 3. We analysed differences in probe accuracies in Experiment 1 using a 2 x 2 within subjects ANOVA. All other differences were evaluated with planned comparisons (two-tailed paired t-tests) and α = 0.05.
REFERENCES


Supplementary Information

Remapped crowding of visual features reveals an oculomotor contribution to object stability across saccades

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Supplementary Figure 1. Remapped crowding for vertical saccades.
To rule out the possibility that the results from Experiments 1-3 are unique to horizontal saccades, we ran a Supplemental Experiment to test whether remapped crowding also occurs for vertical saccades. (a) The critical display used to test remapped crowding for vertical saccades. The saccade target (green square) was 7.8° from the center of the display, and the probe (letter H in this example) was 3.9° from the center of the display. All other stimulus and timing details were as per Experiment 3. (b) The proportion of letters correctly identified when probes and flankers appeared in no-saccade trials and in the pre-saccade interval of saccade trials. Relative to no saccade trials, probe performance was significantly reduced during the pre-saccade interval when flankers surrounded the probe’s remapped location. Thus, remapped crowding also occurs for vertical saccades and is not unique to horizontal saccades or situations in which stimuli are presented on the horizontal meridian. Error bars show one s.e.m. N = 10; ** P = 0.006.
Chapter 6 - General Discussion and Conclusions
In the preceding chapters, I reported novel results showing how eye movement preparation and execution alter object identification in peripheral vision. A key finding, which emerged as a consistent pattern across all experiments, was that the observed changes in peripheral visual processing could be attributed to extra-retinal signals generated during the preparation and execution of oculomotor actions. My studies add significantly to our understanding of the relation of perception to oculomotor control. To summarize the main findings, the spatial extent of visual crowding is reduced at the goal of a saccade (Chapter 2), but expanded contraversive to the direction of a pursuit eye movement (Chapter 3). Following an attentional cue, perception is facilitated for visual targets that appear either at the position of the cue, or in the direction of an impending saccade (Chapter 4). Finally, visual processing during predictive remapping is selective for the features expected to shift on the retina across saccades (Chapter 5). Below, I describe the broad implications of these novel findings and how they contribute to our understanding of visual crowding, visual attention, and predictive remapping. Before summarizing the conclusions of the thesis, I describe ideas for future studies that address potentially important questions arising from my results.

**Implications for visual crowding**

That eye movements affect crowding has important implications for theories of crowding. A prominent view of crowding posits that it results from compulsory interactions between features represented by different visual neurons over a fixed cortical distance in brain areas such as the primary visual cortex (Pelli & Tillman, 2008). This account suggests that features from nearby objects are pooled at least as early as V1, leading to a loss of discriminability of the identity of individual elements (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001). However, the reduction of crowding at a saccade target (Chapter 2) and the expansion of crowding contraversive to smooth pursuit (Chapter 3) imply that the spatial extent of crowding is more flexible than would be expected were information to be lost entirely at the level of V1. Indeed, a recent functional magnetic resonance imaging experiment found that the neural representation of a crowded percept was weakest in V1 and greatest in V4 (Anderson, Dakin, Schwarzkopf, Rees, & Greenwood, 2012). This finding suggests that the maximal site of featural integration is V4, not V1 (Parkes et al., 2001), and generally conforms well with the notion that information is averaged across receptive fields that become progressively larger throughout the visual hierarchy (Freeman & Simoncelli, 2011). Thus, crowding is unlikely to be caused solely by information loss in any one visual area (Whitney & Levi, 2011). The modification of crowding by eye
movement signals support multi-stage models of crowding in which individual features are coherently represented in a first stage of processing, and are then combined at a second stage of processing (Levi, 2008; Levi & Carney, 2009). My results suggest that feedback signals from higher brain areas affect the second stage of processing by determining the area over which information is integrated.

Assuming that crowding results at least in part from the integration of features that fall within common receptive fields in V4 (Anderson et al., 2012; Freeman, Donner, & Heeger, 2011), the reduction in crowding for saccade targets (Chapter 2) may be achieved by changes in the properties of V4 neurons during saccade preparation. This suggestion is based on the well-established influence of oculomotor preparation on V4 neural activity (Moore et al., 1998; Moore & Armstrong, 2003), reviewed in Chapter 1 of this thesis. In particular, the finding that the receptive fields of V4 neurons shift toward the goal of a saccade and shrink in size just prior to an eye movement (Tolias et al., 2001) may be the neural mechanism by which crowding is attenuated during saccade preparation. These receptive field changes occur during the same pre-saccadic time period as the reduction of crowding found in Chapter 2, further supporting a link between the two findings. However, whether changes in V4 alone can account for the pre-saccadic release of crowding, or whether saccade preparation affects form integration across a range of visual areas thought to be involved in crowding (e.g. Anderson et al., 2012) remains an important question. In any case, the modification of crowding during saccade preparation suggests that the neural systems involved in eye movement generation are linked with the neural systems that give rise to crowding. This hypothesis is supported further by our finding of a close correspondence between saccadic precision and the spatial extent of crowding just prior to saccade onset, and preliminary findings from another lab that show a strong correlation between the elliptical profile of saccade endpoints and the elliptical profile of crowding across a range of eccentricities and individuals (Greenwood, Szinte, Sayim, & Cavanagh, 2012).

An important consideration in understanding the neural systems that determine the spatial extent of crowding is whether the mechanisms involved in the changes of crowding at the saccade goal are similar to, or distinct from, the mechanisms that mediate the changes in crowding trailing the pursuit target during smooth pursuit eye movements (Chapter 3). Although I found that saccade and pursuit eye movements affected the spatial extent of crowding differently, it is tempting to speculate that the reduction of crowding at the saccade goal and the expansion of crowding trailing the pursuit target may both
function to facilitate perception of the most behaviorally relevant stimulus, i.e. the target of the eye movement. In the case of saccades, object identification is enhanced for the saccade target. In the case of smooth pursuit, a reduction in discriminability of non-pursued objects close to the fovea may facilitate perception of the pursuit target. This latter hypothesis requires further testing, but nonetheless raises the possibility that the spatial extent of crowding is not simply influenced differentially for each class of eye movement, but that it is influenced more generally according to the specific behavioral goals of the observer.

Perhaps the most surprising result presented in this thesis is the finding that flankers in one hemifield can crowd a visual probe in the opposite hemifield (Chapter 5). Remapped crowding supports the notion that extra-retinal signals related to oculomotor control play a role in visual crowding as described above. Furthermore, this result brings together and extends prominent theories from the crowding literature and remapping literature. First, remapped crowding extends the predictive remapping hypothesis proposed by Cavanagh et al (Cavanagh, Hunt, Afraz, & Rolfs, 2010a). They argued that pre-saccadic changes in the activity of neurons throughout oculomotor and visual brain areas remap the “pointers” that indicate locations of task-relevant information. In my remapped crowding experiments, the pointer indicating the position of the probe is remapped just prior to a saccade to the predicted, post-saccadic location of the probe -- a position flanked by distractors. Thus, visual processing of flankers is prioritized, and perception of the probe is degraded. Critically, by showing that remapped crowding is stronger when flankers are featurally similar to the probe, my results reveal that remapped “pointers” not only indicate the predicted location of objects, but also specify which visual features will appear there following the saccade.

Second, remapped crowding extends models of crowding in which features are pooled at a second stage of analysis following feature extraction (Levi, 2008). That flankers in one visual hemifield can crowd a visual probe in the opposite hemifield during predictive remapping suggests that features can be pooled from non-adjacent locations. Therefore, the area over which features are pooled depends upon specific motor actions, or, more specifically, the pointers involved in remapping the positions of behaviorally relevant objects across saccades (Cavanagh, Hunt, Afraz, & Rolfs, 2010a). These same pointers may be involved in reducing crowding at the goal of saccade (Chapter 2) by “pointing” to the saccade target. During smooth pursuit, these pointers could indicate the position of the pursuit target, increasing the area of crowding located opposite to the
direction of these pointers and therefore contraversive to the direction of pursuit (Chapter 3). Whether the explanatory power of assuming oculomotor pointers determine the extent of feature pooling extends to other crowding phenomena remains to be determined, but nonetheless provides a novel view of the cause of visual crowding.

Implications for visual attention

Although improvements in perception prior to a saccade have been taken as evidence of a relationship between oculomotor selection and visual attention (Deubel & Schneider, 1996; Kowler et al., 1995), my findings suggest a dissociation between changes in perception associated with visual attention and changes in perception associated with eye movements. Directing visual attention towards a crowded target does not always result in a change in critical spacing (Scolari, Kohnen, Barton, & Awh, 2007), and, to date, manipulations of visual attention have been found to have only a modest effect on the spatial extent of crowding (Yeshurun & Rashal, 2010). In my study, in the condition in which observers were required to refrain from making eye movements, observers knew with 100% certainty where the crowded target would appear from trial to trial (and thus were free to devote attention covertly to this location), yet this was the condition in which crowding was strongest (Chapter 2). In contrast, preparing a saccade to the target location reduced the spatial extent of crowding by almost 50%, implying that visual processing benefits associated with the saccade affect crowding much more strongly than benefits associated visual attention. Rolfs and Carrasco (2012) also found that changes in perception during saccade preparation were temporally distinct from changes associated with covert shifts of visual attention alone. Thus, despite a large degree of overlap in the brain regions involved in visual attention and saccades (e.g. Corbetta et al., 1998), the perceptual outcomes and temporal dynamics can be clearly differentiated.

Results from my study of smooth pursuit eye movements and crowding (Chapter 3) also suggest a dissociation between the effects of eye movements and the effects of visual attention on perception in peripheral vision. I found that smooth pursuit eye movements increased the spatial extent of visual crowding contraversive to pursuit direction. Importantly, I found that when the position of a probe was known with 100% certainty, observers’ discrimination accuracy was precisely predicted by performance when the probe position was unpredictable. That is, identification of the probe did not change even when observers were given the opportunity to prioritize visual processing at the probe location. Thus, whereas the pursuit eye movement modified probe identification,
visual attention did not. One might argue that the lack of an effect of visual attention on probe identification during pursuit is explained by the relative inflexibility of visual attention during pursuit eye movements. Across several experiments, Lovejoy and Krauzlis (2009) found that observers’ ability to recognize a visual probe during smooth pursuit was almost perfect at the fovea, and that accuracy dropped sharply when the probe appeared in peripheral vision. They suggested that their finding was indicative of visual attention being tightly focused on the pursuit target. This may explain why, in my experiments, probe identification accuracy did not change when observers knew the probe position relative to when the probe position was unpredictable. Regardless of whether visual attention failed to modify crowding or whether observers’ attention was inflexibly focused on the pursuit target, both accounts are in line with my suggestion that eye movements and visual attention can be dissociated in the way they interact with peripheral visual processing.

Future directions

The relationship between the oculomotor system and visual crowding requires further investigation to establish the degree to which the two are related. Can other characteristics of crowding be explained by assuming a contribution from oculomotor systems? For example, an established characteristic of crowding is that flankers further from fixation than the probe will cause more crowding those closer to fixation (see Figure 2 in Chapter 1). In the test of changes in crowding at the saccade target, I found saccade endpoints have a similar inward-outward anisotropy (Chapter 2). As shown in Figure 1 below, the proportion of saccades that fell short of the target center (yellow shaded area) was greater than the proportion of saccades that overshot the target center (gray shaded area). I chose not to include this analysis or the figure in Chapter 2 because the a priori expectations for the interaction between saccadic endpoint anisotropy and crowding anisotropy are not clear. To better understand this relationship, one could test the pre-saccadic reduction in crowding when a single flanker is positioned closer to fixation than the target, compared with the pre-saccadic reduction when the flanker is positioned more eccentric than the target. It is possible that the inner-bias in saccade endpoints will result in a greater reduction in crowding for inner-flankers than outer-flankers. Such a result would lend further support to the idea that spatial information used to compute saccades plays a role in determining the spatial extent of crowding.
Figure 1. In-out anisotropy of saccade endpoints. This figure shows the frequency distribution of saccade endpoints according to their deviation from the saccade target center. These data are from Experiment 2 in Chapter 2, but were not reported in that chapter. Negative values show the frequency of saccades that fell short of the target center, and positive values show the frequency of saccades that overshot the target center. The proportion of saccades that fell short of the saccade target center (yellow shaded area) is greater than the proportion of saccades that overshoot the target center (gray shaded area). Whether this inner-bias is related to the in-out anisotropy of crowding zones remains to be tested.

The finding that the spatial extent of visual crowding decreases at the goal of a saccade may suggest that the spatial resolution of peripheral vision is modified during saccade preparation. This possibility could be tested directly by measuring a full contrast sensitivity function at the goal of a planned saccade. It is possible that sensitivity to high spatial frequencies will increase as a function of time to saccade. Interestingly, previous studies have found a decrease in sensitivity to low spatial frequencies during saccade preparation (Diamond, Ross, & Morrone, 2000) and execution (Burr et al., 1994). These findings have been taken as evidence for an active suppression mechanism that reduces perception of retinal motion induced by the eye movement itself (Ross et al., 2001), but neither study measured contrast sensitivity functions at the goal of the saccade. Such a study could reveal whether eye movements act to increase spatial resolution for the intended target, while simultaneously reducing sensitivity to low spatial frequencies at non-target locations. Were sensitivity at the goal of a saccade to increase across the entire function, this would be consistent with the recent report by Rolfs and Carrasco (2012) that the strength of a visual signal is enhanced at the goal of the saccade.

My finding that visual processing during predictive remapping is specific to the remapped object raises an important question: Is this selective processing determined by the visual features of the remapped object, or the observer’s expectation about those features? In the experiments in which I tested whether predictive remapping preserves an object’s visual features (Chapter 5), observers monitored for a probe letter that they knew...
was drawn from the letters “T”, “L”, and “H”. Distractors that flanked the probe’s remapped location interfered with probe identification most strongly during predictive remapping when the flankers shared features with the probe. Thus, in these experiments, the flankers that led to the strongest remapped crowding were similar in form to the probe and matched the expectations of the observer, so the unique contributions of these two factors to remapped crowding could not be determined. To test the degree to which an observer’s expectations contribute to remapped crowding, one could manipulate the predictability of the probe’s features relative to those of the flankers. For example, in one block of testing, observers could be instructed to identify a green probe, while in a separate block of testing they could be instructed to identify a visual probe that could be red or green with equal probability. Importantly, in both blocks of testing, the color of a set of flankers on a given trial could be either red or green, again with equal probability. If an observer’s expectation about the features of the probe contribute to remapped crowding, flankers that match the color of the probe should cause greater remapped crowding than flankers that do not match the color of the probe, but only when the color of the probe is predictable. When the color of the probe is unpredictable, remapped crowding should be equivalent for both sets of flankers. Alternatively, however, if predictive remapping is driven in a bottom-up fashion by the features of the probe object, the degree of remapped crowding should be strongest when the flankers are the same color as the probe, regardless of the observer’s expectations. Given the important role of an observer’s expectations in driving shifts of attention (Folk et al., 1992; Folk & Remington, 1998) and the important role of visual attention in predictive remapping (Rolfs et al., 2011), it seems likely that an observer’s expectations will also play a role in determining the degree of remapped crowding.

Future directions for remapping research should also involve identifying the neural correlates of remapped percepts using functional magnetic resonance imaging. However, rather than using simple amplitude estimates of changes in blood oxygen level dependent (BOLD) responses, multi-voxel pattern analysis (MVPA) could be a fruitful technique for these investigations. The aim of MVPA is to decode patterns of activity across large numbers of voxels in response to a given stimulus (Norman, Polyn, Detre, & Haxby, 2006). This approach enables characterization of how a specific stimulus is represented in the brain with greater sensitivity than univariate analyses of changes in the BOLD signal. In MVPA, a subset of the BOLD data is fed into a pattern classifier in order to “train” the classifier to map patterns of activity to experimental conditions. The classifier is then “tested” on a separate subset of the data to see if particular experimental conditions can
be successfully predicted by the multi-voxel patterns alone. Brain regions in which patterns of activity are classified are typically pre-specified (Haxby et al., 2011). A specific brain area is said to be involved in the percept of a stimulus when the classification of voxel activation from that region predicts, with above-chance performance, which stimulus is being viewed (Norman et al., 2006).

MVPA could be used to examine whether brain regions assumed to be crucial to remapping carry featural information across saccades, as would be suggested by my findings in Chapter 5. Previous research suggests that visually evoked activity in the parietal region contralateral to a visual stimulus is remapped to the opposite parietal hemifield following a saccade that would shift the visual stimulus into the opposite visual hemifield, despite the stimulus being extinguished prior to the eye movement (Merriam, Genovese, & Colby, 2003). Given my findings in Chapter 5, it would be expected that this remapped-activity should carry information regarding the stimulus features. In order to test this prediction, different classes of stimuli, for example spiked versus smooth shapes (Williams et al., 2008), would be presented in one visual hemifield in the absence of eye movements. A pattern classifier would be trained to decode patterns of activity in the contralateral parietal cortex that differentiate between the two stimulus classes. In the test phase, the observer would begin each trial by fixating such that the stimulus would fall within the visual hemifield opposite to the hemifield used for training. The observer would then make a saccade to bring the stimulus into the visual field used during the training phase. Critically, however, the visual stimulus would be extinguished prior to the saccade. Thus, activity in the parietal cortex contralateral to the extinguished stimulus location would represent a remapped neural correlate of the stimulus (Merriam et al., 2003). The key question is whether the pattern classifier could decode this remapped activity to predict the category of the stimulus presented prior to the eye movement. If only spatial information is remapped, as proposed by Cavanagh and colleagues (2010a), it should not be possible to decode the stimulus identity from the remapped signal. However, based on my finding that predictive remapping preserves featural information (Chapter 5), I would expect that the remapped activity would be predictive of the type of stimulus presented prior to an eye movement.
Conclusions

The aim of this thesis was to examine the influence of eye movements on object recognition in peripheral vision. The results presented in the preceding chapters shed light on visual crowding and predictive remapping. Crowding has been studied almost exclusively in the absence of eye movements. My studies reveal, for the first time, an important contribution from oculomotor processes. Preparing a saccade enhances discriminability of crowded objects at the goal of the saccade. Smooth pursuit eye movements decrease discriminability of crowded objects contraversive to the direction of pursuit. My studies also provide important insights into predictive remapping. Although saccade preparation systematically biases visual attention in the same direction as an impending saccade following an attentional cue, this is unlikely to be the result of predictive remapping mechanisms. In contrast, I found pre-saccadic visual processing is altered in the opposite direction to an impending saccade in a way that is dependent on the features of the object that will shift on the retina. Taken together, the research presented in this thesis makes clear that vision and action are dynamically linked. Eye movements not only result in a change of the image on the retina, they also change the way in which the visual signal is processed. Critically, the current findings suggest that even when the image on the retina is held constant, the preparation and execution of eye movements dramatically alter the discriminability of objects in peripheral vision.
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Appendix A - Eye movement targets are released from visual crowding

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Behavioral/Cognitive

Eye Movement Targets Are Released from Visual Crowding

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Our ability to recognize objects in peripheral vision is impaired when other objects are nearby (Bouma, 1970). This phenomenon, known as crowding, is often linked to interactions in early visual processing that depend primarily on the retinal position of visual stimuli (Pelli, 2008; Pelli and Tillman, 2008). Here we tested a new account that suggests crowding is influenced by spatial information derived from an extraretinal signal involved in eye movement preparation. We had human observers execute eye movements to crowded targets and measured their ability to identify those targets just before the eyes began to move. Beginning ~50 ms before a saccade toward a crowded object, we found that not only was there a dramatic reduction in the magnitude of crowding, but the spatial area within which crowding occurred was almost halved. These changes in crowding occurred despite no change in the retinal position of target or flanking stimuli. Contrary to the notion that crowding depends on retinal signals alone, our findings reveal an important role for eye movement signals. Eye movement preparation effectively enhances object discrimination in peripheral vision at the goal of the intended saccade. These presaccadic changes may enable enhanced recognition of visual objects in the periphery during active search of visually cluttered environments.

Introduction

Voluntary eye movements are crucial for efficient sampling of the visual environment. During fixation, objects at the fovea receive enhanced processed and are easily recognized, whereas those in the periphery are more difficult to identify, particularly when closely adjacent objects surround them, a phenomenon referred to as visual “crowding” (Bouma, 1970; Pelli and Tillman, 2008). This effect can be experienced by fixating first on the red cross and then on the blue cross in Figure 1A. Note that the letter “Y” is much harder to discern when fixating the red cross than the blue one, even though it is located an equal distance from fixation in the two situations.

Crowding has been assumed to reflect obligatory integration of visual features in early visual areas that represent a region of space which includes both target and nontarget stimuli (Parkes et al., 2001). The extent of this region—the “critical distance”—scales with eccentricity, so that the zone of crowding becomes progressively larger as target stimuli are moved further into the periphery. Critical distance is approximated by Bouma’s law as 0.5 φ, where φ is the eccentricity of the target (Bouma, 1970; Pelli and Tillman, 2008). The spatial extent of crowding can be used to approximate the minimum cortical distance between two objects necessary for accurate object recognition (Pelli, 2008).

Attempts to reduce crowding using spatial cues to indicate the location of the crowded target have yielded mixed findings, and only modest improvements in target discriminability at best (Felisbert et al., 2005; Strasburger, 2005; Scolari et al., 2007; Yeshurun and Rashal, 2010). Thus, it has been suggested that crowding imposes a fundamental limit on conscious vision (Levi, 2008; Whitney and Levi, 2011).

It is well established that responses of visual neurons and perception of uncrowded targets can be modulated by extraretinal signals generated before an eye movement. For example, Moore et al. showed that activity related to an eye movement command in the frontal eye fields (FEF) alters the gain of V4 responses to stimuli presented at the goal of the intended eye movement (Moore and Armstrong, 2003; Moore et al., 2003; Moore and Fallah, 2004). Moreover, Tolias et al. (2001) showed that the receptive fields of V4 neurons shrink in size and shift toward the saccade goal just before a saccadic eye movement. Human psychophysical studies have shown that enhanced identification of uncrowded targets at the goal of a saccade (Remington, 1980) is substantially greater than that arising from visual cues alone (Deubel, 2008). Critically, these neural and perceptual effects are evident before the eyes begin to move, before any change in the retinal location of the target stimulus (Kowler et al., 1995; Deubel and Schneider, 1996; Moore and Fallah, 2004; Deubel, 2008).

The evidence reviewed here suggests that an extraretinal signal involved in saccade preparation (Wurtz, 2008) can enhance perception at the goal of an eye movement. Whether similar perceptual improvements before a saccade occur for crowded targets remains an open question. We therefore tested if visual crowding is reduced when a crowded stimulus is the target of an intended saccade.

Materials and Methods

Overview of experiments. In two experiments, we quantified changes in the magnitude and spatial extent of visual crowding during steady fixa-
**Figure 1.** Demonstration of visual crowding and method used to test crowding before eye movements. **A**, Visual crowding for letter stimuli. In the upper row, the Y in the word “EYES” is virtually impossible to identify while fixating the red cross. In the lower row, the Y on its own is relatively easy to identify while fixating the blue cross, even though it is located at the same eccentricity as the Y in “EYES” above. **B**, Sequence of displays used to quantify the magnitude of crowding before a saccade. At the offset of a blue fixation spot observers executed a saccade to the target and then reported the orientation of the central Gabor. If the fixation spot was red observers maintained fixation and performed the same task on the central Gabor. **C**, Schematic showing the timing of target displays relative to saccade onset. The saccade commences at time 0, and negative times on the x-axis reflect the presaccade intervals over which target stimuli were presented. Saccadic latencies were recalculated continuously online. These latencies were used to determine target-saccade onset asynchronies, such that targets were presented with close to equal probability in each of three intervals before the saccade (−149 to −100 ms; −99 to −50 ms, and −49 to 0 ms; Hunt and Cavanagh, 2011). Dimensions of stimuli in B are not to scale.

which observers executed a saccade to the target placeholder ("saccade" trials). Target presentation durations were brief (<24 ms) and, in saccade trials, were presented at varying times before the eye movement (Fig. 1C, Fig. 2B). Critically, because all orientation judgments were made before the eyes moved, the retinal locations of target and flanking stimuli were identical for the saccade and no-saccade conditions.

**Observers.** Five experienced psychophysical observers (one female) participated in each experiment. Two observers, including one author (W.J.H.), participated in both experiments. All observers had normal or corrected-to-normal vision and gave informed consent. The study was approved by The University of Queensland’s School of Psychology Ethical Review Committee.

**Materials.** Participants sat with their head in a head and chin rest positioned 57 cm from a 20 inch Dell CRT monitor (1600 × 1200 pixels, 85 Hz) in Experiment 1 or 61 cm from a 17 inch Samsung CRT monitor (1280 × 1024 pixels, 85 Hz) in Experiment 2. Stimulus presentation, eye movement recording, and response collection were programmed using the Psychophysics Toolbox Version 3 (Brainard, 1997; Pelli, 1997) and Eyelink Toolbox extensions (Cornelissen et al., 2002) for MATLAB (MathWorks). Eye movements were recorded at 500 Hz with an Eyelink 1000 (SR Research) infrared eye tracker, calibrated using a 9 point calibration procedure.

**Stimuli and procedure.** Each trial began with a fixation spot (width = 0.2°) in the center of a uniformly gray display. As shown in Figure 1B, the target and four flanker positions in Experiment 1 were indicated with black placeholders (1° × 1°). The target in Experiment 1 was 7.7° to the right of the fixation spot, and the center-to-center distance between target and flankers was 1.3°. In Experiment 2, only the target position (7° from central fixation) was indicated with a placeholder, and this placeholder was offset at target onset such that no borders were visible during target presentations. Target and flankling stimuli were Gabors (width = 1°, 2 cpd, 100% contrast) presented for 23.5 ms. Immediately before target presentation, patches of white noise randomized with each screen refresh (85 Hz) were presented at positions corresponding to targets and flankers. In Experiment 1 only, the same dynamic white noise followed target and flanker presentation. Randomly from trial to trial, the combined target and flanker configuration was jittered vertically by ±1° to ensure that observers could not preprogram eye movements throughout each testing session.

A trial began after gaze was detected continuously for 500 ms within a 2° × 2° region centered on the fixation spot. The fixation spot offset after a variable delay of 750–1250 ms (randomly drawn from a uniform distribution), cueing the observer either to make a saccade to the target (blue spot), or to remain fixated (red spot). Runs of saccade and no-saccade trials were alternated in blocks of 12, and testing always began with a saccade block to estimate target presentation times, as described below. In Experiment 1, observers completed 360 trials (180 saccade, 180 no-saccade) in a single testing session. In Experiment 2, each target-flanker separation was tested in a different session, and each observer completed a minimum of two sessions per target-flanker separation. The minimum number of trials completed by each observer in Experiment 2 was 3600.

Using a method similar to that described by Hunt and Cavanagh (2011), the interval between the offset of the fixation spot and target onset was manipulated to maximize the number of trials presented in three time bins before saccade onset (Fig. 1C, Fig. 2B). We estimated the median saccadic latency of a saccade block after each saccade trial, and from this value subtracted 25, 75, or 125 ms to adjust the delay between fixation offset and target onset. During testing only, saccadic latencies were taken as the time between fixation spot offset and the time at which the point of gaze shifted beyond 2° to the right of screen center. Median saccadic latencies were calculated separately for each saccade block. For the first trial of a block we used the median saccadic latency from the previous block. For the first trial of the experiment, median saccadic latency was manually set to 200 ms. These time adjustments were pseudorandomized across a block of trials, such that there were four of each (−25, −75, −125 ms) per block of 12. We then used these time adjustments in the next block of no-saccade trials to ensure stimulus timing was closely matched across saccade and no-saccade blocks. Saccade trial data
were sorted into bins off-line according to the recorded target-saccade onset asynchrony, using a velocity of 30°/s and acceleration of 8000°/s² as criteria for saccade onset. Following target presentation, there was a delay of 500 ms before observers were able to indicate the orientation of the target Gabor (rotated left or right off vertical; unspeeded, two-alternative forced-choice judgment).

Before testing, each observer completed a threshold procedure in which we established the minimum orientation to yield 75% correct identification of an unflanked target Gabor. We took the average orientation yielded by two interleaved QUEST procedures (40 trials each; Watson and Pelli, 1983). The target was presented after a delay of between 12 and 200 ms (randomly drawn from a uniform distribution) following the offset of the fixation spot. Observers were required to maintain steady fixation throughout threshold trials and gaze was monitored on-line. All other trial details during this threshold procedure were as described above.

Statistical analyses. To quantify changes in performance over time and across different target-flanker separations (Experiment 2), we used a permutation analysis described by Rolfs et al. (2005, 2011). Expected performance under the null hypothesis (i.e., that data within each target-flanker condition are temporally invariant) can be estimated by randomly permuting the observed data across time. These permutations were achieved by randomly re-assigning each response to a time bin (without replacement), creating a surrogate time course of data for each individual, from which we derived an average surrogate time course. This procedure was repeated 1000 times to yield a distribution of surrogate means for each time bin, representing an estimate of null performance across time. Using the distributions of permuted data, we calculated 95% confidence intervals around estimated null performance, such that actual data falling beyond these intervals represent significant changes in performance across time. To verify this analysis, we bootstrapped data from each condition to estimate the distribution of the means (Efron and Tibshirani, 1993). In this case, for the number of observations in a given condition for each observer, we randomly sampled data from that condition (with replacement) to create bootstrapped means. By repeating this procedure 1000 times we created a distribution of means from bootstrapped data. From these distributions, we derived confidence intervals around the observed means, where two means falling outside each other’s confidence intervals represents a significant change in performance. This analysis yielded the same significant changes over time as the permutation method.

Curve fitting and critical distance calculations followed previously described analyses (Scolari et al., 2007; Yeshurun and Rashal, 2010). Proportion correct data were modeled using a function with the following equation: \[ pc = a(1 - e^{(-c(d - t))}), \] where \( pc \) is proportion correct, \( a \) is the asymptote, \( s \) is the scaling factor, \( d \) is the target-flanker separation, and \( t \) is the x-intercept. We repeated this procedure for each set of bootstrapped data (see above) to derive the confidence intervals. Critical distance, \( c \), was calculated by: \[ c = 1 - \ln(0.1)/s. \]

We quantified oculomotor precision by fitting an ellipse to saccade endpoints using custom code in MATLAB. We first found the x-y-coordinate of the center of all saccade endpoints, then, unconstrained, found the points in 2D space that created the center-to-edge distances of an ellipse comprising 95% of all points. The axes of the ellipse were calculated by finding the two most extreme pairs of x-y-coordinates on the circumference of the ellipse in horizontal and vertical space.

Eye trace filtering. Trials were excluded if (1) fixation drifted >2° in any direction from the fixation spot; (2) a saccade >2° in amplitude was executed on a no-saccade trial; (3) probe onset occurred earlier than 150 ms or later than 24 ms before a saccade (with the exception of the analysis presented in Fig. 5, see text); (4) the target was presented during an eye-blink; and (5) a saccade endpoint was >2° from the target in Experiment 1, or 4° in Experiment 2. In total, 1373 trials (76%) were included in Experiment 1, and 15,353 trials (79%) were included in Experiment 2.

Results

Experiment 1
We first compared discrimination accuracy for a crowded target to which observers made a saccade with discrimination accuracy for the same target when observers instead maintained fixation centrally. The orientation of the target Gabor was adjusted for each observer using a staircase procedure (Watson and Pelli, 1983) to yield 75% correct responses for targets presented in isolation (i.e., unflanked) when no saccade was planned (see Materials and Methods). As expected, when no saccade was planned the flanking stimuli impaired orientation judgments for the target Gabor, such that observers’ discrimination accuracy fell significantly to

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Figure 2. Influence of saccade preparation on visual crowding. A, Mean percentage correct orientation judgments for a crowded Gabor target during central fixation (black symbol) and at 50 ms intervals before saccade execution (colored symbols). The horizontal red line indicates performance without flanking Gabor. B, Frequency distributions of trials as a function of target-saccade onset asynchrony. Target onset was timed to yield an approximately equal number of observations across three epochs (colored frequency distributions), and trials were screened and divided into 50 ms time bins (individual points). Only trials in which the target-saccade latency was >24 ms were included (i.e., included trials were exclusively those in which the target disappeared before the eyes moved). C, Graph showing mean gaze deviation from screen center during target presentation. Overlapping symbols show that observers maintained fixation close to the screen center in both no-saccade (black symbol) and saccade (colored symbols) trials. D, Mean saccade endpoints corresponded to each of the three jittered target locations (see Materials and Methods). Observers executed eye movements toward the crowded targets with high accuracy, but saccadic errors were generally radially dispersed. Error bars indicate 1 SEM. n = 5.
60 ± 2% (mean ± SEM; two-tailed single sample t test against 75%: \( t_{40} = 5.93, p = 0.004 \); Fig. 2A).

When observers prepared a saccade to the crowded target, orientation judgments improved markedly in the interval between the signal to saccade to the crowded target and the initiation of the saccade (Fig. 2A). When the target and flankers appeared during the 50 ms immediately before saccade onset, orientation judgments were just as accurate as when the target was presented alone (unflanked) with no planned saccade. During this same 50 ms epoch before saccade onset, orientation judgments were also significantly more accurate than in no-saccade trials (two-tailed paired samples t test, \( t_{40} = 4.29, p = 0.013 \)). We screened data from the saccade condition to include only those trials in which the target was offset before the eyes moved (Fig. 2B). Thus, throughout the presaccadic interval, target and flanker stimuli always appeared at exactly the same retinal locations as in the no-saccade trials (Fig. 2C). As shown in Figure 2D, saccades were accurate despite the presence of flanking elements, and saccade endpoints were radially dispersed. The proportion of trials excluded due to saccade error was 5.2, 5.0, and 5.3% for the 0–49, 50–99, and 100–149 ms presaccade conditions, respectively. These values were statistically indistinguishable (pairwise comparisons, all \( ps > 0.69 \), uncorrected), ruling out the possibility that improved performance in the final time bin was artificially inflated by our saccade accuracy exclusion criterion.

To summarize the results of Experiment 1, immediately before a saccade, orientation discrimination accuracy is significantly improved for a crowded stimulus that is the target of an impending saccade. This release from crowding before a saccade yielded target judgments that were just as accurate as those made for unflanked targets at the same peripheral location in the no-saccade condition.

**Experiment 2**

Having established that visual crowding is significantly reduced when a peripheral stimulus is the target of a saccade, we next tested whether the critical distance of crowding around a target is also reduced just before an eye movement. A reduction in critical distance would suggest eye movement signals interact with the distance would suggest eye movement signals interact with the

\[ Efron \text{ and Tibshirani, 1993} \]

To estimate the critical distance of crowding we computed exponential fits to the accuracy data across target-flanker separations, separately for no-saccade trials and for saccade trials in which the target was presented within 50 ms before saccade execution (see Materials and Methods). Figure 4 shows the resulting functions plotted separately for no-saccade trials (gray) and saccade trials (maroon). By convention (Scolari et al., 2007; Yeshurun and Rashal, 2010) the critical distance of crowding is defined as 90% of the asymptotic value for each function (see Materials and Methods). The critical distance for no-saccade trials was estimated at 3.7°. Expressed as a ratio of target eccentricity, this yields a critical distance of 0.53°, conforming well to Bouma’s law (Bouma, 1970; Pelli and Tillman, 2008). In contrast, critical distance during the final 50 ms before a saccade was estimated at 2.0°, or 0.28°, a 47% decrease in the critical distance observed during fixation.

In absolute terms, the critical distance for saccade trials indicates that flankers interfered with identification when they appeared within 2° of the target stimulus. This critical distance estimate is consistent with the accuracy data presented in Figure 3.
3: while accuracy improved significantly when flankers were 2° from the target, no statistically reliable improvements in orientation judgments were observed when target-flanker separations were <2°. The influence of saccade preparation on the critical distance of crowding cannot be attributed to differences in the retinal positions of target and flanker stimuli in saccade versus no-saccade trials. Horizontal and vertical gaze position during target presentation were matched across no-saccade trials and trials in which the target was presented in the final 50 ms before the saccade (Fig. 4B).

In line with studies showing eye movement centers influence visual processing of uncrowded stimuli (Corbetta et al., 1998; Moore and Armstrong, 2003), we propose that oculomotor programming interacts with early visual processes to alleviate crowding. If the reduction in the critical distance of crowding is due to spatially precise selection of the target location immediately before a saccade, then there should be a tight relationship between critical distance and the precision of oculomotor selection. To test this hypothesis, we plotted the accuracy of saccade landing points relative to the target position for all observers (Fig. 5A). The red and purple points show mean saccadic deviation from the target center when flankers were separated from the target by 1° or 5°, respectively. These points fell the same distance from target center, revealing that oculomotor accuracy was unaffected by target-flanker separation. Each black spot in Figure 5A represents the endpoint of a saccade included in the critical distance estimates for Experiment 2. We fitted an ellipse that encompassed 95% of all saccade endpoints (see Materials and Methods). The horizontal extent of the ellipse corresponds to the radial precision of the saccades and the vertical extent denotes the tangential precision. The axes of the fitted ellipse reveal that saccadic precision is poorer in the radial plane than in the tangential plane, with a radial-to-tangential ratio of 1.6. This asymmetry in saccadic precision corresponds closely to the classical radial–tangential asymmetry of critical distance measured using pairs of flankers arranged either radially or tangentially with respect to the target (Toet and Levi, 1992). Moreover, as shown in Figure 5B, the absolute, edge-to-edge spatial extent of crowding when no saccade was planned (gray line) is approximately twice that observed for trials in the 50 ms just before a saccade (maroon line). Note that oculomotor precision (pink line) closely approximates the spatial extent of crowding just before a saccade.

We further tested the extent to which saccade endpoints are related to identification of a crowded target by comparing performance for trials in which saccades deviated from the target center by more than one degree with those in which the saccade fell within one degree of the target center. We performed this

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**Figure 4.** Change in the critical distance of crowding just before a saccade. A. Critical distance of crowding when no saccade is planned (gray fitted curve and vertical line) and in the final 50 ms before a saccade (maroon fitted curve and vertical line). The upper x-axis shows target-flanker separation as a proportion of the target eccentricity, φ. Error bars indicate 95% confidence intervals of the curves, derived from standard bootstrapping procedures (see Materials and Methods; Efron and Tibshirani, 1993). B. Horizontal and vertical gaze position during target presentation, shown as separate colored disks for the no-saccade condition (open symbols) and the 0–49 ms presaccade condition. Colors denote target-flanker separations as in Figure 3. Error bars have been omitted for clarity.

**Figure 5.** Relationship between oculomotor precision and the critical distance of crowding. A. The horizontal and vertical deviations of 8153 saccade endpoints obtained from five observers are plotted on the x- and y-axes, respectively. Position 0°, 0° represents the target center, and the target Gabor extended from −0.5° to +0.5° on both axes. Saccades with negative x-values fell short of the saccade target center, and saccades with positive x-values overshot the target center. An ellipse was adjusted to fit 95% of the saccade endpoints. As shown by the ellipse and its axes, saccadic precision was radially biased. The purple and red points show average deviations of saccade endpoints to targets with flankers at distances of 1 and 5°, respectively. There was no difference between these points; the proximity of flankers to the target did not interfere with oculomotor selection. B. The spatial extent of observers’ oculomotor radial precision closely matches the edge-to-edge spatial extent of crowding within 50 ms before a saccade, and both are approximately half the spatial extent of crowding when no saccade is planned.
analysis separately for three conditions that represent the full range of perceptual performance. We chose (1) the condition in which performance was poorest (100–149 ms time bin, 1° target-flanker separation); (2) the condition in which performance improved the most (0–49 ms time bin, 2° target-flanker separation); and (3) the condition in which performance was best (0–49 ms time bin, 5° target-flanker separation; see Fig. 3). We chose these three conditions to maximize the likelihood of uncovering any effect of saccade accuracy, while limiting the risk of type 1 error due to multiple post hoc comparisons. There was no difference in target discrimination according to saccade accuracy in any of these conditions (ps > 0.81, uncorrected), and the differences in performance were <1.5% within each condition. Thus, performance corresponds best to the overall precision of eye movements (Fig. 5A) rather than the accuracy of saccade endpoints.

Discussion

We have shown that improvements in perception immediately before saccade onset, previously demonstrated with isolated stimuli in sparse displays (Remington, 1980; Kowler et al., 1995; Deubel and Schneider, 1996; Moore and Armstrong, 2003; Deubel, 2008), can also operate to release peripheral targets from visual crowding. By systematically varying target-flanker separations, we also found that the critical distance of crowding established during passive fixation shrinks by approximately half in the 50 ms immediately before saccade onset. The changes in crowding we observed during saccade trials relative to no-saccade trials cannot be attributed to differences in the retinal locations of target and flanker stimuli, as the critical visual events were offset before any eye movements. Moreover, in both saccade and no-saccade conditions observers always knew the precise location of the upcoming target, indicating that the saccade-related mitigation of crowding cannot be ascribed to differences in advance positional information.

The fact that crowding of a target at a fixed retinal eccentricity is significantly attenuated before a saccade implies that extraretinal signals that arise just before the eyes move (Wurtz, 2008) play a key role in modifying the spatial extent of visual crowding, and extend a recent computational modeling report linking crowding and eye movements (Nandy and Tjan, 2012). Enhancement in perceived contrast at the saccade goal (e.g., Rolfs and Carrasco, 2012) might have contributed to the improved discriminability of the crowded targets in our experiments, but our finding that performance improvements varied across target-flanker separations (Fig. 3) suggests that changes in perceived contrast alone cannot account for the results. The change in critical distance just before a saccade (Fig. 4A) reflects the fact that target identification improved most for the smallest target-flanker separations, but did not change for the larger separations. If the presaccadic benefit we have shown were attributable solely to contrast enhancement of the target, this effect should have been equivalent across all target-flanker separations. Moreover, attempts to mitigate crowding by cueing attention to the target, which has also been linked to increased contrast sensitivity (Carrasco et al., 2000), have not yielded reliable reductions in visual crowding (Scolari et al., 2007; Yeshurun and Rashal, 2010).

Changes in the spatial extent of crowding before a saccade suggest that oculomotor signals required for accurate localization of a saccade target can influence responses of visual neurons involved in integrating form information from the peripheral visual field. Such an influence is consistent with evidence for a close functional relationship between oculomotor and visual sensory areas in the primate brain (Wurtz and Mohler, 1976; Umeno and Goldberg, 1997; Moore et al., 1998; Tolias et al., 2001; Moore and Armstrong, 2003; Moore and Fallah, 2004; Gregoriou et al., 2012). In particular, Tolias et al. (2001) found that just before a saccade there is a reduction in the size of the receptive fields of neurons throughout V4, an area thought to be important in crowding (Anderson et al., 2012), as well as a shift of these receptive fields toward the saccade goal. Such a reduction in the size of receptive fields of V4 neurons could result in a corresponding reduction in the critical distance of crowding. Indeed, the mean reduction in receptive field size reported by Tolias et al. (2001) was 2.1°, similar to the 1.7° reduction in critical distance we observed just before a saccade (Fig. 4A). Critically, the changes in receptive field sizes observed by Tolias et al. (2001) were greatest in the final 50 ms before saccade onset, consistent with our findings in human observers.

The observation that crowding is reduced before a saccade is consistent with recent accounts that suggest that crowding arises from imprecise position information for peripheral stimuli. Greenwood et al., (2009) found that the perceived position of target elements can be accounted for by a weighted average of noisy representations of target- and flanker-feature positions. Following this finding, our results can be explained by assuming that operations involved in preparing and executing an eye movement to a crowded target effectively change the weights of target- and flanker-position noise. For example, weightings for flanker stimuli might be reduced just before oculomotor target selection, via suppression of neural activity in FEF associated with distractor stimuli (Schall et al., 1995). In line with this, saccadic accuracy in Experiment 2 was unaffected by the separation between target and flanker stimuli (Fig. 5A). Alternatively, an impending saccade to a crowded target could simply reduce the position noise of the target via a reduction in the size of the receptive fields of V4 neurons that represent the target (Tolias et al., 2001). Performance for crowded targets is well modeled using values for position and identity uncertainty of unflanked targets (van den Berg et al., 2012), suggesting that sharpening of target position estimates could form the basis for reduced crowding before saccades.

Previous studies have linked perceptual enhancements during saccade and nonsaccade conditions to common neural activity in such areas as FEF and posterior parietal cortex, both of which are known to play an active role in saccade generation (Corbetta and Shulman, 2002). Indeed, changes in the gain of V4 neurons occur even when FEF activity is below that required to trigger a saccade (Moore and Armstrong, 2003; Moore and Fallah, 2004). In line with these accounts, both the elliptical shape and radial-tangential asymmetry of saccadic precision we observed in Experiment 2 (Fig. 5) correspond to the classic spatial characteristics of crowding zones measured previously (Toet and Levi, 1992). These observations suggest a functional interaction between oculomotor control systems and visual neurons whose responses are susceptible to crowding in the absence of eye movements. Crucially, our data also reveal that the substantial gains in target discriminability and reductions in critical distance for saccade targets arise exclusively in the last 50 ms before a saccade, consistent with recent psychophysical reports for uncrowded stimuli (Deubel, 2008; Rolfs and Carrasco, 2012; Rolfs et al., 2011). The time course of these perceptual changes raises the possibility that, in addition to the benefits associated with target selection alone, visual centers involved in oculomotor preparation and execution can modulate visual sensitivity during the immediate presaccadic period (but see Gregoriou et al., 2012).

Appendix A
An interesting finding in Experiment 2 was that the spatial extent of crowding observed just before a saccade corresponded closely with the overall precision of saccades (Fig. 5). Yet, observers’ ability to identify the target did not vary according to the accuracy of saccade endpoints. This finding suggests that changes in crowding during saccade preparation do not simply depend on the specific outcome of the saccade motor command. In our experiment, presaccadic changes in the identification of a target at 7° in peripheral vision were relatively uniform when saccades landed within 2° of the target. These data show that the benefits from saccade preparation accrue to a region around the intended endpoint and are not determined by the precision of the executed saccade.

In summary, the current findings are consistent with the idea that oculomotor signals associated with intended eye movements can alter the resolution of object identification within a spatial zone immediately surrounding a peripheral saccade target. This hypothesized link between oculomotor control and visual perception is further supported by the finding that the distribution of saccade errors closely matches the characteristic, radially bi-

References


Appendix A
Appendix B - Visual crowding at a distance during predictive remapping

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Visual Crowding at a Distance during Predictive Remapping

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Summary
When we move our eyes, images of objects are displaced on the retina, yet the visual world appears stable. Oculomotor activity just prior to an eye movement contributes to perceptual stability by providing information about the predicted location of a relevant object on the retina following a saccade [1, 2]. It remains unclear, however, whether an object’s features are represented at the remapped location. Here, we exploited the phenomenon of visual crowding [3] to show that presaccadic remapping preserves the elementary features of objects at their predicted postsaccadic locations. Observers executed an eye movement and identified a letter probe flashed just before the saccade. Flanking stimuli were flashed around the location that would be occupied by the probe immediately following the saccade. Despite being positioned in the opposite visual field to the probe, these flankers disrupted observers’ ability to identify the probe. Crucially, this “remapped crowding” interference was stronger when the flankers were visually similar to the probe than when the flanker and probe stimuli were distinct. Our findings suggest that visual processing at remapped locations is featurally dependent, providing a mechanism for achieving perceptual continuity of objects across saccades.

Results

Experiment 1: Remapped Crowding
Each time we make an eye movement, the retinal image is displaced, yet our perception of the visual world remains stable. The visual system achieves perceptual stability by using the magnitude and direction of an impending saccade to predictively update an internal representation of the visual world. Neurons in primate oculomotor areas, including the lateral intraparietal area (LIP), frontal eye fields (FEF), and superior colliculus (SC), begin to respond to visual stimuli outside their receptive fields if an impending saccade will bring the stimulus into the receptive field [1, 4–6]. Such anticipatory activity might provide a neural mechanism for predictive remapping of stimuli to facilitate transsaccadic perception [7]. However, whether presaccadic activity of remapping neurons conveys information about an object’s identity, such as its orientation and shape, has been the subject of intense debate [8–19]. Here we demonstrate that visual processing at predictively remapped locations is contingent on the visual appearance of the remapped object.

We exploited the phenomenon of visual crowding [3, 20] to determine whether processing at remapped locations is sensitive to features of the remapped object (see Figure 1A). A crowded object is difficult to identify because its features are integrated with those of the flanking elements prior to recognition [21]. Flankers that share features with a crowded object impair identification of the object more than flankers with non-shared features [22], and the magnitude of crowding decreases as the flankers are moved further away [3]. Crucially, in the current study, we presented a probe stimulus in one visual hemifield and distractors in the opposite visual hemifield flanking the predicted postsaccadic retinotopic location of the probe (Figure 1B). We further manipulated the similarity of flankers and probes to determine whether featural similarity modulated interference by distractors at the probe’s future retinotopic location during the period of predictive remapping (Figure 1C; and see Figures S1C and S1D available online).

After first establishing a standard crowding effect (Figure S1A), we compared observers’ accuracy for displays in which probe and flanker items shared visual features with their accuracy for displays in which probe and flanker features were different. As expected [22], letter probes were released from crowding when nonshared-feature flankers surrounded the probe. Specifically, probe identification accuracy was lower when flankers and probes shared features (0.50 ± 0.03; mean ± SEM; red dashed lines in Figure 2B) than when they did not (0.74 ± 0.02; blue dashed lines in Figure 2B; \( t = 11.56, p = 3.18 \times 10^{-4} \)).

To measure visual processing during remapping, we required observers to identify a letter probe flashed briefly in the interval immediately prior to execution of a goal-directed saccade to a predictable location (see Figure 1C). The probe appeared in one of four possible flanker conditions: (1) directly flanked by distractors that shared features with the probe (“shared-feature” distractors); (2) directly flanked by distractors that were featurally distinct from the probe (“non-shared-feature” distractors); (3) alone in one hemifield, with shared-feature distractors presented in the opposite hemifield; or (4) alone in one hemifield, with nonshared-feature distractors presented in the opposite hemifield.

Predictive remapping is highly dependent on the time course of stimulus presentation relative to saccade onset [1, 2, 23, 24]. To motivate observers to execute saccades with predictable latencies, therefore, we required observers to report the identity of a brief, masked Gabor at the saccade target in addition to the letter probe (see Supplemental Experimental Procedures). Results from the saccade task are presented in Figure S2.

For critical “remapped crowding” trials (Figure 2A), we compared the accuracy of probe identification when no saccade was planned with accuracy during a brief period just prior to a saccade. As shown in Figure 2B, relative to no-saccade trials, probe performance was significantly reduced during the presaccadic interval when both shared-feature flankers (\( t_s = 6.24, p = 0.003 \)) and nonshared-feature flankers (\( t_s = 3.13, p = 0.035 \)) surrounded the remapped location of the probe.
These results indicate that an object's identity can be degraded by flankers in the contralateral visual field due to predictive remapping. We refer to this presaccadic perceptual effect as "remapped crowding."

A second important finding shown in Figure 2B is that remapped crowding was significantly stronger in the shared-feature condition than in the nonshared-feature condition, suggesting that, as in normal crowding, visual processing at remapped locations is sensitive to feature information. This difference was confirmed by a significant interaction between flanker features (nonshared versus shared) and saccadic condition (no saccade versus presaccade; $F_{1,4} = 30.51, p = 0.005$). Whereas, in the no-saccade condition, probe performance was equivalent across flanker features ($t_4 = 0.8, p = 0.471$), in the presaccade condition, performance deteriorated more when flankers shared features with the probe than when they were featurally distinct ($t_4 = 6.01, p = 0.004$).

We examined the time course of interference from remapped crowding by dividing the presaccade interval into 100 ms bins measured from saccade onset (see Supplemental Experimental Procedures and Figures S1C and S1D). As shown in Figure 2C, the difference in probe identification accuracy for shared-feature and nonshared-feature conditions emerged 100–200 ms prior to saccade onset ($t_4 = 3.82, p = 0.019$) and was greatest 0–100 ms before the saccade ($t_4 = 3.75, p = 0.020$).

The results of experiment 1 demonstrate that, just prior to a goal-directed eye movement, identification of a letter probe is degraded when flankers surround the remapped location of the probe, even though at the time of presentation they appear in opposite hemifields. This remapped crowding effect is greater when flankers share features with the probe than when they are featurally distinct. Our evidence supports the conclusion that predictive remapping leads to crowding at a distance, arising from integration of feature information from the flankers and the remapped object in the opposite visual field.

**Experiment 2: The Extent of Feature Specificity in Remapped Crowding**

In experiment 1 the probe and shared-feature flankers were drawn from the same set of letters (L, T, and H) from trial to trial. It is possible, therefore, that at least some of the errors in probe identification might have arisen from decision noise associated with selecting between these possible letter identities [25, 26]. We ruled out this potential contribution in experiment 2 by employing shared-feature flankers, Landolt Cs, that were never probes (see Figure 3A).

As expected [22, 27], when probes were directly flanked by distractors, the standard crowding effect was significantly stronger in the shared-feature condition than in the nonshared-feature condition ($t_4 = 5.49, p = 0.005$; dashed lines in Figure 3B). These results demonstrate a standard crowding effect from elementary features of flankers and probes in the absence of shared categorical identities.

As shown in Figure 3B, when the probe and flankers appeared in opposite visual hemifields, probe performance was lower during the presaccade interval of saccade trials than during fixation trials. Crucially, however, this decrement in accuracy for saccade trials was significant in the shared-feature condition ($t_4 = 4.29, p = 0.013$), but not in the nonshared-feature condition ($t_4 = 2.02, p = 0.114$). Moreover, an analysis of trials in which the probe was presented during the critical period of remapping (0–100 ms prior to the saccade) revealed a significant interaction between flanker features and saccade condition ($F_{1,4} = 8.39, p = 0.044$). No effect of flanker similarity was observed in no-saccade conditions ($t_4 = 0.31, p = 0.772$). In contrast, accuracy was significantly lower during the period of predictive remapping when flankers surrounding the remapped location shared features with the probe than when the flankers were featurally distinct ($t_4 = 2.82, p = 0.048$; see Figure 3C). The size of this decrement was 9%, comparable to the 10% difference found for similar and distinct flankers under our standard crowding condition.
Remapped Crowding

Although observers’ accuracy at identifying the orientation of the Gabor differed across conditions, further analyses suggest it is unlikely these differences contributed to the remapped crowding effect (see Figure S3). Furthermore, there were no differences in saccadic latencies or amplitudes across conditions.

Experiment 3: The Spatial Extent of Remapped Crowding

Flankers degrade object recognition most strongly when they fall within an area that is approximately half the eccentricity of the probe [20], a region referred to as the “critical distance of crowding” [3]. To examine the spatial extent of feature processing at remapped locations, in experiment 3 we varied the distance of the flankers from the remapped location of the probe. Flankers were either inside (1.3°) or outside (2.6°) the critical distance of the probe’s remapped location (see Figure 4A). If remapped crowding depends on the remapped location of the probe, observers’ performance should be worse when flankers are 1.3° from the probe’s remapped location than when they are 2.6° from the probe’s remapped location.

During steady fixation and when flankers and probe appeared in the same hemifield, observers were less accurate in identifying the probe in the 1.3° flanker condition than in the 2.6° flanker condition (t9 = 2.11, p = 0.064; see dashed lines in Figure 4B). A similar trend was observed during the presaccadic interval (t9 = 2.03, p = 0.073). These trends accord well with previous results on the effect of probe-flanker distance in crowding (for a review, see [3]). Results from the saccade task are presented in Figure S4.

As can be seen in Figure 4B, when flankers surrounded the probe’s remapped location, probe identification accuracy was lower during the presaccadic interval than during steady fixation in both the 2.6° condition (t9 = 2.47, p = 0.032) and the 1.3° condition (t9 = 4.48, p = 0.002). Note that probe identification accuracies in the no-saccade conditions were lower than those in the previous experiments. The probe was likely harder to identify in this experiment due to its greater eccentricity of 3.9° compared with 2.6° in the last experiments. Critically, as shown in Figure 4C, the time course of the presaccadic decrement was markedly different across the two spatial separations. At 0–100 ms prior to the saccade, there was an interaction between flanker spacing and saccade condition (F1,9 = 5.57, p = 0.043); probe identification was significantly poorer for the 1.3° flanker condition than for the 2.6° flanker condition during predictive remapping (t9 = 2.78, p = 0.021), but there was no such difference in the no-saccade condition (t9 = 0.14, p = 0.888). Just as recognition of a visual object in the periphery depends on the proximity of surrounding objects [20], remapped crowding depends on the proximity of visual information to the remapped location of the probe.

Discussion

We found that, just prior to a saccade, the presence of visual distractors surrounding a probe letter’s predicted postsaccadic retinotopic location interferes with observers’ ability to identify the probe. Importantly, this interference is modulated by the visual similarity of the distractors and the probe, as in standard crowding: flankers that are similar to a probe impair performance relative to flankers that are dissimilar to a probe. In a further experiment, we also observed remapped crowding for vertical saccades, suggesting the effect is not unique to the horizontal meridian (see Supplemental Results). Our results reveal that visual features are preserved during remapping. We describe this effect as a “preservation” of visual features, rather than as “feature remapping” per se, because our data do not distinguish between competing accounts of the underlying mechanisms. Instead, our findings call attention to a fundamental regularity in the effects of remapping: just prior to saccade initiation, visual processing at the future retinotopic location of a task-relevant visual object is tuned to the features that most closely match the object.
The temporal profile of the remapped crowding effect measured here closely matches the time course of activity of remapping neurons in LIP [1], area V3 [5], FEF [6, 28], and SC [4], as well as predictive remapping of spatial attention [2, 23, 24]. Hunt and Cavanagh [23] found a similar time course of interference from masks presented at the future retinotopic location of probes. They attributed this “remapped masking” effect to a shift in the priority of visual processing from the probe location to the mask location just prior to an eye movement. Because masking depends on disruption of transient signals, however, no strong conclusions could be drawn about featural information at the remapped location. Our finding that remapped crowding depends on the similarity between flanker and probe stimuli makes remapped crowding distinct from transsaccadic [29] and presaccadic [23] remapped backward masking.

The spatial characteristics of remapped crowding are markedly different from those of standard crowding. In standard crowding, the probe and flankers appear in close spatial proximity [20]. By contrast, in remapped crowding, the flankers appear in the opposite visual hemifield to the probe. Given this difference between the physical arrangements of stimuli,
the analogous reduction in identification accuracy in the standard and remapped conditions is most likely attributable to a common form of spatiotemporal integration of probe and flanker stimuli (see the Supplementary Material of [3]). During predictive remapping, there is a brief window of time during which visual processing is prioritized at the location of the probe and, concurrently, at its predicted location [2]. On this account, remapped crowding arises because visual information is drawn from both the probe and the flankers, resulting in visual interference. Such an interpretation is in line with evidence from a recent study, in which we found that oculomotor signals play an important role in visual crowding [30], and is consistent with the notion that feature preservation during remapping is mediated by higher brain areas, such as FEF [15].

A link between an object's position and identity could be mediated in a top-down fashion by brain areas involved in both remapping and visual selection, potentially negating the need for feature information to be conveyed via the remapping signal itself [7, 15]. The FEF, for example, contain remapping neurons [6] and specify the locations of visual objects with task-relevant features [31]. Thus, just prior to a saccade, neurons in such remapping areas can signal the remapped position of an object with task-relevant features. Reciprocal links between FEF and area V4 allow dynamic, spatiotemporal changes in featural processing [32] at remapped locations [15]. Top-down mediation of feature preservation during remapping provides a mechanism by which transsaccadic object continuity could be achieved via purely retinotopic representations [11–13, 15], without the need to transfer feature gain settings of low-level visual neurons, as previously suggested [10, 33]. Our account is in line with recent studies showing that the degree of postsaccadic remapping can be modulated by instructing observers to attend to the remapped location of objects [34–36] (but see [13]), as well as a recent brain imaging study showing that a world-referenced representation of motion depends on the allocation of spatial attention to the motion stimulus [37].

We have shown that, during eye movement preparation, visual processing is altered to anticipate the appearance of task-relevant features at the predicted postsaccadic location of a visual object. Under natural conditions, top-down preservation of features during remapping would allow an uninterrupted and stable representation of visual objects across shifts of gaze, because relevant object features are primed at remapped locations in expectation of these features arriving there following an eye movement.

Supplemental Information

Supplemental Information includes four figures, Supplemen
tal Results, and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.03.050.

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Supplemental Inventory

Supplemental Figures
Figure S1 shows data from a pilot experiment in which we established standard crowding and remapped crowding effects, and the timing of stimuli according to saccade onset in the main experiments. Figures S2–S4 show results from analyses of the Gabor orientation judgment task, saccadic latencies, and saccade amplitudes for the three main experiments. In Figures S2–S4, pre-saccade trials included only those in which the probe was presented within 100 ms of saccade onset, when remapped crowding was strongest in all experiments. All differences in Gabor accuracy were analysed with 2 x 2 repeated measures ANOVAs, and pairwise t-tests were used to explore any significant interactions. Saccadic latencies and saccade amplitudes were evaluated using two-tailed paired t-tests with α = 0.05.

Supplemental Results
Here we report results from a Supplemental Experiment in which we tested for remapped crowding with vertical saccades (see Discussion in the main text).

Supplemental Experimental Procedures
**Figure S1, Related to Figure 1. Standard Crowding, Remapped Crowding, and Stimulus Timing**

(A and B) Data from a pilot experiment (N = 10). (A) While observers remained fixated in the center of the display, identification accuracy for a probe flanked by letters (red bar) was significantly lower than for a probe presented alone (blue bar; p = 0.004). (B) In the no-saccade condition, the presence of distractors in the hemifield opposite the probe had no effect on probe identification accuracy relative to probe-alone trials (p > 0.10). For trials in which an eye movement had to be executed, however, participants’ accuracy in identifying probes during the pre-saccade interval was significantly reduced when distractors occupied the probe’s remapped location relative to probe-alone trials. Statistical analyses confirmed a significant two-way interaction between saccade condition (no-saccade versus pre-saccade) and flanker condition (probe-alone versus remapped crowding; F$_{1,9}$ = 7.97, p = 0.02). Specifically, the difference in accuracy
between probe-alone and remapped crowding conditions was significant only during the pre-saccade interval ($t_9 = 3.58, p = 0.006$). Furthermore, while the decrease in accuracy from no-saccade to pre-saccade trials was significant for the remapped crowding condition ($t_9 = 3.29, p = 0.009$), there was no such difference for the probe alone condition ($t_9 = 0.99, p = 0.347$). The dashed black line shows performance for the standard crowding condition. Note that it was only in the pilot experiment that the “remapped crowding” display contained two probe letters, one in each hemifield, as shown here. Error bars in (A) and (B) represent one SEM. *** $p = 0.001$; ** $p < 0.01$.

(C) Overview of the timing of probe onset relative to fixation offset in critical “remapped crowding” trials, aligned to saccade onset on the x-axis.

(D) Saccade data from a representative observer in Experiment 1. Frequency of saccadic latency is plotted in orange. Onset asynchrony between probes and saccades is shown in pink. Probe onset latencies were normally distributed around 100 ms prior to the saccade. This method yielded an approximately equal number of observations across 100 ms time bins (see Supplemental Experimental Procedures).
Figure S2, Related to Figure 2. Experiment 1: Gabor Judgment Accuracies, Saccadic Latencies, and Saccade Amplitudes

(A) Gabor judgment accuracy. There were no significant differences in Gabor judgement accuracy across conditions.

(B) Saccadic latencies. Saccadic latencies were equivalent for nonshared- and shared-feature conditions. This implies spatial attention was deployed to the Gabor equally across conditions.

(C) Saccade amplitudes. There was no difference in saccade amplitude across conditions. This implies the Gabor was equally attended across saccade and fixation trials. Error bars in all panels show one SEM.
Figure S3, Related to Figure 3. Experiment 2: Gabor Judgment Accuracies, Saccadic Latencies, and Saccade Amplitudes

(A) Gabor judgment accuracy. We found a marginally significant interaction between flanker condition (nonshared vs shared) and saccade condition (no-saccade vs pre-saccade) for Gabor judgment accuracy ($F_{1,4} = 6.83, p = 0.059$). Follow-up pairwise $t$-tests (without correction for multiple post-hoc comparisons) revealed that, compared with fixation, observers were marginally more accurate at judging the orientation of the Gabor during the pre-saccade interval with shared-feature distractors ($t_{4} = 2.33, p = 0.081$). Furthermore, during the pre-saccadic interval, Gabor judgments were more accurate in the shared-feature condition than in the nonshared-feature condition ($t_{4} = 3, p = 0.04$). It may have been the case, therefore, that improved performance in the Gabor task for the shared-feature condition led to worse performance in the probe identification task during the pre-saccade interval. Indeed, we found a marginally significant correlation between improvement in Gabor accuracy and reduction in probe identification accuracy in the shared-feature condition ($r = 0.82, p = 0.089$). However, Gabor judgment accuracy was not causally related to probe identification accuracy: there was no such correlation for the nonshared-feature condition ($r = -0.21, p = 0.73$); nor was this correlation present in the shared-feature condition of either of the other main experiments (Experiment 1: $r = -0.46, p = 0.439$; Experiment 3: $r = -0.18, p = 0.623$).

(B) Saccadic latencies. Saccadic latencies were equivalent in the two remapped crowding conditions.

(C) Saccade amplitudes. There was no difference in saccade amplitude across conditions. Error bars in all panels show one SEM. * $p < 0.1$, ** $p < 0.05$. 
Figure S4, Related to Figure 4. Experiment 3: Gabor Judgment Accuracies, Saccadic Latencies, and Saccade Amplitudes

(A) Gabor judgment accuracy. There was a main effect of saccade condition (no-saccade vs pre-saccade) on Gabor judgement accuracy ($F_{1,9} = 8.97, p = 0.015$). Critically, however, there was no interaction between flanker condition and saccade condition.

(B) Saccadic latencies. Saccadic latencies were equivalent for nonshared- and shared-feature conditions.

(C) Saccade amplitudes. There was no difference in saccade amplitude across conditions. Error bars in all panels show one SEM.
Supplemental Results

Supplemental Experiment
To test whether the findings from Experiments 1–3 might be unique to horizontal saccades, we ran a Supplemental Experiment (N = 10) to test whether remapped crowding also occurs for vertical saccades. The critical displays used were similar to the remapped crowding display shown in Figure 4A, but were rotated 90° such that all placeholders fell on the vertical meridian. The saccade target was 7.8° from the center of the display, and the probe was 3.9° from the center of the display. Flankers only appeared within the critical distance of the probe’s actual location or remapped location. All other stimulus and timing details were as per Experiment 3 (see Supplemental Experimental Procedures). When flankers surrounded the probe’s remapped location, the proportions of letters correctly identified in no-saccade trials and pre-saccade trials were 0.56 ± .05 (M ± SEM) and 0.45 ± .05, respectively. That is, relative to no-saccade trials, probe performance was significantly reduced during the pre-saccade interval when flankers surrounded the probe’s remapped location (p = 0.006). Thus, remapped crowding also occurs for vertical saccades and is not unique to horizontal saccades or situations in which stimuli are presented on the horizontal meridian.

Supplemental Experimental Procedures

Observers
Twelve observers (4 females, 2 authors) participated in the experiments (five observers in Experiments 1 and 2, and 12 observers in Experiment 3). All observers had normal or corrected-to-normal vision. The study was approved by The University of Queensland’s School of Psychology Ethical Review Committee.

Materials
Participants sat with their head in a head and chin rest positioned 57 cm from a 22-inch widescreen Dell LCD monitor (1920 x 1200 pixels, 60 Hz) in Experiments 1 and 2, and a 20-inch Dell CRT monitor (1600 x 1200 pixels, 60 Hz) in Experiment 3. Stimulus presentation, eye movement recording and response collection were programmed using the Psychophysics Toolbox Version 3 [38, 39] and Eyelink Toolbox [40] for MATLAB (MathWorks). Eye movements were recorded at 500 Hz with an EyeLink 1000 (SR Research) infrared eye tracker, calibrated using a 5-point calibration procedure.

Stimuli and Procedure
Each trial began with the presentation of a fixation dot (width = 0.2°) at the center of a uniform gray display (31.2 cd/m²). Four placeholders (0.9° x 0.9°) in Experiments 1 and 2, and six placeholders in Experiment 3, were positioned to the left and right of the fixation spot, along the horizontal meridian. The distance from the fixation dot to the center of the nearest placeholder, and between the centers of adjacent placeholders, was 1.3°. There was a gap of 0.4° between adjacent placeholders. All placeholders
were outlined in black with the exception of either the far left or far right placeholder, which was outlined in green to indicate the saccade goal and the location of the Gabor. The side of the saccade goal was selected with equal probability across trials and presented in a pseudorandom order. The distance from the fixation dot to the center of the saccade goal was 5.2° in Experiments 1 and 2, and 7.8° in Experiment 3. To reduce perceptual distortions of space around the time of the saccade (e.g. [41]), and to eliminate transients associated with the onset and offset of the probe and any flankers, all placeholders were filled continuously with animated white noise [2], except during the target frame (Figure 1C). White noise was randomised on each screen refresh (each pixel value was pseudorandomly and independently drawn from a normal distribution, M = 128, SD = 50).

Each trial began only if gaze was maintained within a 2° x 2° area centered around the fixation spot for 500 ms. The fixation spot disappeared after a uniformly variable delay (750-1250 ms), cueing participants to execute the saccade. The saccade target (a Gabor oriented 22.5° left or right from vertical), letter probe, and any distractors were presented in a single frame during the pre-saccade interval (see below), and were immediately followed by dynamic white noise inside each placeholder. After 500 ms of white noise, participants reported the Gabor orientation with a button press (left or right arrow). If the orientation of the Gabor was reported correctly, the text, “T L or H?” was presented; participants then made a three-alternative forced-choice judgment on the identity of the letter probe via button press (left, down, or right arrow, for T, L and H, respectively). Observers were instructed that the letter probe to be identified would always appear in the placeholder located mid-way between fixation and the saccade target (i.e., the third placeholder from the end of the array in Experiments 1 and 2, and the fourth placeholder from the end of the array in Experiment 3). During testing, no feedback was given about letter probe performance. To control for any effects of flankers on probe identification that were not specific to an impending saccade, we included blocks of trials in which observers undertook the same task but were required to maintain their gaze centrally at the offset of the fixation point.

The saccade target was always located at the extreme left or right end of the array of placeholders. Participants practiced until they could execute the required eye movement and judge the orientation of the saccade target while performing above chance on the letter probe task (see below). If participants reported the orientation of the Gabor incorrectly, they were provided with on-screen feedback and informed that the trial would be repeated at the end of the block. After responses were made and any feedback given, the next trial commenced immediately. Saccade and fixation blocks of at least 16 trials were alternated, giving a minimum of 480 trials per participant. The colour of the fixation spot changed to indicate whether the observer was required to execute a saccade (indicated in blue) or remain fixated (indicated in red).

The target frame, including the letter probe, Gabor, and any distractors, was presented for 17 ms. Letter probes, distractor letters (Experiment 1) and square Landolt C symbols (Experiments 2 and 3) were constructed from rectangles (0.9° x 0.3°) arranged to form each symbol (T, H, L, C). Oval distractors in Experiments 1 and 2 had a diameter of
0.9°, and a line width of 0.3°. In Experiment 2, Landoldt Cs were always oriented with the gap on the right to ensure their identities were as consistent over trials as the dissimilar feature distractor identities (Os). In Experiment 3, the direction of each Landoldt C was randomised from trial to trial. In all experiments, probes and distractors were white (100% contrast). Based on data from a pilot study, the Gabor (1.4 cpd, 100% contrast) was oriented 22.5° left or right off vertical. Correct identification of the saccade target required close allocation of spatial attention toward the saccade goal, and away from the letter stimuli in the remapped crowding condition [42].

The interval between the saccade cue (the offset of the fixation spot) and the target frame was adjusted so the target frame was presented during the pre-saccade interval on the majority of trials (see Figure S1B and S1C) [23]. This interval was calculated by subtracting 100 ms from the median saccadic latency. To time the target frame, saccadic latencies were calculated online as the time between the offset of the fixation spot and the moment gaze deviated from this fixation point by more than 2°. Each experiment began with a block of saccade trials, and the median saccadic latency of the first trial of the first saccade block was estimated at 200 ms. Median saccadic latencies were calculated from all preceding saccades in the current block only. Reported saccadic latencies, and those used for all analyses, were re-calculated offline using the native EyeLink saccade detection criteria. This method of timing target presentations worked well and yielded close to 50% of trials in each time bin (see below and Figure S1D). The interval between the saccade cue and target frame from the most recent saccade trial was used for the following block of no-saccade trials.

Observers completed a minimum of 60 trials per distractor condition in all experiments, collapsed across probe side (left or right). The same number of trials was completed for each condition during fixation. All participants completed at least one block of 20 trials in which all stimuli were displayed as described above, but the task was to execute a saccade and report the orientation of the Gabor only. This practice block was repeated until accuracy at the Gabor orientation task exceeded 75%. Observers also completed at least one practice block of saccade and letter identification tasks, and then an entire run of trials as practice. For the pilot experiment, participants did not complete an entire run of practice trials. This difference in practice likely accounts for the overall higher accuracy in “no-saccade” trials for the main experiments (e.g. Figure 2B) relative to the pilot experiment (Figure S1B). Data from practice blocks were discarded.

Data Preprocessing and Statistical Analyses

Only trials in which observers correctly identified the orientation of the Gabor were included in analyses. Trials were discarded for the following reasons: (1) no saccade was executed or the saccade endpoint was greater than 2° from the center of the saccade target in saccade trials; (2) saccadic latency was shorter than 100 ms; (3) a saccade greater than 2° was executed within 500 ms of the removal of the fixation spot on fixation trials; (4) the target frame was presented during an eye-blink. Of the remaining trials, “pre-saccade” trials were those in which the onset of the target frame preceded the saccade by more than 17 ms, and by less than 200 ms. Trials in which the target frame onset occurred outside of these periods were excluded. For Experiment 3,
data were excluded for one observer due to poor performance at identifying the orientation of the Gabor (mean accuracy = 67%), and for one observer for whom there were less than 10 observations for each of two conditions. In total, 86.3% of trials were included in Experiment 1, 88.8% in Experiment 2, and 89.3% in Experiment 3. Pre-saccade trials were binned according to their onset time relative to the saccade (see Figure S1D). Of all included pre-saccade trials meeting the above criteria, 48.1% occurred 0-100 ms prior to the saccade in Experiment 1, 51.7% occurred 0-100 ms prior to the saccade in Experiment 2, and 49.4% occurred prior to the saccade in Experiment 3.

Supplemental References