Visual crowding is anisotropic along the horizontal meridian during smooth pursuit

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Humans make smooth pursuit eye movements to foveate moving objects of interest. It is known that smooth pursuit alters visual processing, but there is currently no consensus on whether changes in vision are contingent on the direction the eyes are moving. We recently showed that visual crowding can be used as a sensitive measure of changes in visual processing, resulting from involvement of the saccadic eye movement system. The present paper extends these results by examining the effect of smooth pursuit eye movements on the spatial extent of visual crowding—the area over which visual stimuli are integrated. We found systematic changes in crowding that depended on the direction of pursuit and the distance of stimuli from the pursuit target. Relative to when no eye movement was made, the spatial extent of crowding increased for objects located contraversive to the direction of pursuit at an eccentricity of approximately 3°. By contrast, crowding for objects located ipsiversive to the direction of pursuit remained unchanged. There was no change in crowding during smooth pursuit for objects located approximately 7° from the fovea. The increased size of the crowding zone for the contraversive direction may be related to the distance that the fovea lags behind the pursuit target during smooth eye movements. Overall, our results reveal that visual perception is altered dynamically according to the intended destination of oculomotor commands.

Introduction

In humans, only the central retina—the fovea—is capable of the high-resolution acuity needed to process the visual environment in detail. Thus, when an object moves through space relative to an observer, smooth pursuit eye movements are necessary to keep the moving object relatively stable on the fovea for detailed processing. Pursuit eye movements are responsible for a number of perceptual phenomena, including increased sensitivity to color and high spatial frequencies (Schütz, Braun, Kerzel, & Gegenfurtner, 2008), suppression of motion streaks (Bedell & Lott, 1996; Tong, Aydin, & Bedell, 2007; Tong, Patel, & Bedell, 2005), and distortions of space (e.g., Mitrani & Dimitrov, 1982). It is unclear, however, whether changes in visual processing during smooth pursuit are uniform throughout the visual field or whether they depend on the direction of the eye movement. For example, investigations employing manual response measures suggest that visual processing is enhanced ahead of the pursuit stimulus (van Donkelaar, 1999; Van Donkelaar & Drew, 2002). Conversely, studies employing saccadic latency measures have concluded that pursuit results in saccade inhibition in the direction opposite to the eye movement (Kanai, van der Geest, & Frens, 2003; Tanaka, Yoshida, & Fukushima, 1998). In the present study, we used a sensitive measure of visual processing, visual crowding (Bouma, 1970), to determine whether smooth pursuit alters object identification according to the position of the stimulus relative to the direction of pursuit.

The few studies that have investigated identification of objects in peripheral vision during smooth pursuit suggest object perception in the periphery is poorer during pursuit than during steady fixation (for a review, see Schütz, Braun, & Gegenfurtner, 2011). In one such
behind the pursuit target. These findings suggest that when observers pursued a string of letters that spanned the horizontal meridian, the speed of pursuit was partly selective according to the direction of pursuit.

In a similar investigation, Lovejoy, Fowler, and Krauzlis (2009) tested whether observers’ ability to discriminate an object in peripheral vision during pursuit depends on the position of the object relative to the direction of pursuit. In their experiments, 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 between the pursuit target and the probe, regardless of whether probes were presented in the direction of pursuit, or in the opposite direction. When the likely position of an upcoming probe was indicated by 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.

However, because performance was at chance for conditions in which the target was more than 2° from the pursuit stimulus, the study by Lovejoy et al. (2009) may not have been sensitive to small changes in perception, or to changes in perception much beyond the fovea.

In support of the notion that visual processing is not spatially uniform during smooth eye movements, several studies have found differences in the latency of saccades to targets contraversive to the direction of pursuit compared with saccades to targets in the same direction (Kanai et al., 2003; Tanaka et al., 1998). In these studies, observers were required to pursue a moving stimulus that jumped either forward (i.e., in the same direction as the pursuit eye movement) or backward (opposite to the direction of pursuit), and the observer was required to make a saccade to this new stimulus position. Tanaka et al. (1998) found that saccadic latencies were longer when the required saccade was contraversive to pursuit than ipsiversive to pursuit. Kanai et al. (2003) extended these findings to show that, relative to saccades in the same direction as pursuit, latencies were prolonged when the required saccade position fell anywhere within the visual hemifield opposite to the direction of pursuit. They further showed that this asymmetry disappeared when the required saccade direction was predictable, suggesting the asymmetry in saccadic latency with respect to pursuit direction is not driven by visual factors, but instead by higher-level factors involved in the control of saccadic eye movements.

In the present study, we tested whether smooth pursuit eye movements affect the spatial area over which distractors reduce discriminability of a peripheral stimulus. Our ability to recognize an object in the periphery is largely determined by the spacing between it and any surrounding objects (Bouma, 1970). As shown in Figure 1, 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. This 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 (Pelli, 2008), or because the resolution of visual attention is too coarse to resolve crowded objects (He, Cavanagh, & Intriligator, 1996). 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 (Levi, 2008). Thus, critical spacing quantifies the spatial extent of crowding (Pelli, 2008). Critical spacing scales linearly with an object’s retinal eccentricity, so that it becomes progressively larger for more eccentric targets (Bouma, 1970). When expressed as a proportion of target eccentricity, φ, critical spacing is approximately invariant throughout the visual field (Pelli & Tillman, 2008) ranging from approximately 0.1φ–0.5φ across observers (Toet & Levi, 1992). Along the vertical meridian, crowding is anisotropic; its spatial extent is greater for objects in the upper visual field than for those in the lower visual field (He et al., 1996).

Crowding, as measured by critical spacing, has provided a useful tool to measure changes in visual perception resulting from eye movements. We recently found that, during saccadic eye movement preparation, critical spacing is reduced at the goal of the saccade (Harrison, Mattingley, & Remington, 2013a). In that study, we proposed an account of crowding in which oculomotor programming plays a causal role in determining the area over which information is combined, linking the neural systems involved in eye movements and those involved in perception (see also Harrison, Retell, Remington, & Mattingley, 2013b; Rolfs & Carrasco, 2012). Under this hypothesis, vision can be altered according to the goal of an oculomotor command: The most behaviorally relevant stimulus, the saccade target, receives enhanced processing allowing it to be more easily discriminated from flanking elements. Thus, smooth pursuit may also alter visual crowding in a way that facilitates the eye movement.

The results of Khurana and Kowler (1987) and Lovejoy et al. (2009), described above, suggest that object identification in peripheral vision is degraded during smooth pursuit. These findings are typically interpreted as evidence that visual attention is tightly focused on the pursuit target. Because drawing attention away from a crowded target reduces its discriminability (Yeshurun & Rashal, 2010), focusing attention on the pursuit target might be predicted to increase crowding throughout the visual field during smooth eye movements. Whether changes in visual processing during smooth pursuit will attenuate crowding ahead of the pursuit target (e.g., Van Donkelaar & Drew, 2002), or exacerbate crowding behind the pursuit target (e.g., Kanai et al., 2003) remains an open question. A change in crowding during pursuit would reveal that the neural circuits involved in generating smooth pursuit eye movements interact with those that give rise to crowding. Moreover, any increase in crowding during pursuit would contrast with changes around the time of saccadic eye movements, in which crowding of peripheral targets is significantly attenuated (Harrison et al., 2013a), and suggest that involvement of the oculomotor system is contingent on the specific motor task.

### Methods

#### Overview

We compared the spatial extent of crowding during smooth pursuit with the spatial extent of crowding when no eye movement was made. To test whether crowding during pursuit is altered differentially according to the position of the object relative to the direction of pursuit (Lovejoy et al., 2009), we further compared the spatial extent of crowding on the side of the fovea ipsiversive to the direction of the eye movement (e.g., on the right of the fovea during rightward pursuit), with the extent of crowding on the side of the fovea contraversive to the direction of the eye movement (e.g., on the left side of the fovea during rightward pursuit). During smooth pursuit trials, observers were required to pursue a spot that translated across the display at 10°/s, 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 (Gervais, Harvey, & Roberts, 1984), distractor letters were drawn from a set of letters that excluded the probe letter. To mitigate retinal motion of the probe and flankers during pursuit, which may exacerbate crowding (Bex, Dakin, & Simmers, 2003), 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. The velocity of the pursuit target and Gaussian distribution of probe onset time were such that probes were presented in the center of the display on average (Figure 2). For no-eye movement trials, observers performed the same orientation discrimination task, but all stimuli remained stationary in the center of the display.
Observers

One author (WH) and two experienced psychophysical observers (KS and JR) participated in the experiments. Observers KS and JR were naive 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 and procedures comply with the Declaration of Helsinki.

Setup

Observers sat 57 cm from a 17-inch Samsung CRT monitor (1280 × 1024 pixels, 85 Hz; Samsung, Seoul, South Korea) with their head in a head and chin rest. Experiments were programmed using the Psychophysics Toolbox Version 3 (Brainard, 1997; Pelli, 1997) and Eyelink Toolbox (Cornelissen, Peters, & Palmer, 2002) in MATLAB (MathWorks, Natick, MA). Eye movements were recorded at 500 Hz with an EyeLink 1000 (SR Research, Osgoode, Ontario, Canada), calibrated using a 9-point calibration procedure every 40 trials or as otherwise described (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. For the trial to continue, observers were required to maintain their gaze within a 2° × 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°/s. After a normally distributed time interval (µ = 1000 ms, σ = 250 ms; Figure 2), 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° × 0.5° region, and, for Experiments 1 and 2, appeared to the left or right of the fixation point with equal probability, at an eccentricity of 7° and 3°, respectively. Four different distractors flanked the target, each of which could have appeared to the left, right, above, or below the target. On each trial, the four 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). The target-flanker separation was adjusted according to the method of constant stimuli. In Experiment 1, the center-to-center target-flanker separation was one of nine possible distances, starting with a smallest distance of 0.75° and then increasing in half-degree steps from 1°–4.5°. In Experiment 2, the target-flanker separation ranged from 0.55°–1.35° in 0.1° steps. In one testing session for KS and two for JR, this range was set to 0.75°–1.55°. Flanker contrast was set to 50% in all experiments. Based on pilot investigations, probe contrast was set to 50% for Experiment 1 for all observers, and 5% for WH and 10% for KS and JR 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 × 4 probe orientations × 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. WH completed eight testing sessions for Experiments 1 and 2 (3,456 trials per experiment). KS and JR each completed four testing sessions for Experiment 1 (1,728 trials) and eight testing sessions for Experiment 2 (3,456 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, the velocity of the eye movement relative to the velocity of the pursuit target, 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 2 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 trial-to-trial 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 2).

Statistical analyses

We modeled accuracy data from the main experiments using the Psignifit 3.0 toolbox, which takes into account the number of trials per condition for curve fitting and confidence interval generation (Fründ, Haenel, & Wichmann, 2011). As described by Wichmann and Hill (2001), the psychometric function had the form:

\[ y = 0.25 + (1 - 0.25 - b)^*1/(1 + e^{-2c}) \]

where \( y \) is proportion correct responses, \( b \) is the lapse rate, \( c \) is the midpoint of the function (threshold), and \( d \) is the slope (precision).

To test whether pursuit eye movements affected the spatial extent of crowding, we performed bootstrapping analyses (Efron & Tibshirani, 1993) using the bootstrapped distributions derived from Psignifit. Two observed means that fell beyond each other’s bootstrapped confidence intervals were considered to be significantly different from one another. 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 for pursuit trials, and, from the resulting values, subtracting the difference between contraversive and ipsiversive values from no-eye movement conditions. The same subtraction procedure was performed for precision scores to create the two-dimensional distributions shown in Figure 5.

Control experiments

Observers WH and KS 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 to account for the results found in Experiment 2 (below). Experimental procedures were as described for Experiment 2, and in the Results and discussion, with the following differences. While observers tracked the pursuit target, probe and flanker stimuli were presented simultaneously both contraversive and ipsiversive to the direction of pursuit. 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. 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
Results and discussion

Experiment 1

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 (Collewijn & Tamminga, 1984; Kerzel & Ziegler, 2005; Lovejoy et al., 2009; e.g., Meyer, Lasker, & Robinson, 1985), we used observers’ eye position during probe presentation to calculate the actual retinal eccentricity of the probe on each trial, \( \phi \), and quantified each tested probe-flanker spacing as a proportion of \( \phi \) (Pelli, 2008). The fovea systematically trailed the pursuit target on pursuit trials by an average of 0.16° ± 0.06° (mean ± SD), 0.28° ± 0.05°, and 0.12° ± 0.05°, for KS, WH, and JR, respectively. Because the direction of smooth pursuit was held constant within testing blocks (see 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 (Wallis & Bex, 2012). 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 (Yeshurun & Rashal, 2010).

Figure 3A shows observers’ orientation identification accuracy as a function of probe-flanker spacing. As expected (Bouma, 1970), the proportion of correct orientation identifications increased with larger probe-flanker distances, and this was true for both the no-eye movement and pursuit conditions. We calculated critical spacing by fitting performance for each condition with a two-parameter log function. For each function, we took critical spacing as the probe-flanker distance at which performance reached 0.625 proportion correct (midway between chance and perfect performance [Kooi, Toet, Tripathy, & Levi, 1994; Wallis & Bex, 2012]; see Methods). Critical spacing values are shown as vertical lines in Figure 3A, and are described in detail below.

To determine whether smooth pursuit modified critical spacing for objects 7° from the pursuit target, we used a bootstrapping analysis to simulate distributions of critical spacing for each condition and for each observer (see Methods; Efron & Tibshirani, 1993). Results from this analysis are shown in Figure 4A, 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 rightward, such that crowding contraversive to the direction of pursuit is plotted leftward (blue), and crowding ipsiversive to pursuit is plotted rightward (purple). Although for observer WH critical spacing was greater for pursuit trials than for no-eye movement trials, across observers there were no reliable changes in crowding during pursuit relative to when no eye movements were made.

For a small subset of pursuit trials, the letter probe was presented when the pursuit target deviated from the display center by more than 5° (Figure 2). It is possible, therefore, that at large target-flanker separations the probe or outer-flanker was presented close to
the edge of the display, which may have had an unquantified effect on performance. To rule out this possibility, we re-analyzed our data after excluding all trials in which the pursuit target deviated from the center of the display by more than 5°. We thus included only trials in which the probe and flankers appeared well away from the edge of the display. The new exclusion criterion did not change our results: Crowding during pursuit was not systematically different from crowding during steady fixation, nor were there critical spacing differences between contraversive and ipsiversive pursuit conditions.

We next compared the difference in critical spacing according to the position of the probe relative to the direction of smooth pursuit. Using the values derived from the log functions plotted in Figure 3A, 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 psychometric function (see Methods), which indicates the precision of responses. These values—critical spacing and precision—are plotted against each other in Figure 5A. 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 bootstrapping 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 5A). These data show that the extent of crowding for objects at 7° from the pursuit target is equivalent contraversive and ipsiversive to the direction of pursuit.

**Experiment 2**

Because changes in peripheral visual processing may be restricted to regions closer to the fovea than 7°...
eccentricity (Lovejoy et al., 2009; Van Donkelaar & Drew, 2002), 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 3B, and are presented as in the first experiment. We again calculated probe-flanker spacing according to the actual retinal eccentricity of the probe, φ. Consistent with the first experiment and with previous studies (Collewijn & Tamminga, 1984; Kerzel & Ziegler, 2005; Lovejoy et al., 2009), 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. The average deviations for KS, WH, and JR were 0.14° ± 0.06° (mean ± SD), 0.3° ± 0.04°, and 0.05° ± 0.03°, respectively. Therefore, the observers’ fovea was closer to contraversive probes than to ipsiversive probes.

When gaze is fixed, reducing the retinal eccentricity of the probe while holding the physical probe-flanker spacing constant reliably improves performance (Bex et al., 2003; e.g., Bouma, 1970; Levi, Hariharan, & Klein, 2002; Strasburger, 2005; Toet & Levi, 1992; Wallis & Bex, 2012). However, as shown in Figure 3B, orientation identification at a given probe-flanker spacing was actually worse for contraversive than for ipsiversive probes during pursuit for all observers, despite contraversive probes being closer to the fovea. As shown by the vertical lines in Figure 3B, for pursuit trials critical spacing for contraversive probes was greater than for ipsiversive probes for all observers.

Figure 4B shows the results from the bootstrap analysis of critical spacing when the probe was 3° from the fixation point. (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.
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 and WH (p < 0.0001), but not for JR (p = 0.14).

The bottom panel of Figure 5B 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 significant (p = 0.029). In summary, when probes were 3° from the pursuit target, the spatial extent of crowding increased, and precision of responses decreased, only for probes contraversive to the direction of smooth pursuit.

Because retinal motion affects crowding (Bex et al., 2003), we tested whether differences in retinal motion across conditions contributed to the asymmetry of crowding during pursuit, as shown in Figures 4B and 5B. 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 during probe presentation (Schwartz & Lisberger, 1994; Tanaka & Lisberger, 2001).

Figure 6 shows pursuit gain as stacked density plots and box-and-whisker plots. As expected (Meyer et al., 1985), median gain (box plot bands) was 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 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.

**Mislocalization control experiment**

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, briefly flashed stimuli can be mislocalized during pursuit (Blanke, Harsch, Knöll, & Bremmer, 2010; Brenner, Smeets, & van den Berg, 2001; Kerzel, Aivar, Ziegler, & Brenner, 2006; Mitrani & Dimitrov, 1982; Rotman, Brenner, & Smeets, 2004; van Beers, Wolpert, & Haggard, 2001). Crowding is tuned to perceived rather than physical location (Dakin, Greenwood, Carlson, & Bex, 2011; Maus, Fischer, & Whitney, 2011), 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 contra- and ipsiversive to the direction of the eye movement (e.g., Mitrani & Dimitrov, 1982). 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 arose because contraversive probes were perceived as more distant from the pursuit target than ipsiversive probes, we conducted a control experiment to test for asymmetries in the perceived position of the crowded probe (see Methods).

Figure 7A shows the proportion of trials in which contraversive stimuli were reported as being further away from the pursuit target than concurrent ipsiversive stimuli. 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 $-0.019^\circ$ and $-0.017^\circ$, respectively (see dashed lines in Figure 7A), 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 less than our conservative estimates of the minimum PSE required to nullify the critical distance differences for each observer ($-0.35^\circ$ for KS, and $-0.72^\circ$ for WH; see Methods for calculation details).

To summarize, results from the mislocalization 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.

**Visual attention control experiment**

We conducted a second control experiment in which we tested whether the anisotropy of crowding during pursuit is due to directional differences in visual attention. Directing visual attention away from a crowded probe can increase critical spacing (Yeshurun & Rashal, 2010). Studies of smooth pursuit suggest that the distribution of visual attention during pursuit can be anisotropic (Kowler, 1989; Lovejoy et al., 2009; Tanaka et al., 1998; van Donkelaar, 1999). Kanai et al. (2003) found that asymmetries in saccadic latency relative to pursuit direction can be reduced when observers have prior knowledge about the upcoming saccade-target location. In our experiments, there were no explicit constraints on observers’ visual attention and the probe appeared to the left or right of the pursuit target with equal probability (see Methods).

 Probe discrimination accuracy was tested at the probe-flanker spacing corresponding to each observer’s critical spacing for crowding contraversive to the direction of pursuit (see Methods). This probe-flanker spacing was expected to be sensitive to manipulations
of visual attention. Moreover, by using the contraversive critical spacing for both contraversive and ipsiversive probe presentations, we were able to use the fits shown in Figure 3B to derive clear predictions about expected performance. If knowledge of probe location has no effect on its identification, 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 match the contraversive critical spacing when visual attention was unconstrained in Experiment 2. Because we used the contraversive critical spacing distance, predicted performance for contraversive probe discrimination is 0.625 by definition, and greater for ipsiversive probes.

Predicted performance for observers KS and WH is shown on the gray background of Figure 7B. Visual crowding again depended on pursuit direction, such that discrimination accuracy for contraversive probes was significantly poorer than for ipsiversive probes ($p < 0.0001$). 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. Thus, unlike the anisotropy in saccadic latencies during pursuit that are mitigated when observers have prior knowledge about an upcoming target position (Kanai et al., 2003), changes in visual crowding during pursuit seem to be less influenced by similar higher cognitive factors.

General discussion

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 $3^\circ$ from the pursuit target, but not for objects $7^\circ$ from the pursuit target. Control analyses and experiments revealed that differences in retinal motion, perceived position, and visual attention cannot account for the anisotropy. 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 (Bouma, 1970; Pelli & Tillman, 2008; Pelli, Palomares, & Majaj, 2004; Toet & Levi, 1992; Wallis & Bex, 2012), 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 that are close to the fovea but that are unlikely to be behaviorally relevant (i.e., objects behind the pursuit target). This selective exacerbation of crowding may facilitate perception of the pursuit target, and therefore the pursuit eye.
However, for neither experiment was this correlation contraversive to pursuit direction, on the other hand, and the relative change of critical spacing. Results of this correlation for Experiments 1 and 2 are shown in Figure 8. Indeed, there was a strong correlation between the average distance between an observer’s fovea and the pursuit target, on the one hand, and the relative change of critical spacing. We therefore conducted a post-hoc test of whether foveal error is related to changes in critical spacing. Error bars show one standard error.

movement itself, by reducing the visual salience of trailing background objects. This suggestion is further supported by data from a study by Lovejoy et al. (2009) that show identification accuracy for probes presented in the center of a pursuit target is independent of foveal error. We therefore conducted a post-hoc test of whether foveal error is related to changes in critical spacing. Results of this correlation for Experiments 1 and 2 are shown in Figure 8. Indeed, there was a strong correlation between the average distance between an observer’s fovea and the pursuit target, on the one hand, and the relative change of critical spacing contraversive to pursuit direction, on the other. However, for neither experiment was this correlation statistically significant ($p s > 0.16$), likely owing to our limited sample size. Nonetheless, these trends are consistent with the notion that changes in crowding during pursuit represent a perceptual compensation for the fovea systematically lagging the pursuit target.

We found changes in crowding contraversive to the pursuit direction for probes $3^\circ$ from the pursuit target, but not for probes $7^\circ$ from the pursuit target. Thus, not only were changes in crowding anisotropic, they were limited to a region close to the fovea. However, we cannot determine if this result was due to something unique about our testing conditions. For example, the eccentricity at which changes in crowding occur during pursuit may be determined by a combination of factors, such as physiology, pursuit velocity, and foveal error. In our experiments, the pursuit target velocity was limited to a region close to the fovea. However, we limited sample size. Nonetheless, these trends are consistent with the notion that changes in crowding during pursuit represent a perceptual compensation for the fovea systematically lagging the pursuit target.

However, faster pursuit typically results in a greater distance of the fovea from the pursuit target (Meyer et al., 1985), and the distance from the fovea at which changes in crowding occur may be determined solely by foveal lag (Figure 8).

The absence of any reliable change in identification accuracy when observers knew the probe location in the second control experiment is consistent with the suggestion that visual attention is relatively inflexible during pursuit (Lovejoy et al., 2009). Although Lovejoy et al. found some evidence of attentional cueing effects in the same direction as pursuit, closer inspection of their data suggests an alternative explanation. Their results suggest that observers’ identification accuracy for a probe ahead of the pursuit target was higher when followed by a predictive cue than by a nonpredictive cue, whereas there was no such difference when probes trailed the pursuit target. However, when stimuli were stationary and observers were required to maintain steady fixation, cueing differences were observed both to the left and the right of fixation. Therefore, compared with a no-eye movement condition, smooth pursuit led to worse performance contraversive to pursuit direction, but did not affect performance ipsiversive to pursuit direction. Thus, their data reveal a loss of discriminability for objects contraversive to pursuit direction, as per our current findings, and within a similar range from the pursuit target (approximately $2^\circ$ in their experiments). Taken together, our findings and those of Lovejoy et al. suggest that changes in low-level factors, specifically the area over which visual information is integrated, outweigh contributions from higher-level attention processes that are under an observer’s control.

To rule out completely the possibility that visual attention affects crowding during pursuit, a more systematic approach to controlling attention may be necessary. One way to achieve this would be to vary the relative priority observers are instructed to give to the pursuit and visual discrimination tasks. For example, Souto and Kerzel (2011) combined an eye movement task with a perceptual judgment task and found that instructing observers to prioritize their smooth pursuit eye movements led to worse perceptual performance. Conversely, having observers prioritize the perceptual task led to better perceptual performance, but with longer pursuit latencies and erroneous eye movements. In principle, therefore, it is possible that voluntary shifts of attention could modify anisotropic crowding effects during pursuit when less priority is given to the pursuit task. However, any such modulation by reducing the priority given to the pursuit task would be in line with our hypothesis that changes in crowding facilitate the eye movement. If the pursuit task is less important, so, too, should be the need for facilitation of the pursuit eye movement.

Figure 8. Correlation between foveal lag and change in critical spacing. Experiment 1 is plotted in red, and Experiment 2 is plotted in green, with different symbols showing each observer as per Figure 5. The y-axis shows the contraversive-ipsiversive critical spacing difference for pursuit trials after controlling for the same difference for no eye movement trials. Correlations between foveal lag and Δ critical spacing were 0.96 and 0.97, and slopes were 0.22 and 0.37, for Experiments 1 and 2, respectively. Error bars show one standard error.
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 (Bedell & Lott, 1996; Tong et al., 2005, 2007). For example, Bedell and Lott (1996) 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 with the eyes stationary. Tong et al. (2007) further showed that streak suppression is greatest when probe position and retinal motion are contraversive to the direction of the eye movement. To the best of our knowledge, it is currently unknown whether streak suppression interacts with crowding. A priori, it might be assumed that streak suppression should enhance identification of a probe because it is perceived more clearly than one for which streaks are less suppressed. Such an assumption would predict an increase in crowding ipsiversive to pursuit direction where streaking, and therefore visual interference, should be least suppressed. Clearly, this is the opposite of what we found. Perhaps instead 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. Our suggestion that crowding may mitigate visual streaking is consistent with the finding that streak suppression depends on spatially proximate and dense stimuli (Chen, Bedell, & Öğmen, 1995), the same conditions under which crowding is strongest. This potential relationship between suppression of streaking and visual crowding during pursuit, as well as in the absence of eye movements, will be an important avenue for future research.

Whether crowding is altered during vertical or oblique smooth pursuit eye movements remains an open question. There are differences in the dynamics and neural correlates of vertical versus horizontal smooth pursuit eye movements (Rottach et al., 1996), and so it is possible that crowding will be affected differently for vertical and horizontal eye movement directions. Because the neurophysiology is different for vertical and horizontal eye movements (Chubb & Fuchs, 1982; Keller & Heinen, 1991; Partsalis, Zhang, & Highstein, 1995), unique changes in crowding for each direction of pursuit may shed light on the brain areas involved in crowding. However, as we have speculated above, changes in crowding may facilitate the behavioral goal of foveating a moving stimulus, and we expect this to be the case regardless of the direction of motion.

Taken together, our findings are consistent with the idea that oculomotor goals can modify visual processing (Moore, Armstrong, & Fallah, 2003). Saccade preparation has been shown to alter receptive field sizes of neurons in V4 (Tolias et al., 2001), and to reduce critical spacing at the goal of an intended saccade (Harrison et al., 2013a). Here we have extended this earlier work by showing that the generation of smooth pursuit eye movements also interacts with the compulsory integration of visual features over a region of space (Pelli, 2008). The spatial profile of crowding during saccade preparation is markedly different from that during pursuit, however, so whether a common neural mechanism is involved remains an open question.

We found no change in crowding ipsiversive to the pursuit direction. Without further investigation we can only speculate why this was the case. We note a potential relationship of our findings of increased crowding contraversive to the direction of pursuit and the increased latency for contraversive compared to ipsiversive saccades during pursuit (Kanai et al., 2003; Tanaka et al., 1998). In previous work we have documented a relationship between the magnitude and critical distance of crowding with an impending saccade (Harrison et al., 2013a). It is possible that involvement of the saccade system underlies our findings even in the presence of an ongoing pursuit eye movement. Such an explanation may explain why we found no changes in crowding ipsiversive to pursuit, because saccades in that direction are relatively unaffected by the preceding pursuit eye movement. Recent computational modeling has also linked crowding with saccadic eye movements (Nandy & Tjan, 2012). Nandy and Tjan outlined a model in which crowding in the absence of eye movements arises because the image statistics learned in peripheral vision are distorted by saccades. It is unclear whether this model can explain the changes in crowding during the execution of eye movements we report here and elsewhere (Harrison et al., 2013a), but it is possible that the transient change in perception around the time of eye movements depends on the image statistics learned over a period of time.

Regardless of the specific neural circuitry involved, the finding that smooth pursuit alters the spatial extent of crowding according to the direction of the eye movement suggests that brain areas involved in crowding are dynamically influenced by oculomotor activity.

In conclusion, the current findings suggest that extraretinal signals involved in the generation of smooth pursuit eye movements modulate the spatial extent of crowding. Relative to when the eyes are stationary, form information is integrated over a larger area for objects close to the fovea and positioned opposite to the direction of a pursuit eye movement. This anisotropic change in crowding could be related to streak suppression contraversive to the direction of
pursuit, and might reflect the operation of processes that help to compensate for the fact that the fovea typically trails the pursuit target.

**Keywords:** smooth pursuit, visual crowding, eye movements, visual perception, visual attention, peripheral vision

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