Characterizing the role of disparity information in alleviating visual crowding

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The ability to identify a target is reduced by the presence of nearby objects, a phenomenon known as visual crowding. The extent to which crowding impairs our perception is generally governed by the degree of similarity between a target stimulus and its surrounding flankers. Here we investigated the influence of disparity differences between target and flankers on crowding. Orientation discrimination thresholds for a parafoveal target were first measured when the target and flankers were presented at the same depth to establish a flanker separation that induced a significant elevation in threshold for each individual. Flankers were subsequently fixed at this spatial separation while the disparity of the flankers relative to the target was altered. For all participants, thresholds showed a systematic decrease as flanker-target disparity increased. The resulting tuning function was asymmetric: Crowding was lower when the target was perceived to be in front of the flankers rather than behind. A series of control experiments confirmed that these effects were driven by disparity, as opposed to other factors such as flanker-target separation in three-dimensional (3-D) space or monocular positional offsets used to create disparity. When flankers were distributed over a range of crossed and uncrossed disparities, such that the mean was in the plane of the target, there was an equivalent or greater release of crowding compared to when all flankers were presented at the maximum disparity of that range. Overall, our results suggest that depth cues can reduce the effects of visual crowding, and that this reduction is unlikely to be caused by grouping of flankers or positional shifts in the monocular image.

Introduction

Visual crowding, the increased difficulty in recognizing objects when surrounded by neighboring objects, sets a sensory limit on peripheral object recognition (Bouma, 1970; Levi, 2008; Pelli, 2008; Stuart & Burian, 1962). Knowledge of the properties of visual crowding may reveal important aspects of the underlying processes involved in object recognition and have significant implications for patients with central vision loss, who rely exclusively on their peripheral vision.

In attempting to understand crowding in healthy individuals, a number of key characteristics have been reported. First, the spatial extent of crowding is proportional to the eccentricity of the target object (Bouma, 1970). This relationship, termed Bouma's law, is determined by the underlying organization of visual cortex (Pelli, 2008). Second, more peripherally located objects exert a greater crowding effect than equally spaced, less peripheral objects (inward-outward asymmetry; Bouma, 1973), although this depends on where spatial attention is directed (Petrov & Meleshkevich, 2011). Third, crowding is stronger when objects lie along the radial axis connecting the target and fovea compared to the tangential axis, leading to elliptical peripheral crowding zones where the long axis points towards the fovea (Toet & Levi, 1992; see also Nandy & Tjan, 2012, figure 1).

Crowding has been reported for a range of tasks including vernier acuity (Westheimer & Hauske, 1975), visual acuity (Flom, Heath, & Takahashi, 1963), stereoacuity (Butler & Westheimer, 1978), and orientation discrimination (Westheimer, Shimamura, & McKee, 1976), and has been demonstrated with a wide

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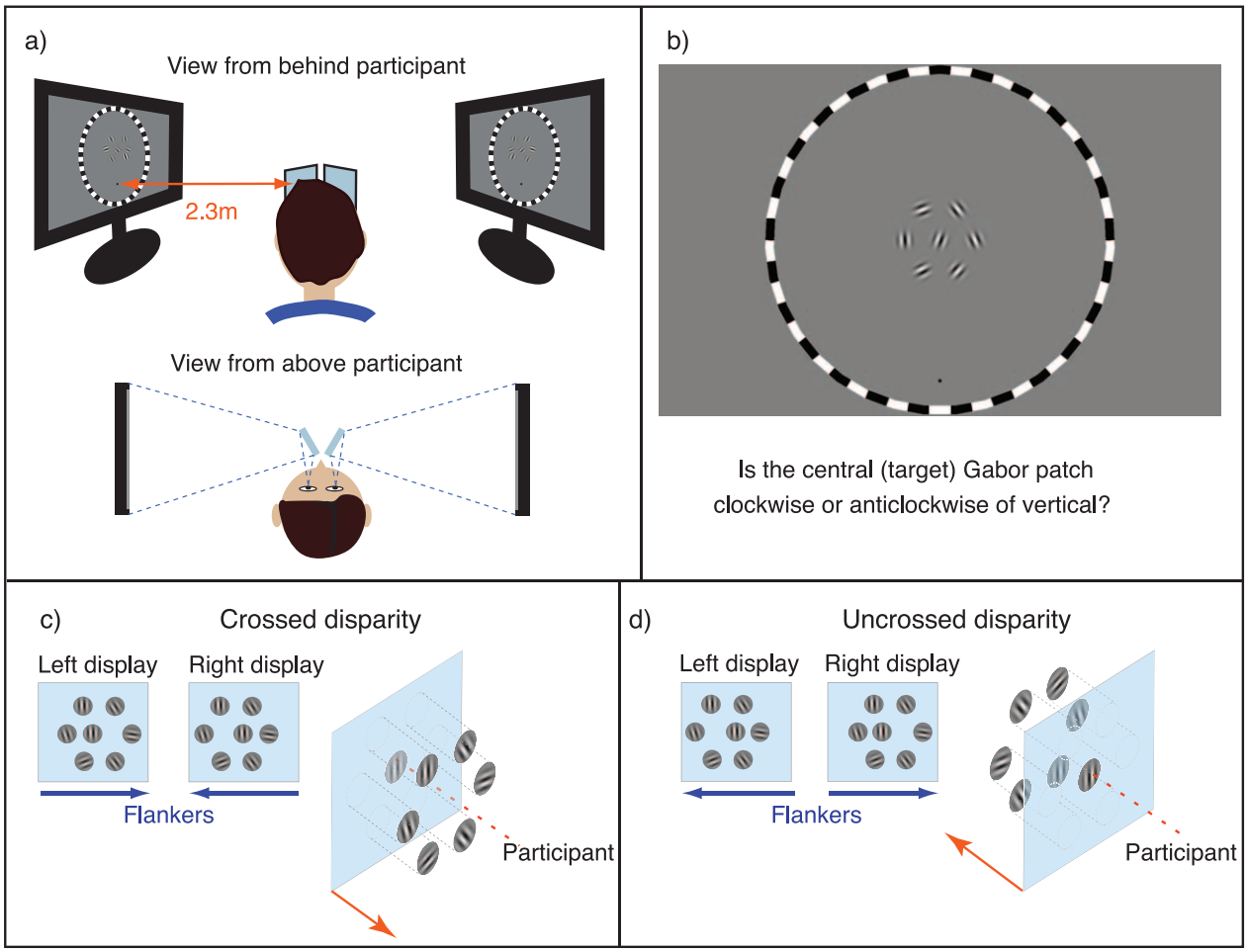


Figure 1. (a) Apparatus arrangement. Participants were positioned equidistant between two displays, which were viewed through a two-mirror stereoscope, such that the left display was viewed by the left eye only and the right display by the right eye only. (b) Example stimulus presentation. A Gabor patch target was positioned 3° above a fixation dot and surrounded by six flanking Gabor patches. A black and white annulus was constantly displayed to aid fusion. Participants were required to decide whether the target was oriented clockwise or anticlockwise of vertical. (c) Gabor flankers appeared in front of the screen (represented by the light blue plane) and closer to the participant (red arrow) when presented with crossed disparity by displacing flankers seen by the left eye to the right and flankers seen by the right eye to the left (blue arrows). (d) Gabor flankers appeared behind the screen and further away from the participant (red arrow) when presented with uncrossed disparity by displacing flankers seen by the left eye to the left and flankers seen by the right eye to the right (blue arrows).

range of different stimuli, from simple Gabor patches (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001), through to more complex objects, such as faces (Louie, Bressler, & Whitney, 2007).

The strength of crowding is dependent not only on the spatial separation of flankers from the target, but also on the properties of the flankers; flanking objects that are more similar to the target generally exert a larger crowding effect. For instance, flankers that differ from a target in terms of spatial frequency (Chung, Levi, & Legge, 2001), orientation (Andriessen & Bouma, 1976; Levi, Hariharan, & Klein, 2002), color (Gheri, Morgan, & Solomon, 2007; Kennedy & Whitaker, 2010; Kooi, Toet, Tripathy, & Levi, 1994; Põder, 2007), contrast polarity (Chung & Mansfield, 2009; Kooi et al., 1994), size (Nazir, 1992), shape (Kooi et al., 1994; Nazir, 1992), complexity (Zhang, Zhang, Xue, Liu, & Yu, 2009), or direction of motion (Gheri et al., 2007) have been shown to exert less crowding than those that are otherwise similar. In addition, studies have demonstrated that crowding is reduced when flankers are presented at a single depth, in front of (Felisberti, Solomon, & Morgan, 2005; Sayim, Westheimer, & Herzog, 2008), or behind (Felisberti et al., 2005; Kooi et al., 1994; Sayim et al., 2008) the target, compared to when the target and flankers are presented in the same depth plane.

While the aforementioned studies demonstrated a release from crowding when flankers were presented in a single depth in front and/or behind the target, here we

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characterize disparity-based crowding mechanisms by measuring the effect of flanker-target disparity for a broad range of disparities. By measuring performance on an orientation discrimination task, we show that crowding systematically decreases with increasing flanker-target disparity, and a complete release of crowding is achieved when flankers are presented at sufficiently large disparities. We also find that crowding is greater when flankers are presented in front of a target, compared to behind. Additionally, by measuring the effect of distributing flankers over a range of disparities, we show that crowding effects are not based on the average disparity of flanker elements.

Methods

Participants

Three experienced psychophysical observers and two naive participants with normal or corrected-to-normal vision participated in the study (20–45 years; median 32 years, one female, four males). Informed consent was obtained from all participants. The experimental procedures adhered to the tenets of the Declaration of Helsinki and were approved by a local ethics committee at the School of Psychology, The University of Nottingham.

Apparatus

Stimuli were generated on an Apple Macintosh computer (Apple Inc., Cupertino, CA) using custom software written in Python (Peirce, 2007) and presented on two 22-in. Samsung 2233RZ LED monitors (Samsung, Seoul, South Korea) with a refresh rate of 120 Hz, resolution of 1680 × 1050 pixels, and mean luminance of 145 cd/m^2. The monitors were photometrically calibrated using a Minolta CS-110 photometer (Konica Minolta, Mississauga, Ontario, Canada) and viewed through a stereoscope constructed using two front-surface mirrors (Figure 1a). A forehead and chin rest were used to hold participants' heads in position and maintain a constant viewing distance of 2.3 m, at which each pixel subtended a visual angle of 0.4 arcmin.

Stimuli

A central target Gabor patch ($SD = 0.1°$, carrier grating spatial frequency = 6.0 or 3.6 c/°) surrounded by an annulus of six flanking Gabor patches (Figure 1b) were presented on both displays. The target Gabor patch on each display was presented 3° above a small fixation dot, which was visible with both eyes and on which fixation was maintained during each testing block. The peak Michelson contrast of the target and flanking Gabor patches was 0.99. Each display was viewed independently by one eye. An alternating black and white peripheral annulus was present throughout testing on each display to aid fusion.

Flanking Gabor patches were presented in crossed disparity (such that they appeared in front of the screen and the target; Figure 1c) by displacing flankers seen by the left eye to the right and those seen by the right eye to the left, by an equal amount. Flankers were presented in uncrossed disparity (such that they appeared behind the screen and the target; Figure 1d) by moving flankers seen by the left eye to the left and those seen by the right eye to the right, by an equal amount. Based on an interpupillary distance of 65 mm, a one pixel displacement of an object on one screen relative to the other equated to a stereo-angle of 25 arcsec. Unless otherwise stated, the target and flankers had a random phase, while all flankers had a random orientation around 360°. In addition, unless otherwise stated, both the phase and orientation of flanker and target stimuli were matched on each screen. Flankers were otherwise identical to the target.

Procedure

Prior to testing, the stereoscope mirrors were independently positioned for each participant to ensure accurate alignment of nonius lines. Peripheral orientation discrimination thresholds were quantified by calculating the just noticeable difference (JND) for judgments between clockwise and anticlockwise of vertical for the target Gabor patch. The orientation of the target Gabor patch was manipulated according to the method of constant stimuli, with 10 presentations of nine linearly spaced orientations randomly ordered within each testing block. Stimuli were presented for 500 ms (60 frames). Psychometric functions were constructed for each condition, based on a minimum of 180 trials. All testing was carried out in a darkened room.

Uncrowded orientation discrimination thresholds were determined for each individual by presenting the target in the absence of flanking Gabors. All six flanking Gabors were presented with the target Gabor for all measurements of crowded thresholds.

Data analysis

Psychometric functions were fitted with the following logistic function using the method of Ordinary

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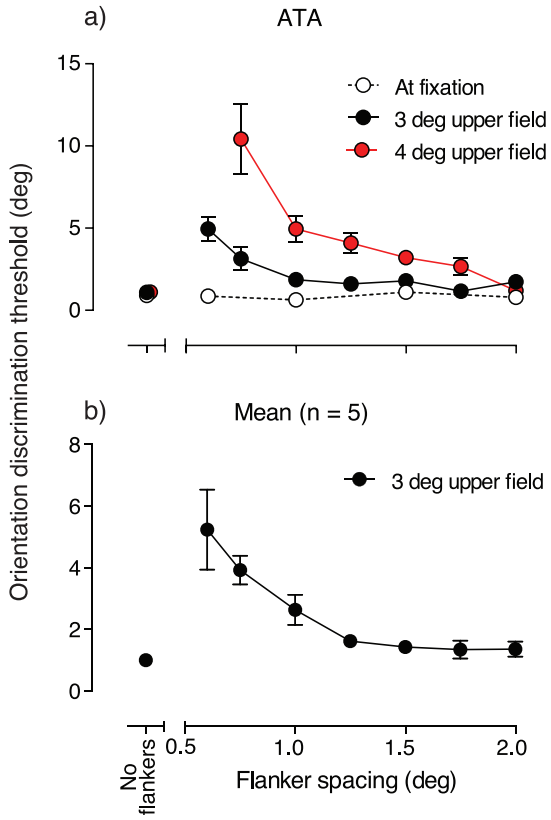


Figure 2. (a) Orientation discrimination thresholds at three different eccentricities plotted as a function of flanker separation. (b) Mean orientation discrimination threshold at an eccentricity of 3° as a function of flanker separation ($n = 5$). Error bars indicate ±1 *SE*.

Least Squares, in order to estimate the orientation discrimination threshold:

$$P_{CW} = \frac{100}{1 + e^{\frac{PSE-a}{b}}}$$

where P_{CW} is the percentage of clockwise responses; *PSE* is the point of subjective equality, the orientation of the target stimulus corresponding to the 50% response level on the psychometric function, a is the orientation of the target stimulus, and b provides an estimate of the orientation discrimination threshold (approximately halfway between the 27% and 73% response levels). *PSE*, *a* and *b* were free parameters.

Results

To examine the effect of flanker disparity on crowding, we first needed to determine the magnitude of crowding for each participant when objects were presented at the same depth. Orientation discrimination thresholds were measured for different flanker separations, with the target and all flankers presented in the same plane as the screen (i.e., 0 arcsec disparity). Figure 2a shows orientation discrimination thresholds plotted as a function of flanker-to-target separation at three different eccentricities (0°, 3°, and 4°) for an individual participant. Crowding did not occur when the target was presented at fixation: Thresholds remained the same regardless of the separation of flankers or whether flankers were present or absent. When the target was presented at 3° or 4° from fixation, thresholds increased with decreasing flanker separation. For a given flanker separation, thresholds were generally higher at greater eccentricities. Figure 2b shows mean data for five participants for an eccentricity of 3°. As the individual data indicated, thresholds increased with decreasing flanker separation. When flankers were a distance of approximately 1.5° from the target, orientation discrimination thresholds were at a similar level to when no flankers were present. These data are in agreement with previous findings showing that visual crowding increases with decreasing distance between target and flankers and increasing eccentricity (Bouma, 1970).

Importantly, measuring the effect of crowding in a single depth plane allowed selection of a flanker-to-target separation where significant crowding was present for each participant, prior to measuring the effect of flanker disparity on visual crowding. A flanker-to-target separation was selected that led to an approximately threefold increase in threshold, relative to the unflanked threshold, for each individual (corresponding to a center-to-center separation of 1° for DPM, PVM, and DS and 0.75° for ATA and MM).

In order to make comparisons between disparity-based modulation of crowding and sensitivity to changes in flanker disparity, stereoacuity thresholds were measured at an eccentricity of 3° using a similar procedure to that used to measure orientation discrimination thresholds. However, rather than judging the orientation of the target Gabor, participants were required to judge whether the flankers were in front or behind the central target, which remained in the same depth plane as the screen. Individual flanker-to-target separations, quantified in Figure 2, were also used for this procedure. Across all participants, mean stereoacuity at 3° was 242 arcsec (± 37 *SE*).

To determine the effect of flanker depth on crowding, the flanker-to-target separation was held constant, while the disparity of the flankers was changed. In separate conditions, flankers were presented at a different disparity ranging between −800 to 800 arcsec (where negative and positive numbers indicate crossed and uncrossed disparities, respectively). Figure 3 shows individual orientation discrimination thresholds as a function of flanker disparity, where horizontal dotted lines correspond to unflanked

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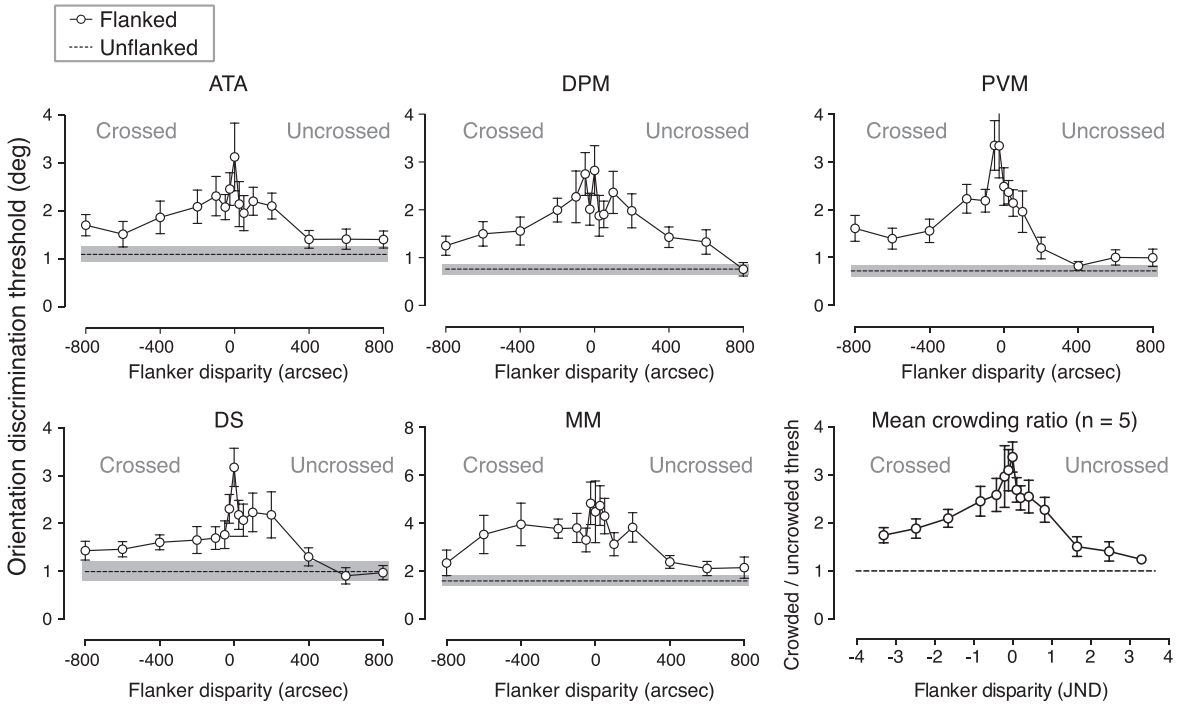


Figure 3. Orientation discrimination threshold plotted for individual participants and the mean crowding ratio (crowded/uncrowded orientation discrimination threshold) as a function of flanker disparity. Negative flanker disparities correspond to crossed disparities, while positive flanker disparities correspond to uncrossed disparities. Horizontal dashed lines show the uncrowded threshold, i.e., when no flankers were presented (gray region shows ±1 *SE*). The bottom right panel shows crowding (quantified as a ratio of crowded to uncrowded orientation discrimination threshold) as a function of flanker disparity (quantified in mean stereoacuity threshold [JND] units). Error bars indicate ±1 *SE*.

thresholds (gray shaded regions show ±1 *SE*). For all participants, thresholds reduced with increasing crossed or uncrossed flanker disparity. For large disparities (beyond 200 arcsec), thresholds were lower when flankers were presented in uncrossed disparity (behind the target) compared to when they were presented in crossed disparity (in front of the target). Thresholds were comparable to uncrowded performance when flankers had a disparity of 800 arcsec. In other words, crowding was completely released when flankers were presented sufficiently far enough behind the target, such that they had no effect on the orientation judgment of the target. There was a mean anticlockwise bias (−0.7°), which remained fairly constant across all flanker disparities, apart from when the disparity of the flankers was 0 arcsec, when anticlockwise bias increased to a maximum level of 1.7°.

Crowding is often quantified as a crowding ratio (crowded/uncrowded threshold). The bottom right panel in Figure 3 shows the mean crowding ratio as a function of flanker disparity. Flanker disparity is quantified in terms of mean stereoacuity threshold (JND) units. These data show that crowding was alleviated when flankers were presented at a different depth to the target, even for subthreshold changes in flanker disparity.

When the disparity of the flankers was increased, they moved along a path perpendicular to the plane of the screen. This meant that, as well as the disparity changing, the distance of the flankers to the target in three-dimensional (3-D) space also increased. To test whether this could account for the reduced effect of crowding we observed, we repeated the experiment, but held the 3-D flanker-to-target distance (red lines in Figure 4a) constant while disparity was increased. By reducing the flanker-to-target separation in the *x*-*y* plane (plane of the screen) while increasing disparity, flankers moved along an arc on the surface of an imaginary sphere, maintaining a constant distance from the target (see Figure 4a). Figure 4b shows that the same pattern of results was found when the 3-D distance between the target and flankers was held constant (red symbols) compared to when this distance increased with disparity (gray symbols). This suggests that for the conditions tested, it was the disparity of the flankers that determined the degree of crowding, rather than how far away they were from the target in 3-D space.

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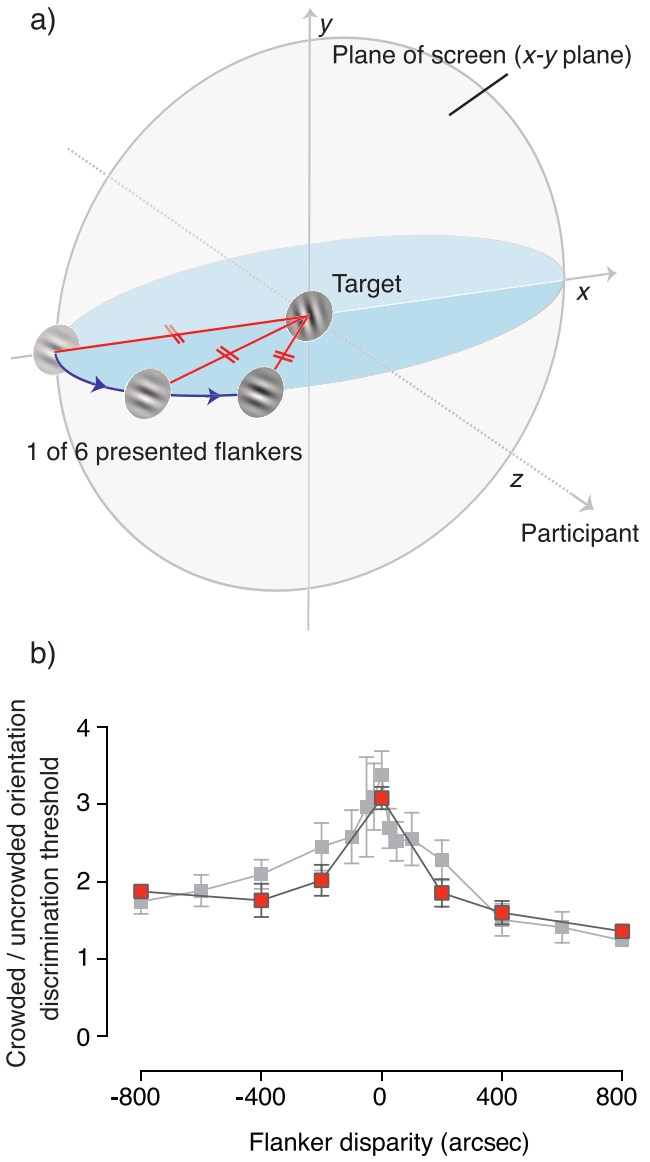


Figure 4. (a) Schematic showing the path of one of the six presented Gabor flankers, which moves along an arced path (blue arrows) such that the distance from the target (red lines) remains constant. This was achieved by reducing the flanker-to-target disparity in the *x-y* plane as disparity increased. (b) Mean crowding ratios plotted as a function of flanker disparity when distance between flankers and target in 3-D space was held constant ($n = 4$), as depicted in a (data shown in red). Data shown in gray indicates results from an earlier condition, where flankers were moved along a path perpendicular to the plane of the screen, such that flanker-to-target distance in 3-D space increased with disparity. Error bars indicate ± 1 *SE*.

Although the target always appeared to be in the center of the flankers when viewed binocularly, if viewed monocularly, the relative offset of the target and flankers could change depending on the disparity level. We wondered whether this change in the physical relationship of the target to flankers viewed by each eye could have contributed to the change in crowding observed. To test this possibility, participants performed the task monocularly, since in these conditions the offset between the target and center of the flankers would be present but disparity would be absent. Two participants completed this control experiment and showed an approximate 50% increase in thresholds when flankers were presented monocularly (randomly to each eye) with a positional offset corresponding to a disparity of 800 arcsec, compared to when they were presented binocularly with no disparity.

To investigate this further, we compared orientation discrimination thresholds when all flankers were presented with a binocular disparity of 800 arcsec to conditions where all flankers were displaced by an equivalent amount, but in the same direction in each eye (blocked, so that all flankers were shifted to the left for half the trials, then all flankers shifted to the right for the remaining trials). In the former case, the flankers appeared at a different depth to the target. In the latter case there was no disparity and the flankers appeared at the same depth as the target. In both cases, the task was performed binocularly, the target and flankers were presented to both eyes, and the absolute horizontal offset of the target relative to the center of the flankers was the same in each eye. If the reduction in crowding were due to the shift in position of the target relative to the flankers, as viewed by either eye, the same result would be expected for the two conditions. Figure 5a shows that thresholds are lower when flankers are presented at a different depth to the target, indicating that disparity information was responsible for the release of crowding.

Next, we compared orientation discrimination thresholds when flankers were presented at a different depth to the target using two different methods. The first method was the same as that used earlier, i.e., changing the relative position of the flankers presented to each eye. The second method changed the relative phase of the flankers presented to each eye. The phase of each of the flankers presented to the left eye was individually randomized on each trial. The phase of each of the flankers presented to the right eye was $\pm 0.25\lambda$ of its corresponding flanker presented to the left eye, depending on whether the flankers were of crossed or uncrossed disparity. For both methods, the spatial frequency of the target and flanking Gabor patches was set to 3.6 c/° to enable a larger disparity to be produced by the phase shift, while still producing a sufficient number of visible cycles in each Gabor patch. In addition, for both methods, all flankers were vertically oriented to allow the same disparity (240 arcsec) to be applied to all flankers. There was only a position shift of the Gabor flankers relative to the target using the first method. Figure 5b shows the mean threshold for each method. Similar to earlier condi-

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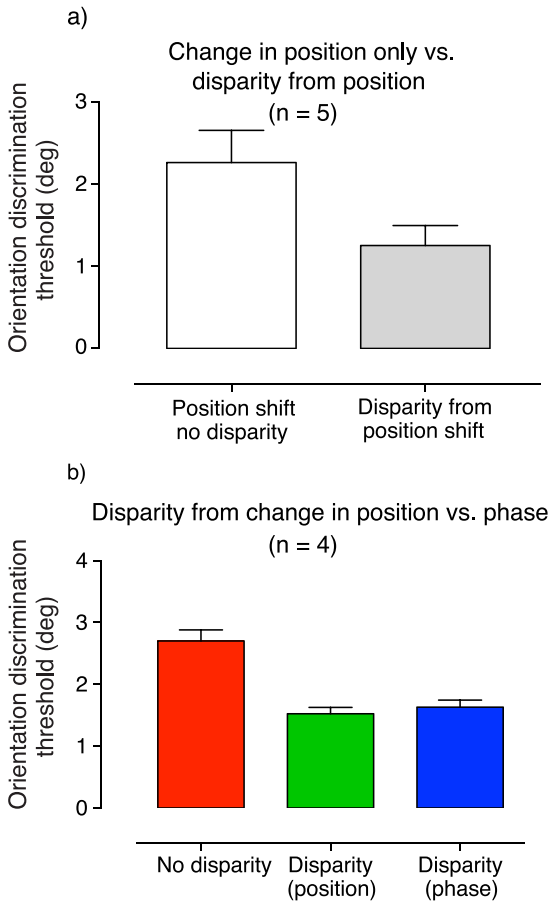


Figure 5. (a) Mean orientation discrimination thresholds when flankers were presented with a disparity of 800 arcsec by shifting the position of the Gabor flankers in *opposite* directions on each display (disparity; gray column), compared to when they were shifted by an equivalent amount in the *same* direction on each display (no disparity; white column). (b) Orientation discrimination thresholds when flankers were presented in the same plane as the screen (red column), and when presented with a disparity of 214 arcsecs, induced either by changing the relative position or relative phase of the carrier frequency of the Gabor flankers on each display. Error bars indicate ±1 *SE*.

tions, we ensured significant crowding was present for each participant by using an appropriate flanker-to-target separation. This was 0.6° for two participants, 0.75° for one participant, and 1.0° for one participant. Separations were smaller, on average, due to the reduced effect of crowding when all flankers are oriented vertically.[1] The mean threshold when flankers were presented in the same plane as the screen is also shown, which was different to that in earlier conditions, because of changes in spatial frequency and orientation characteristics of the stimuli. Both methods of producing depth resulted in a similar reduction in threshold.

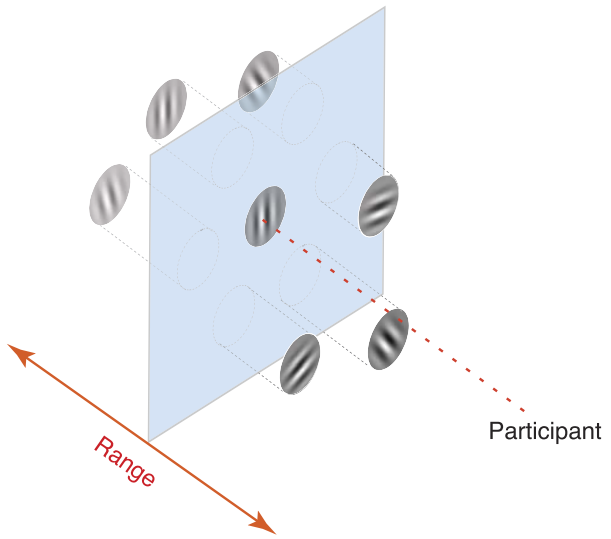


Figure 6. Position of Gabor flankers when distributed across a range of disparities relative to the target and the plane of the screen (pale blue surface). One flanker is positioned with a crossed disparity equal to half the total range and one flanker is positioned with an uncrossed disparity half the total range. Remaining flankers are distributed in equal disparity intervals between these flankers. In all cases, the average disparity is equal to the disparity of the target (i.e., 0 arcsec).

In all experiments described to this point, all flankers were presented in the same depth plane. Evidence exists for averaging or pooling of disparity information (Parker & Yang, 1989; Rohaly & Wilson, 1994). To investigate how disparity information from the flankers is pooled, we measured how crowding was affected when flankers were distributed over a range of different depths. Figure 6 illustrates how flankers were distributed evenly over a range of crossed and uncrossed disparities. Disparity ranges used were 200, 400, 800, and 1600 arcsec. Flanker disparities for each disparity range are listed in Table 1.

Figure 7 shows individual and mean orientation discrimination thresholds relative to the range of the flanker disparity distribution. In each case, the average disparity of the range is 0 arcsec, i.e., equivalent to that of the target and the plane of the screen. If crowding were determined by the average disparity of the distribution, thresholds would not change with the distribution range and would correspond to the level shown by the horizontal dotted line in each plot. However, thresholds decreased as the range of the distribution increased. The rate of threshold reduction was relatively large over a range of 0–200 arcsecs and began to plateau above 200 arcsecs. For two participants (DS and MM), thresholds reached the same level as that recorded when no flankers were presented (horizontal dashed line). These data suggest that the level of crowding is not dictated by the average

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Disparity range (arcsec)	Flanker disparities (arcsec)
0	All 0
200	−100, −60, −20, 20, 60, 100
400	−200, −120, −40, 40, 120, 200
800	−400, −240, −80, 80, 240, 400
1600	−800, −480, −160, 160, 480, 800

Table 1. Flanker disparities for each disparity range.

disparity of flanker elements and that the release of crowding is not specific to situations where all flankers are presented in the same depth. They also suggest that the effect of disparity appears to operate over a relatively small range (in the order of 200 arcsec). This could mean that combining or pooling of disparities is only effective over that range or something else affects thresholds beyond approximately 200 arcsec.

The bottom right panel in Figure 7 includes predictions based on the data when all flankers were in a single plane (shown in Figure 3). The red, green, and blue points indicate predicted thresholds for when all flankers are presented at the smallest disparity of the range, the largest disparity of the range, and the mean disparity of the range (computed separately for crossed and uncrossed disparities), respectively. In each case, the threshold is the mean of that predicted by crossed and uncrossed disparities of individual data shown in Figure 3. These results suggest that the threshold is not determined by the smallest, largest, or average disparity of the disparity range, although the largest disparity comes closest.

We measured performance with a disparity range of 1600 arcsec, setting the disparity of the flankers with the lowest disparities to 0 arcsec (previously ±160 arcsec) in two participants. If crowding is determined by the closest flankers to the target in terms of disparity, we would expect thresholds to change (be higher) compared to the standard 1600 arcsec range condition. However, we found thresholds to be almost the same in each case: 1.45° with two flankers at 0 arcsec compared 1.65° with the standard 1600 range condition, adding weight to the suggestion that thresholds are not determined by the flankers with the smallest disparity in the range.

When flankers were distributed over a range of disparities, flankers were shifted in opposite directions on each screen. Unlike previous conditions, the amount by which each of the six flankers was shifted varied, according to the specific disparity of the flanker within the range. Therefore, not only did the relationship between the target and flankers change on each screen

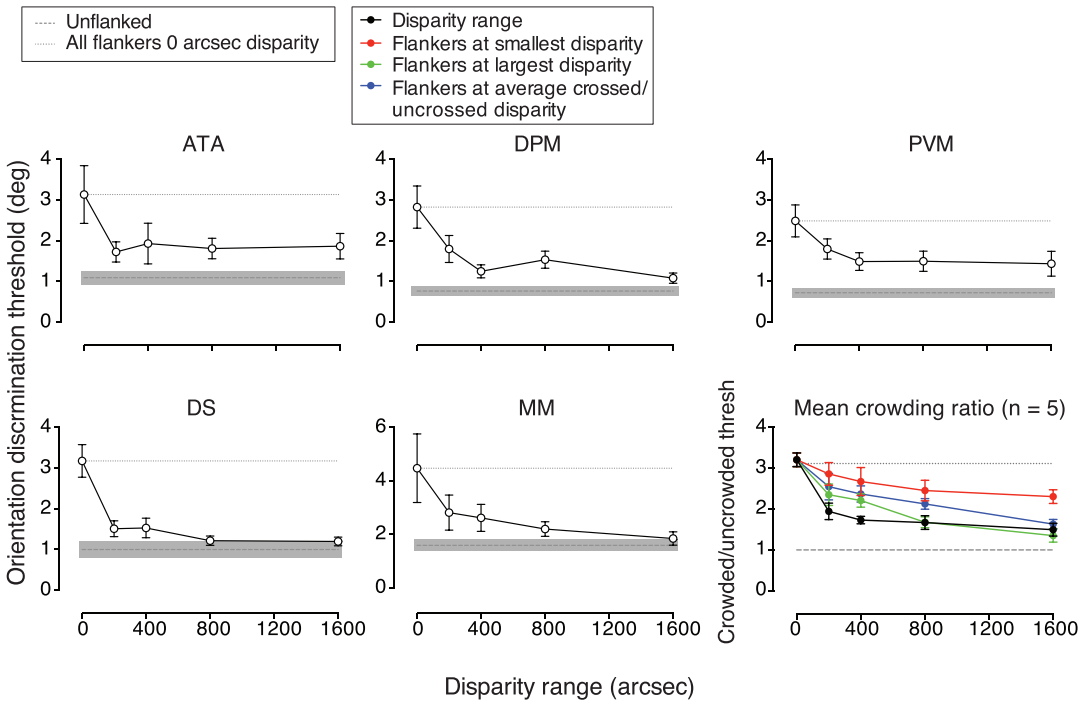


Figure 7. Orientation discrimination thresholds plotted as a function of disparity range. Flankers were evenly distributed across the disparity range. In all cases, the average disparity was 0 arcsec (i.e., that of the target). The horizontal dotted line represents the orientation discrimination threshold that would be predicted if performance corresponded to the mean disparity of all flankers (i.e., 0 arcsec). The horizontal dashed line represents the orientation discrimination threshold when no flankers were present. The bottom right panel contains predictions for having flankers at the smallest disparity of the range (red), largest disparity of the range (green), and the average disparity, computed separately for crossed and uncrossed disparities (blue). Error bars and gray region indicate ±1 *SE*.

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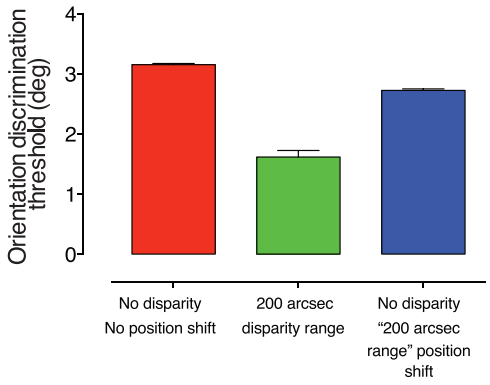


Figure 8. Mean orientation discrimination threshold (i) when all flankers were presented with a disparity of 0 arcsec (red column), equivalent to the 0 arcsec condition in Figure 3, (ii) when flankers were distributed over a 200 arcsec disparity range (green column), and (iii) when they were shifted by an amount equivalent to that required to produce a 200 arcsec range but in the same direction in each eye, i.e., no disparity (blue column) for two participants. Error bars indicate ±1 *SE*.

(monocularly), but the relationship between each of the flankers also changed on each screen, ungrouping the circular arrangement of the flanker array. We wondered whether these monocular changes might have produced the change in thresholds observed when flankers were distributed over a disparity range. It can be seen in Figure 7 that crowding reduced rapidly when flankers were distributed over a range of 0–200 arcsec and plateaued thereafter. We repeated the range condition, shifting flankers by an equivalent amount to that when flankers were distributed over a disparity range of 200 arcsec, but in the same direction on each screen—such that there was no disparity (blocked, so that all flankers were shifted to the left for half the trials, then all flankers shifted to the right for the remaining trials). The results of this manipulation are shown in Figure 8. Thresholds were not reduced to the same extent as when flankers were presented in different depth planes. Therefore changes in disparity make the majority of the contribution to the release of crowding observed when flankers are distributed over a range of 200 arcsec, as opposed to monocular position shifts. It could be that monocular position shifts contribute to the reduction in crowding found for larger disparity ranges (where position shifts will be larger). However, larger disparity ranges beyond 200 arcsec have a limited effect on further releasing crowding.

Discussion

Crowding was reduced when flankers were presented at a different disparity to the target compared to when targets and flankers were presented at the same depth (see Figure 3). This is consistent with results from a previous study (Kooi et al., 1994), which showed that presenting a target at a single fixed depth in front of flankers increased the accuracy of responses and decreased the spatial extent of crowding for a peripheral letter recognition task, compared to when they were presented in the same plane (Kooi et al., 1994). Similar results have been reported for a foveal Vernier alignment task (Sayim et al., 2008). Unlike these studies, that presented flankers at a *single* fixed, crossed and/or uncrossed disparity relative to the target, we measured crowding over a *range* of crossed and uncrossed disparities. This approach revealed a disparity-based tuning function for crowding: Crowding is maximal when the flankers are presented in the same plane as the target, and crowding decreases with increasing crossed or uncrossed flanker disparity, indicating that the strength of crowding changes with the *extent* to which the flankers differ in depth.

One previous study has measured the effect of spatial interference on task performance using a foveal stereoacuity task and nearby contours distributed over a range of disparities relative to the target (Butler & Westheimer, 1978). Participants were required to judge the depth of a bar relative to a reference bar, which appeared in the same plane as fixation. Maximum threshold elevation occurred when orthogonal line flankers were placed in the same plane as the reference bar. Increasing crossed or uncrossed flanker disparity led to reduced thresholds. However, the bandwidth of the tuning function was much narrower compared to our results, with a halving of thresholds when an average disparity of approximately 23 arcsec was introduced between the reference and flanker bars (Butler & Westheimer, 1978). Moreover, in contrast to Sayim et al. (2008), they found no effect of flanker disparity on a Vernier alignment task in the same subjects. The task specificity, narrow spatial tuning, and the fact that the flanker effects are greatest when there is a temporal offset between target and flanks, suggests that the type of spatial interference reported by Butler and Westheimer (1978) may be more closely related to stereo-based masking than visual crowding (Pelli, Palomares, & Majaj, 2004; Whitney & Levi, 2011). Butler and Westheimer (1978) used flankers that were orthogonal to the target rather than being random in orientation. It is possible that crowding, if present, would be greatly reduced in this situation.

As we measured both stereoacuity and orientation discrimination thresholds for the same conditions and in the same participants, it is possible to consider crowding effects in terms of disparity sensitivity. Do we need to be able to reliably detect a disparity change in order to alleviate crowding? Interestingly, a systematic change in crowding was observed for *subthreshold*

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changes in flanker disparity. This is evident in the bottom right panel of Figure 3, which plots crowding as a function of flanker disparity quantified in mean stereoacuity threshold (JND) units. This implies that an awareness of the relative flanker-target configuration is not required for crowding release (see also Greenwood, Bex, & Dakin, 2009). In fact, most subjects required an approximately threefold stereo-threshold change in disparity before crowding was released to baseline levels. Our control experiment (see Figure 4) shows that crowding is not determined by the 3-D distance between target and flankers, but by the relative flanker-target disparity.

The effect of flanker disparity on crowding was asymmetric for crossed and uncrossed disparities (see Figure 3). Crowding was lower when flankers were presented with uncrossed disparities compared to crossed disparities, which was most apparent at large disparities. In other words, crowding was lower when the target appeared in front of the flankers compared to when it appeared behind the flankers.

Could the asymmetry in crowding for crossed and uncrossed disparities be due to different sensitivity to crossed and uncrossed disparities? We measured sensitivity to crossed and uncrossed disparities separately for two participants. For one participant (ATA), thresholds were 208 and 126 arcsec for uncrossed and crossed disparities respectively. For the second participant (PVM), thresholds were 306 and 199 arcsec for uncrossed and crossed disparities, respectively. Both participants were more sensitive to crossed disparities than uncrossed disparities, consistent with previous literature that suggested that crossed disparities are processed more efficiently than uncrossed disparities (Lasley, Kivlin, Rich, & Flynn, 1984; Manning, Finlay, Neill, & Frost, 1987). If the release from crowding was based on relative disparity sensitivity, thresholds should be lower when flankers are presented in crossed disparity compared to uncrossed disparity—in direct contrast to our results. This suggests that differences in stereoacuity to crossed and uncrossed disparities is unlikely to be responsible for the asymmetry in the release of crowding for crossed and uncrossed disparity flankers.

Felisberti et al. (2005) previously investigated the effect of flanker disparity (~260 arcsec in front or behind) on crowding for a peripheral orientation discrimination task, with variable results. For one participant, crowding was reduced when the target appeared either in front or behind the flankers. For another, crowding only reduced when the target appeared behind the flankers, and for a third it did not matter whether the target and flankers were presented at the same or different depths (i.e., no change in crowding). The variability in these results may be due to the fact that each participant demonstrated a different level of threshold elevation for the target-flanker separation employed (Felisberti et al., 2005). Here we took a different approach: Rather than fixing stimulus conditions such that the threshold elevation varied amongst individuals, we adopted stimulus configurations that ensured a consistent and significant threshold elevation when flankers were presented with the target for each participant. Flanker-target separations were chosen on the basis of thresholds being elevated approximately threefold. We then proceeded to establish the characteristics of disparity-based crowding. However, it is possible that the level of asymmetry for crossed versus uncrossed disparity is related to the magnitude of crowding. In situations where crowding effects are small (e.g., larger target-flank distances) the asymmetry may be less pronounced. To verify this, crowding was remeasured for one participant at a larger eccentricity (4.5°) where threshold elevation was greater (i.e., more crowding), and we found that the degree of asymmetry between crossed and uncrossed disparities was consistent in direction but much more marked in magnitude. We speculate that the degree of asymmetry may be proportional to eccentricity, though clearly more data would be required to quantify the precise relationship.

A potential source for the asymmetry in disparity-based crowding could be that asymmetries in disparity may act as a cue to occlusion relationships between objects. Closer objects can be assumed to occlude objects perceived to be further away. Flankers presented at crossed disparities relative to the target may have acted like a perceptual occluder, even though they never physically obscured the target, in a similar way that depth ordering of stimuli modulates motion-induced blindness (Graf, Adams, & Lages, 2002).

Another potential explanation for the asymmetry in disparity-based crowding is that the changes in depth drive perceived changes in flanker contrast. We know that the reverse is true: In the absence of other cues to depth, objects that are lower in contrast appear further away than those of higher contrast (O'Shea, Blackburn, & Ono, 1994). Therefore, it is likely that real changes in disparity alter the apparent spatial properties of objects. This effect—higher contrast and/or larger size when flankers appeared nearer than the target—was reported (but not quantified) by virtually all participants. Flanker contrast can influence the magnitude of crowding (Chung et al., 2001; Pelli et al., 2004), although the spatial extent of crowding is invariant to flanker contrast (Pelli et al., 2004). By manipulating the contrast of flankers and the target for a letter identification task, Chung et al. (2001) showed that when flankers had a higher contrast compared to the target, there was always more crowding. This is different to what is found for other stimulus parameters, where crowding is maximal when the flankers are most similar to the target, e.g., in terms of orientation

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(Andriessen & Bouma, 1976; Levi et al., 2002), spatial frequency (Chung et al., 2001), or color (Gheri et al., 2007; Kennedy & Whitaker, 2010; Kooi et al., 1994; Põder, 2007), and suggests that any perceptual increases in flanker contrast could modulate the magnitude of crowding.

Alternatively, the asymmetry in the crowding function could be associated with an asymmetry in the allocation of spatial attention. Previous work suggests that such an asymmetry exists for judgments relating to depth. For instance, visual search is more efficient when a target appears in front of a background (O'Toole & Walker, 1997). Similarly, distractors located closer than fixation produce more interference than those located further away (Andersen & Kramer, 1993), suggesting that the allocation of spatial attention is biased towards space closer to the participant—a finding supported by electrophysiological recordings (Parks & Corballis, 2006). In a similar vein, recordings from V1 neurons in awake, behaving monkeys (Zipser, Lamme, & Schiller, 1996) show that neural activity is dependent on the figure-ground configuration of stimuli. When a stimulus is surrounded by a texture that is perceived to be further away, neural responses are enhanced. This may form the neurophysiological substrate for preserving the orientation signal in the uncrossed flanker disparity condition and generating the observed asymmetric release from crowding.

In a series of control conditions (see Figure 5), we investigated whether the change in the physical relationship between the target and flankers viewed by each eye could have contributed to the observed changes in crowding. Monocular presentation of the stimuli, with comparable flanker-target offsets to the binocular presentation conditions but with no disparity cues, resulted in a 50% increase in threshold, similar to previous findings (Sayim et al., 2008). However, presenting stimuli to one eye may lead to an increase in threshold due to other factors, such as an absence of binocular summation. Furthermore, the stimuli will not be precisely localized in depth when presented monocularly. Indeed, Kooi et al. (1994) found a significant threshold elevation when stimuli were presented monocularly with no offset, compared to when they were presented binocularly with no disparity (Kooi et al., 1994). Therefore, to control for this, we presented target and flanker stimuli to both eyes, but shifted them in the same direction in each eye, such that the absolute positional shifts were the same as the original experiment (data in Figure 5), but the participant did not perceive the flankers in depth. A greater reduction in crowding was found when flankers were presented in depth, despite an equivalent offset between the target and flankers on each screen. We also showed that flanker disparity induced by a method that did not require a position shift of the flankers resulted in the same reduction in crowding. These results confirm that crowding was released due to differences in disparity, rather than changes in the relative flanker-target positional offset.

Previous studies have shown that targets that stand out more from flankers receive less crowding than those that are perceived to group with flankers (Saarela, Sayim, Westheimer, & Herzog, 2009). Could the reduction in crowding that occurs with increasing flanker-target disparity be due to the target popping-out from flankers, which group by disparity? Presenting objects at different disparities has been shown to cause target pop-out for a visual search task (Nakayama & Silverman, 1986). Additionally, presenting noise in a different depth plane to signal dots leads to better performance on a motion coherence task compared to when they are presented in the same plane, suggesting that stereoacuity can be utilized to segment motion cues (Snowden & Rossiter, 1999). If grouping of flankers according to disparity were responsible for the reduction in crowding, we would expect crowding to be lowest when all flankers are presented at the same flanker-target disparity as each other—since grouping between the flankers would be stronger. However, we found that distributing flankers over a range of disparities led to an equivalent or greater release of crowding compared to when all flankers were presented at the maximum disparity of that range (see Figure 7). This suggests that grouping and target-pop out were not responsible for the release of crowding caused by flanker-target disparity.

Increasing the disparity range of the flankers, even over a relatively small range, decreased orientation discrimination thresholds (see Figure 7). This result was not predicted by the disparity of the smallest, largest, or average disparity of the flanker set, or determined by ungrouping on the basis of the position of the flankers in the x-y plane. Previous studies have demonstrated disparity averaging for differences of up to approximately 114 arcsec (Parker & Yang, 1989). Our findings are broadly consistent with this range, although the exact range over which disparity averaging occurs is likely to depend on the eccentricity tested and stimulus characteristics, such as the disparity relative to fixation (Parker & Yang, 1989). When the disparity range of flankers was 200 arcsec ($\pm$100 arcsec), crowding was still observed, but the magnitude was greatly reduced and was very close to zero (uncrowded threshold) by $\pm$800 arcsec. For crowding to occur, disparity signals need to arise from a narrow range of disparities centered on the target. Flankers located beyond a disparity of 200 arcsec have a limited influence on target perception. In order to develop a more complete model of the averaging process, it would be necessary to develop a stimulus arrangement that includes a large number of flanking elements, so that the statistical moments of disparity distributions can be more readily

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separated to reveal the parameters that determine the magnitude of crowding exerted. This may also reveal details of the underlying mechanisms that read out from the disparity averaging process (Webb, Ledgeway, & McGraw, 2007).

Conclusions

In this study we characterized the tuning of disparity-based crowding. Systematic changes in crowding occur across a range of flanker disparities. We show that, for relatively large disparities, crowding is lower when a target appears in front of flankers, compared to when it appears behind. Crowding effects are not mediated by changes in the monocular images or the 3-D distance between target and flankers, but by changes in flanker-target disparity. However, subjects do not have to be aware of changes in the relationship between target and flankers for changes in crowding to take place. Crowding is not dictated by mean flanker disparity or the closest element, and there appears to be a limited pooling range. Grouping by disparity is also unlikely to play a major role in the observed effects. Future crowding models should involve mechanisms that operate at a stage after binocular combination of inputs, account for the asymmetry for crossed and uncrossed flanker disparities, and the graded influence of target-flanker similarity on crowding strength.

Keywords: crowding, stereoacuity, disparity, orientation, figure ground, peripheral visual field, pooling

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Footnote

[1] In a separate control experiment, when all flankers were presented in the plane of the target, we found a mean ($\pm SD$) threshold of 3.2 ($\pm$0.34) deg when flankers were randomly oriented, compared to 1.3 ($\pm$0.15) deg when they were all vertically oriented.

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