

Orientation-crowding within contours

James C. Glen

UCL Psychology and Language Sciences,
University College London, London, UK



UCL Institute of Ophthalmology,
University College London, London, UK
National Institute for Health Research

Steven C. Dakin

Biomedical Research Centre at Moorfields Eye Hospital,
London, UK



We examined how crowding (the breakdown of object recognition in the periphery caused by interference from “clutter”) depends on the global arrangement of target and distracting flanker elements. Specifically we probed orientation discrimination using a near-vertical target Gabor flanked by two vertical distractor Gabors (one above and one below the target). By applying variable (opposite-sign) horizontal offsets to the positions of the two flankers we arranged the elements so that on some trials they formed contours with the target and on others they did not. While the presence of flankers generally elevated orientation discrimination thresholds for the target we observe maximal crowding not when flanker and targets were co-aligned but when a small spatial offset was applied to flanker location, so that contours formed between flanker and targets only when the target orientation was cued. We also report that observers’ orientation judgments are *biased*, with target orientation appearing either attracted or repulsed by the global/contour orientation. A second experiment reveals that the sign of this effect is dependent both on observer and on eccentricity. In general, the magnitude of repulsion is reduced with eccentricity but whether this becomes attraction (of element orientation to contour orientation) is dependent on observer. We note however that across observers and eccentricities, the magnitude of repulsion correlates positively with the amount of release from crowding observed with co-aligned targets and flankers, supporting the notion of fluctuating bias as the basis for elevated crowding within contours.

Introduction

Object discrimination using peripheral vision is significantly poorer than for foveal vision. This is especially the case when objects are surrounded by

irrelevant visual structure (“clutter”), which can have a profound effect on recognition. Such *crowding* limits peripheral vision. Crowding is not attributable to known decreases in acuity and occurs when a flanking element falls within an area surrounding the target known as its interference zone, hindering discrimination of the target’s features. This zone is primarily defined by the critical distance between the target and flanker element(s), which is thought to be roughly half the eccentricity of the target (Bouma, 1970). It is important to note that while crowding affects discrimination of element features, detection of the element remains unaffected.

Crowding has been demonstrated with many features such as color, shape, contrast polarity (Kooi, Toet, Tripathy, & Levi, 1994), spatial frequency (Chung, Levi, & Legge, 2001), position (Greenwood, Bex, & Dakin, 2009) and orientation (Hariharan, Levi, & Klein, 2005). While most early crowding research emphasized the role of local interactions (between adjacent elements) it is now clear that the global arrangement of features is important (Livne & Sagi, 2007; Saarela, Sayim, Westheimer, & Herzog, 2009). Crowding is particularly powerful when distractor and target co-align to form an extended visual contour (Livne & Sagi, 2007). Conversely, where flankers are arranged to promote perceptual grouping with one another a release from crowding is seen, as the target “jumps out.”

As to the mechanism of crowding, it is now widely acknowledged that visual crowding involves inappropriate pooling of constituent element features (Dakin, Cass, Greenwood, & Bex, 2010; Greenwood et al., 2009; Parkes, Lund, Angelucci, Solomon, & Morgan, 2001). For example, discrimination of the orientation of a near-vertical central target is impaired when the element is surrounded by vertical distractor elements because

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the observer bases their judgment on what is effectively the average orientation of the target and distractors (Parkes et al., 2001). Thus in crowded displays, target and flanker orientation signals are not lost completely but are pooled together. Dakin et al. (2010) presented evidence that this averaging process has a probabilistic component: Stimulus separation defines not only the strength of crowding but the probability that it occurs. Furthermore the model as described had elongated averaging zones promoting stronger averaging within contours. This is in accord with work described above suggesting that crowding and *contour-integration* are related phenomena (Livne & Sagi, 2007; May & Hess, 2007). We return to this point below.

Crowding is not the only phenomenon where surrounding structure influences orientation-processing. In the *tilt illusion* (Gibson, 1937), perceived target-orientation is repelled from the orientation of a surrounding/abutting grating. However, by increasing eccentricity it is possible to change repulsion to assimilation so that the orientation of the target is drawn towards that of the interfering stimulus (Mareschal, Morgan, & Solomon, 2010). The critical eccentricity for this switch to arise depends on stimulus separation: The switch arises at greater eccentricities for wider separations (Mareschal et al., 2010).

Although both crowding and the tilt illusion lead to a distortion of target orientation, it is currently uncertain the extent to which these phenomena share an underlying mechanism. Assimilative tilt effects cause target orientations to appear more like those of the flanking stimuli; because it is known that crowding occurs between similar elements (Chung et al., 2001; Hariharan et al., 2005; Kooi et al., 1994), the conditions that lead to assimilation will also lead to increased crowding (Mareschal et al., 2010). Furthermore, one of the candidate theories of crowding is *averaging* (Parkes et al., 2001; Greenwood et al., 2009), whereby the identity of a crowded feature is not lost (e.g., by being swamped by noise) but rather is diluted by averaging with features of the flankers. Clearly such an averaging mechanism could also be used to explain assimilative tilt-illusions (e.g., Dakin, Williams, & Hess, 1999); if the orientations of the target and flanking stimuli are averaged, the observer's perception is of the target being drawn towards the orientation of the flanking stimuli as seen with assimilation.

Focusing on oriented stimuli, it has been noted previously that strong crowding arises not only when target and flanker have similar orientations but also when they are positioned and oriented to form a *contour* (Livne & Sagi, 2007; May & Hess, 2007; Chakravarthi & Pelli, 2011). Specifically, Livne and Sagi (2007) showed a release from crowding when flankers grouped into contours, while Chakravarthi and Pelli (2011) showed that such effects depended

mainly on contour-grouping between target and flankers. May and Hess (2007) went so far as to suggest that the integration fields supporting contour detection might explain interference zones for crowding. Beyond this little is known about the nature of “contour-crowding” and specifically what impact it has on local orientation coding (of constituent features). This is critical if we are to better understand the role of contour integration in crowding and relate its mechanism to other phenomena involving a disruptive influence of oriented-context, such as the tilt illusion. Here we investigate how being located within a crowded contour influences orientation-processing of the constituent elements and note strong similarities between the influence of global contour-orientation and the influence of oriented surrounds (i.e., as in the tilt illusion) on perceived orientation of a Gabor target.

Methods

Apparatus

Experiments were run on an Apple MacBook Pro (Apple Inc., Cupertino, CA) computer within the MatLab programming environment (Mathworks Inc., Natick, MA). Code from the Psychophysics Toolbox (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007) were used to display stimuli which were presented on an 18-inch Dell CRT monitor (Dell Computers, Round Rock, TX) linearized to 14-bit grayscale (using a Bits++ video processor, Cambridge Research Systems, Cambridge, UK). Viewing distance was set at 46.5 cm. At this distance one pixel subtended 2.5 arcmin, or alternatively 24 pixels subtends one degree of visual angle. Stimuli were presented on a plain background with a mean luminance of 50 cd/m². Stimuli were viewed monocularly through the subject's dominant eye. Observers made their responses using a USB keypad.

Observers

In Experiment 1 we used eight observers (the two authors and six naïve participants). Experiment 2 tested four observers from the first experiment (the two authors and two naïve participants). All had normal or corrected-to-normal vision. Authors are experienced psychophysical observers, other participants were not.

Stimuli

Stimuli consisted of a single Gabor element (the *target*) flanked above and below by a pair of vertical Gabors (the *flankers*). Targets were near-vertical Gabor

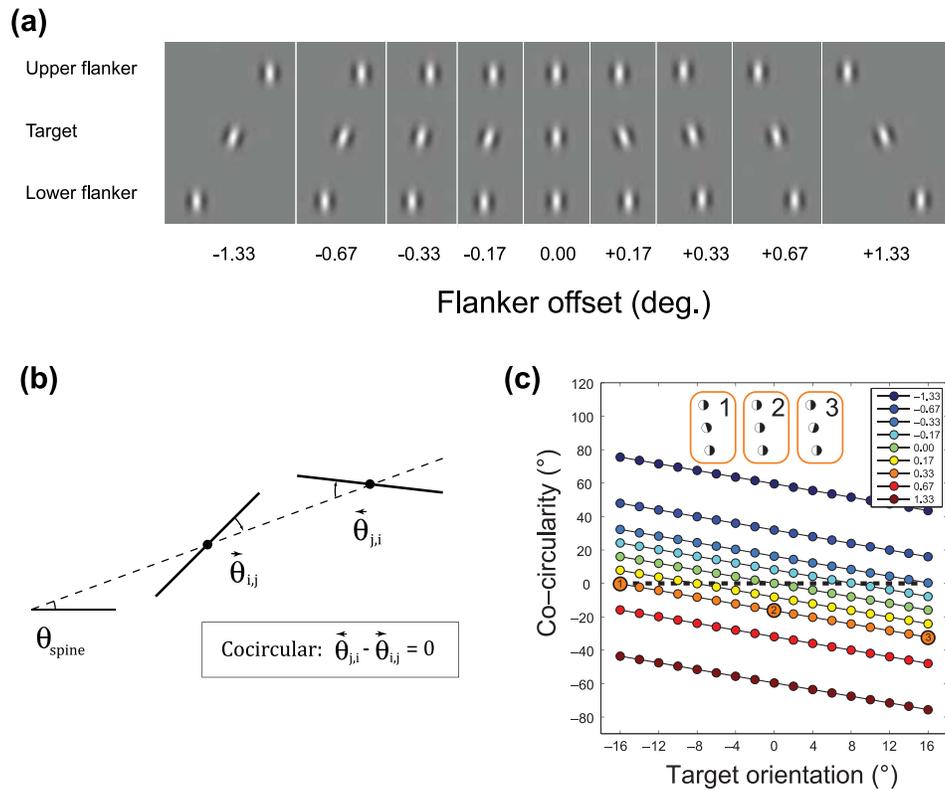


Figure 1. (top row) Illustrates the stimulus layouts used in the experiment corresponding to the 9 different flanker offset conditions. All target orientations in this image are contour consistent, with the special case of colinearity at 0° offset. (bottom row) The cocircularity of all stimulus-configurations (with a stimulus gain of 2.0). Different colors show different flanker offset conditions and a given point corresponds to a particular target orientation. Insets 1, 2, and 3 are schematic depictions of the stimuli corresponding to orange points labeled 1, 2 and 3.

elements ($1.5\text{ c}/^\circ$ carrier, envelope $SD = 0.24^\circ$) presented in the upper visual field at 8 deg. (Experiment 1) and 4° and 12° (Experiment 2) for 250 ms per trial. Flankers were similar but had carrier orientation fixed at vertical. Flankers were positioned with a vertical offset of $\pm 2.33^\circ$ (i.e., above and below the target) and a variable horizontal separation. Nine horizontal offsets were tested; ± 1.33 , ± 0.67 , ± 0.33 , ± 0.17 and 0° (for examples see Figure 1). Under the 4° eccentricity condition in Experiment 2 the vertical offset was reduced to $\pm 1.25^\circ$, so as to keep the flankers within the critical distance for crowding. Seventeen levels of target orientation were used (default -8 to $+8$ in 1-degree steps, around vertical) which were varied systematically between trials. The particular orientation values used were set by the stimulus gain-parameter (i.e., the multiplier applied to the values -8 to $+8$) used for each participant.

This set of parameters will lead to a set of stimuli that systematically differ in the degree to which they will form contours, which can, in turn, be quantified using a measure of *cocircularity* (Elder & Goldberg, 2002; Parent & Zucker, 1989; Figure 1b). For two

oriented elements (indexed i and j) located at (x_i, y_i) and (x_j, y_j) the orientation of the spine connecting them is:

$$S_{i,j} = \tan^{-1} \left(\frac{y_j - y_i}{x_j - x_i} \right) \quad (1)$$

and if the orientation of the two elements is θ_i and θ_j then we can define their cocircularity as:

$$C_{i,j} = (\theta_i - S_{i,j}) - (S_{i,j} - \theta_j) \quad (2)$$

This expression approaches zero for combinations of orientation and position that are consistent with a cocircular contour (including the special case of *colinearity* when both $\theta_i - S_{i,j} = 0$ and $S_{i,j} - \theta_j = 0$ and becomes large (with a maximum value of $\pm 90^\circ$) when elements' positions/orientations are contour-inconsistent. Figure 1c plots cocircularity as a function of target orientation for the various flanker-offset conditions we tested. The plots show that although the flankers have a fixed vertical orientation, each target-flanker pairing within the stimulus can be co-circular (i.e., cocircularity = 0°) with appropriate combinations of target tilt (which is systematically varied within a run) and flanker-offset.

Note that this stimulus design leads to small differences in the distance between target and flanker across different flanker offsets: Separation of co-aligned elements is 2.33° rising to 2.69° for the maximum flanker offset. Given that the critical target-flanker separation for a stimulus presented at 8° is around 4° (Bouma, 1970) flankers are sufficiently deep inside the targets' interference zone that this small (maximum of 15%) difference in separation is unlikely to contribute significantly to the pattern of results reported.

Design

Both experiments had a within-subjects design. Target orientation was set to a value around vertical: specifically with an orientation that was one of 17 possible offsets from vertical, over a range that was set—using the results from a pilot run—individually for each observer. A method of constant stimuli (MOCS) was used with 16 trials at each of the 17 levels of orientation for the nine flanker offsets and the single unflanked condition. The nine flanker offset and unflanked conditions were randomly interleaved to give $272 \times 10 = 2,720$ trials per run. All participants completed two runs. Prior to this participants performed a minimum of 272 practice trials to familiarize themselves with the task.

Procedure

Participants were instructed to fixate a centrally-presented cross throughout the experiment. A trial consisted of a 250 ms presentation of the test stimulus immediately followed by a blank screen that remained until the observer responded. The observer used the keypad to indicate if the target appeared tilted clockwise or counterclockwise of vertical. Once the observer had responded the next stimulus was displayed. No feedback was given to the observer. The program recorded the number of clockwise and counterclockwise responses along with the corresponding stimulus level. These data were later fit to estimate measures of bias and threshold.

Specifically psychometric functions were obtained by plotting the probability that the participant responded that the target was oriented clockwise (y -axis) against the orientation of the target (x -axis). The data were then fit (minimizing least-squares error between model and data) with a cumulative Gaussian function. The *slope* of the function gives the orientation threshold of participants (the orientation yielding 82% correct discrimination), while shifts of the psychometric function left or right indicate bias. This shift measures

the orientation yielding 50% correct discrimination and is also known as the point of subjective equality (PSE). Note that in graphs, error bars associated with threshold and bias data are the 95% confidence intervals derived using a bootstrapping procedure (Efron & Tibshirani, 1993) which operated on the pooled data for a given observer across all runs. The bootstrap ran 512 repetitions.

Results

Experiment 1

Figure 2a shows psychometric functions for orientation discrimination across all conditions collected from a naïve observer (EH). The leftmost pair of psychometric functions (collected in *absent* and *co-aligned* flanker conditions) demonstrates that crowding occurs with co-aligned flankers. Specifically, the red function (unflanked condition) is steeper than the green function (co-aligned flankers) consistent with crowding elevating thresholds from 5.8° to 9.7° . The rightmost four graphs in Figure 2a show performance with flankers offset (to the left and right within each graph) by increasingly large distances. Note the signature of crowding (shallower psychometric functions) in all these plots.

Figure 2c and 2b shows threshold and bias estimates derived from flanked conditions for two observers, plot as a function of flanker separation (with corresponding estimates from the unflanked conditions shown as dashed lines). Threshold results confirm the presence of crowding at all flanker separations but also indicate a general decrease with increasing flanker offset. This decrease is in line with previous research indicating that the magnitude of crowding is proportional to the proximity of the distractors to the target (Andriessen & Bouma, 1976; Bouma, 1970; Dakin et al., 2010; Felisbert, Solomon, & Morgan, 2005; Levi, Hariharan, & Klein, 2002; Pelli, Palomares, & Majaj, 2004; Wilkinson, Wilson, & Ellemberg, 1997). However a key feature of our data is the presence of “notches” in threshold functions. In all but one of our eight observers the highest thresholds were measured not with zero-offset/co-aligned configurations but with the smallest nonzero flanker offsets ($\pm 0.17^\circ$ and $\pm 0.33^\circ$) although for participant EH this peak is seen to be closer to $\pm 0.67^\circ$.

Considering the crowded thresholds we observe at this eccentricity (i.e., ~ 4 – 16°) and inspecting Figure 1c we note that the only flanker-offset conditions likely to lead to contour consistent stimuli (i.e., with a cocircularity of 0°) are $\pm 0.33^\circ$ (when the target is cued at 16°), $\pm 0.17^\circ$ (target cued to 10°) and 0° (i.e., co-aligned, with

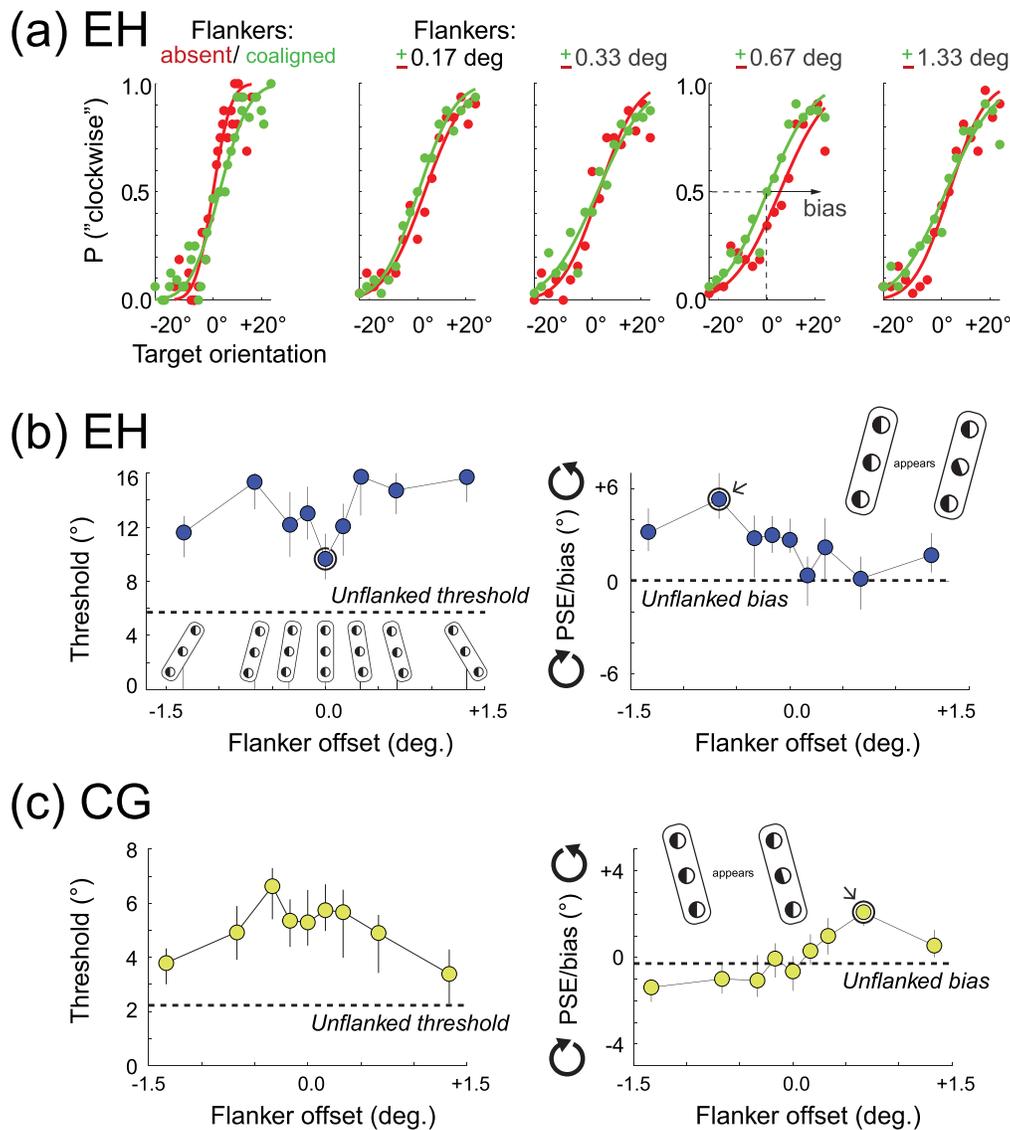


Figure 2. (a) Example psychometric functions from Experiment 1. Each point plots the proportion of times observers responded “clockwise” (y-axis) against the orientation of the target (x-axis). Cumulative Gaussian functions were then fitted to these data (solid lines). (b) Shows (left plot) discrimination thresholds and (right plot) bias (point of subjective equality; PSE) for naïve observer EH across all conditions with error bars indicating 95% confidence intervals. Note the threshold ‘notch’ at co-alignment and the negative, repulsive bias trend. (c) Threshold and bias for author CG, again showing the release from crowding at co-alignment. The positive trend in bias here shows assimilation of the target-orientation with the contour-orientation.

a target orientation of 0°). Given that crowding of co-aligned stimuli only arises with cues of 0°—when observers must be guessing anyway—our finding that flanker offsets of ±0.17 and ±0.33 lead to highest thresholds is consistent with contour-formation being involved in the crowding process (Livne & Sagi, 2007; Chakravarthi & Pelli, 2011).

To measure statistical confidence in these notches, we used bootstrapping (similar to the procedure for estimating error bars) to generate 1,024 new data sets. For each of these sets we calculated a measure of “notch-depth” that quantifies the (relative) facilitation resulting from co-alignment of target and flankers

$$F = \frac{\tau_0}{\max(\tau)} \tag{3}$$

where 0 is the bootstrapped threshold at 0.0° flanker-offset and $\max(\tau)$ is the largest threshold across all flanker-offset conditions, for that instance of the bootstrap. The data of only 2/8 observers—JO and HG—do not lead to 95% of F -estimates exceeding a value of 1.0, indicating the presence of a significant notch in the other six observers.

The right halves of Figures 2b and c display changes in estimated bias. Observers exhibited quite different trends in bias tending towards being either repulsive or

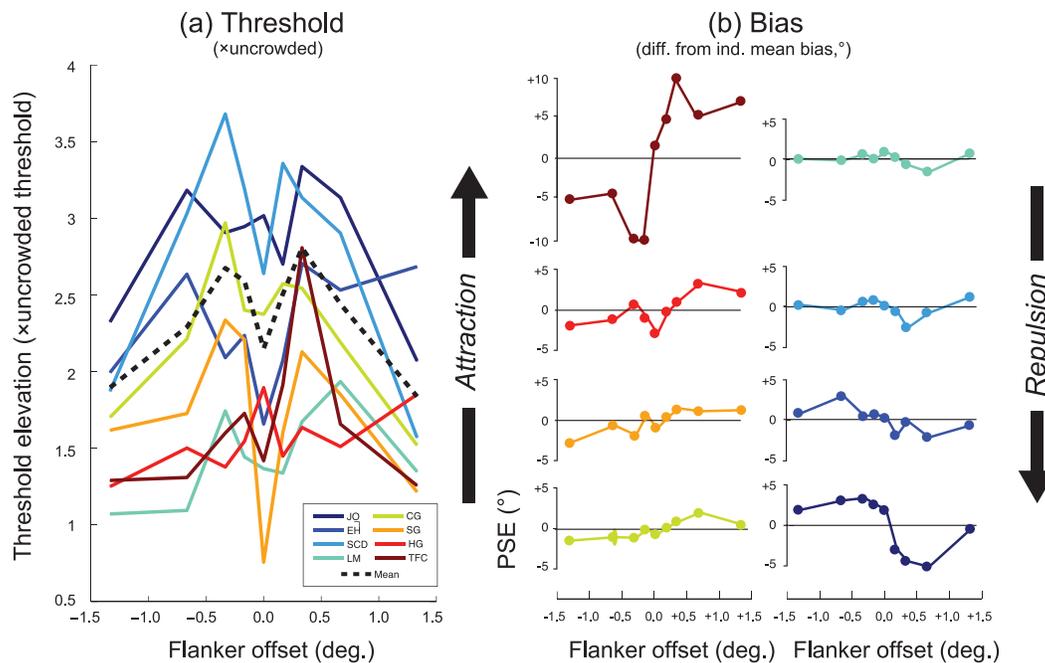


Figure 3. (a) Threshold elevation and (b) bias plotted against the nine stimulus separation conditions. The dashed line in (a) is an average of the thresholds for the eight participants. Bias in (b) was calculated by subtracting the mean bias (for each observer) from the individual bias estimates and has been ordered according to the magnitude and sign of the resulting normalized bias.

assimilative. Figure 2b shows EH has a general negative trend in bias consistent with their perceiving the target orientation as being repulsed from the contour orientation (a straight line passing between the two flankers and the center of the target; see schematic inset in Figure 2b). Conversely CG shows a positive trend associated with the target orientation being assimilated or drawn towards the contour orientation (Figure 2c inset schematic).

To assess the statistical significance of these trends we used the same bootstrapped data-sets used to analyze notch-depth, and then quantified bias modulation as:

$$B = \sum \beta_+ + \sum -\beta_- \quad (4)$$

where β_+ and β_- are biases derived from bootstrapped data with positive and negative flankers, respectively. By multiplying the biases by the sign of the offset we arrive at a *bias modulation index* that is positive when the data show attraction and negative when they show repulsion. The data of only 1/8 observers—LM—led to a distribution of B -estimates where the value 0.0 fell within the 95% confidence intervals, indicating the presence of significant bias modulation in the other 7/8 observers.

Figure 3 displays data from all eight participants. Figure 3a plots threshold elevation (original thresholds expressed as a multiple of uncrowded threshold) against flanker separation. Solid lines show results from different observers, the dashed black line the average

across all participants. Although there was variation across participants, most showed a clear bimodal shape with all but one displaying a release from crowding at or around co-alignment. For the averaged data two separate peaks were seen at offsets of -0.33° and $+0.33^\circ$ and a trough at 0° . The peaks had threshold elevations of 2.4 and 2.5 respectively. The trough was substantially lower than the peaks, with a threshold elevation of 1.9. Beyond offsets of $\pm 0.33^\circ$ the threshold elevation falls away.

We suggest that the observed release from crowding at co-alignment likely arises from decrease in repulsive bias (in line with previous work on position; Greenwood et al., 2009). This bimodal threshold pattern cannot solely be attributed to varying stimulus separation, indicating that there is an effect of target-flanker configuration on the magnitude of crowding.

In analogy to the presentation of threshold elevation in Figure 3a, data in Figure 3b are derived by taking raw bias estimates from the nine flanker conditions and subtracting the mean bias across all conditions for a given observer. Results have been presented following rank-ordering to make presentation clearer. The ordering was done based on the bias modulation index B (Equation 4) calculated using each observers raw (i.e., not bootstrapped) data. This index quantifies how repulsive/assimilative normalized bias was for each observer. For a given observer the index allowed the biases to be ordered from most positive (assimilative) to most negative (repulsive). While most participants showed a biphasic pattern of bias, within this there

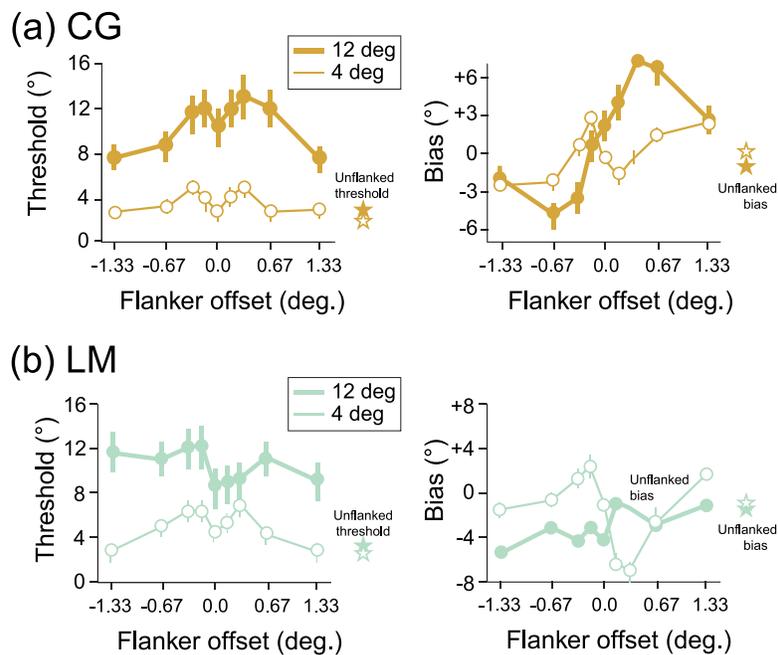


Figure 4. Results from Experiment 2: Threshold and bias for crowded orientation discrimination from two observers at two target-eccentricities. Note that for thresholds collected at 12° (thick lines, graphs in left column) we observe substantial crowding with flanker separations out to $\pm 1.33^\circ$ consistent with larger interference zones at this eccentricity. Overall thresholds show the same “notch” as for data collected at 8° indicating a consistent release from crowding with target-flanker co-alignment. For bias data we note a change in the sign of bias—arising from the influence of contour orientation on perceived target-orientation—from predominantly repulsive (at 4°) to more assimilative (at 12°).

were two clear subpatterns. The first of these was a positive trend, with negative flanker offsets leading to predominantly negative bias and positive offsets to positive bias. This same-sign bias indicates an assimilative effect and was observed in 4/8 data sets. The second sub-pattern was a negative trend that indicates a predominantly repulsive effect. This pattern was observed in 3/8 participants. The next experiment tests the idea that this pattern of results depends on stimulus-eccentricity.

Experiment 2

This experiment tested the hypothesis that eccentricity influenced the direction of the bias observed in Experiment 1. We ran essentially the same experiment with the target presented at either 4° or 12° (again, in the upper visual field). As stated in the Methods, stimulus separation was reduced to 1.25° in the 4° eccentricity condition, so that flankers still fell within the targets’ (now smaller) interference zone. The results were averaged across repetitions in the same manner as above.

Data from two representative observers are shown in Figure 4. Considering threshold data first (left column), because the spatial extent of crowding increases with eccentricity (Bouma, 1970) it came as no surprise that the threshold for orientation discrimination for a target

presented at 12° (thick circles) was elevated relative to uncrowded performance even with our larger flanker-target separation of 1.33° . Apart from this difference the overall pattern of threshold elevation measured with targets at 4° and 12° is similar to results presented in Figures 2 and 3 (measured with 8° targets) with greatest crowding arising (on average) with flanker offsets of $\pm 0.33^\circ$ and a release observed both for greater separations and for the zero-separation (co-alignment) conditions.

Considering bias data (Figure 4, right column) results at 4° were very consistent: Unflanked levels of bias were always low, (LM = -0.9° ; CG = 0.2° ; SCD = -0.6° ; EH = 0.5°) and all observers showed a pattern of results dominated by a repulsion of the target orientation from the overall contour orientation. Maximal repulsion was typically observed at the smallest flanker separations and 3/4 participants saw a change from repulsive to assimilative bias at larger flanker offsets. We note that this pattern of results is in accordance with work on the tilt illusion for peripheral stimuli, where Mareschal et al. (2010) note that repulsive bias changes to assimilative bias with increasing stimulus separation.

The pattern of bias for observers at 12° is more idiosyncratic. While participant CG displayed clear assimilation with all flanker offsets, SCD showed strong repulsion, while data from participant LM shows a

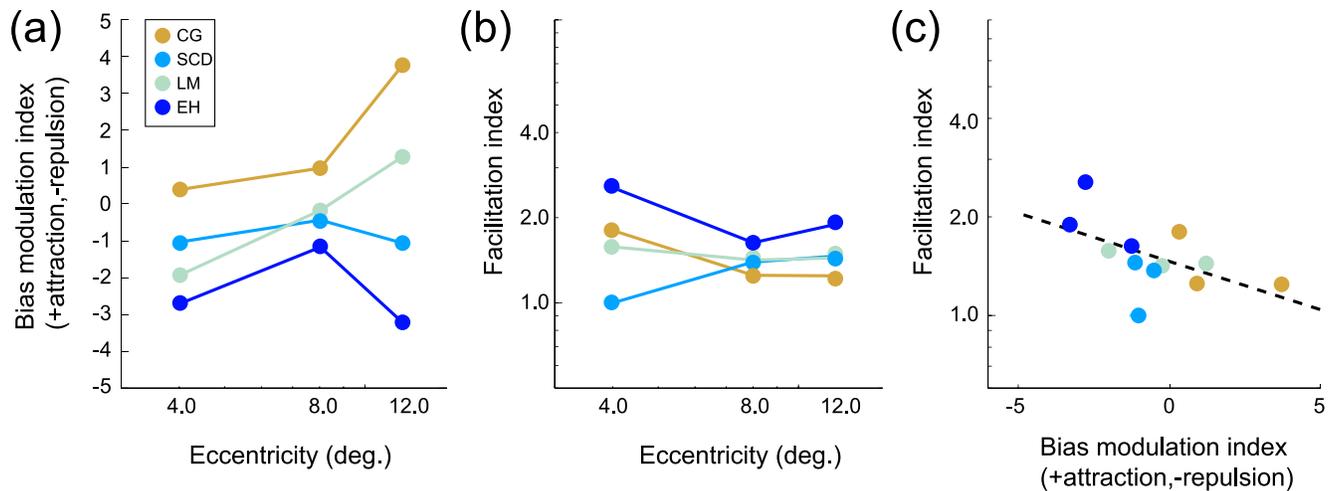


Figure 5. Indexes of (a) bias-modulation (positive denotes attraction, negative denotes repulsion) and (b) facilitation (threshold decrease with co-alignment) plot for all observers as a function of eccentricity. Note (a) the general reduction of repulsion (i.e., positive/upwards trend) with increasing eccentricity in contrast to (b) near-constant levels of facilitation. (c) Plotting one index against the other reveals a tendency for strong repulsion to associate with higher levels of facilitation.

positive trend, but was all negatively biased irrespective of flanker position (i.e., showing both assimilation and repulsion). Finally, EH showed a similar pattern of repulsion at 12° as at 4°. To make sense of these data, we computed the bias modulation index B (Equation 4) as an overall index of the magnitude and direction of bias at each of the three tested eccentricities for each observer. Indices are plotted in Figure 5a and one can see that while repulsion switches to attraction (i.e., the repulsion index becomes positive) only in 2/4 observers, we do see a general trend for the magnitude of repulsion to decrease.

We also computed an index of facilitation F (Equation 3) that quantifies the depth of the notch (at zero flanker-offset) in the threshold functions (e.g., Figure 4, left column). These results, plot in Figure 5b, show that the amount of facilitation is fairly constant with increasing eccentricity. Figure 5c plots the repulsion against the facilitation index for all observers/conditions and reveals that they are moderately negatively correlated ($R = -0.54$, $p = 0.068$) so that more facilitation (i.e., more release from crowding with co-alignment) was associated with stronger repulsion. Since there is no a priori reason to expect these measures to be associated we take this as suggestive that the underlying explanation for crowding (i.e., elevated thresholds) with spatially offset flankers is fluctuating bias (Dakin et al., 2010; Greenwood et al., 2012).

Discussion

We measured participants' ability to perform crowded orientation discrimination where flanking and

target elements could combine to form shapes that differed in the extent to which they were consistent with the presence of an underlying contour. We report three main findings.

- Contour structure affects discrimination threshold. We observe most crowding not when target and flankers positions are aligned but when they are slightly misaligned so that they form contours only when the target is cued.
- Contour structure produces bias; global orientation (i.e., the arrangement of target and flankers) influences perceived target orientation. In some conditions the target orientation is assimilated with the global orientation, in others it is repulsed from it.
- Eccentricity influences the sign of the bias observed. We observed a clear reduction in repulsive bias with increasing eccentricity broadly in line with previous work looking at the tilt illusion (Mareschal et al., 2010).

Contours and crowding

The degree to which features are consistent with a contour influences the extent to which they crowd one another. Notably, Livne and Sagi (2007) and Chakravarthi and Pelli (2011), showed that conditions that promoted grouping between the target and flankers led to strong crowding while conditions that led to flanker-grouping broke crowding (since target and flankers became clearly segregated). Our threshold measurements confirm that conditions promoting contour-grouping between target and flankers (at smaller spatial

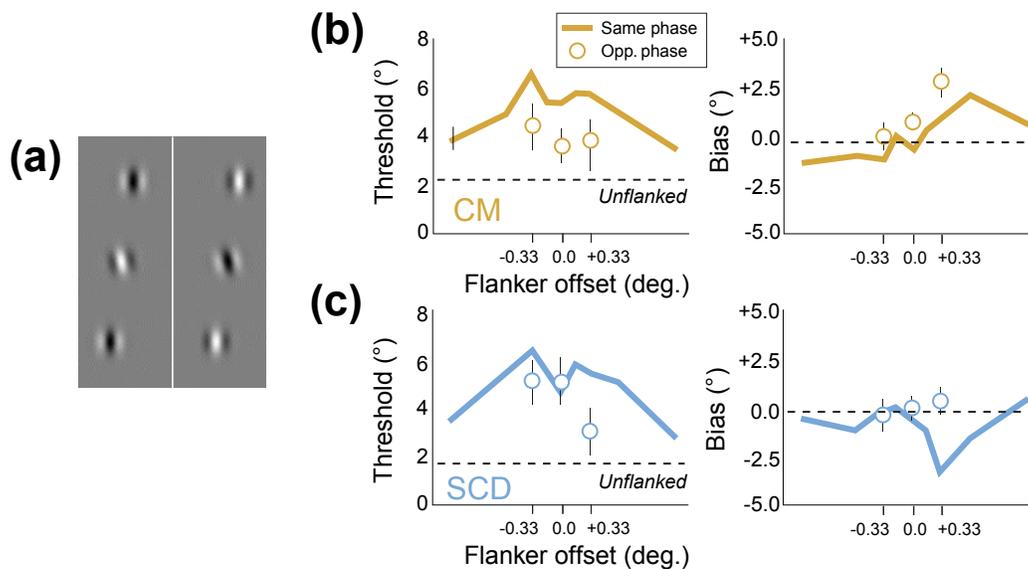


Figure 6. (a) Two examples of stimuli composed of alternating contrast polarity elements. (b, c) Open symbols show thresholds and biases from two observers judging the orientation of the central target element at three flanker offsets. For reference solid lines show data from the comparable same-polarity condition. Polarity alternation reduces (b) threshold and (c) bias.

offsets) maximized crowding. Specifically from Figure 1 (bottom row) it can be seen that offsets of $\pm 0.17^\circ$ and $\pm 0.33^\circ$ resulted in cocircularity approaching zero (i.e., were conducive to contour formation) at target offsets in the range of those presented in the experiments. This was thought to be responsible for the increase in threshold (especially at $\pm 0.33^\circ$).

One candidate explanation for this elevation is that the orientation of the contour contaminates the target orientation. Our bias results suggest that the influence exerted by the contour orientation on perceived target orientation (either attractive or repulsive) can differ depending on observer and eccentricity. Results from Experiment 2—which reveal a tendency for strength of crowding to be associated with strength of bias induced by configuration—suggests a common neural mechanism. Specifically, these results are consistent with our earlier suggestion that loss of orientation information within crowded contours can be modeled as a fluctuating (trial-by-trial) bias that results from crowding having a probabilistic (all-or-nothing) component (Dakin et al., 2010).

If inappropriate contour linkage leads to crowding then conditions that are known to interfere with contour processing may lead to a release from crowding. Manipulation of contrast polarity is an interesting manipulation in this regard. It is known that alternation of contrast polarity along a contour disrupts detection of peripherally-presented contours in some observers (Hess & Dakin, 1997) but not others (Nugent, Keswani, Woods, & Peli, 2003). In terms of crowding, alternating contrast polarity reduces crowding of *T*-orientation discrimination (Chakravarthi &

Cavanagh, 2007; Chung & Mansfield, 2009; Kooi et al., 1994) but does not greatly reduce crowding of Landolt C orientation discrimination by bars or Gaussians (Hariharan et al., 2005; Hess, Dakin, Kapoor, & Tewfik, 2000). Based on the disruptive influence of contrast-polarity on contour integration in at least some observers (Hess & Dakin, 1997; Nugent et al., 2003) we suggest that differences in the impact of contrast-polarity alternation on crowding arise from the central role of inappropriate contour-linking in the crowding of “tumbling T” targets (Dakin et al., 2010) but not of Landolt C targets.

We have conducted a preliminary investigation of the impact of contrast-polarity alternation on our results. We ran the two authors with stimuli composed of polarity-alternating elements (Figure 6a; the contrast-polarity of the target was set randomly from trial-to-trial and flankers were opposite contrast-polarity to this) at three flanker offsets (-0.33 , 0.0 and 0.33°). All other experimental details were as described previously for Experiment 1. Consistent with contour linking being responsible for the reported pattern of crowding, polarity alternation does improve performance by reducing threshold (Figure 6b) in one observer (although also modestly increasing bias) and through a combination of modest threshold-reduction and bias-reduction in the other observer (Figure 6c). Clearly further work is required but we would specifically predict that observers’ benefit from inverting the contrast polarity of flanking elements in crowded displays will inversely correlate with their ability to detect alternating contrast polarity contours in the peripheral visual field (Hess & Dakin, 1997; Nugent et al., 2003).

Furthermore, Chung and Mansfield (2009) showed that contrast polarity inversion both reduced crowding of tumbling T targets but also failed to improve reading rates (e.g., of letter-trigrams) in the periphery. This finding is surprising if reading is limited by the visual span (Legge et al., 2007) which is itself limited by crowding (Pelli et al., 2007). Chung and Mansfield (2009) suggest that their finding could have arisen from differences in task-demands of T -orientation discrimination (crowding task) and trigram-letter identification (reading task). We speculate that the difference may actually be a consequence of physical properties of text. Typographers have long known that the chance alignment of spaces across lines of text can form “rivers” that are distracting. We suggest that the visual appearance of written language may have evolved to minimize the impact of spurious contour formation between the strokes of adjacent letters (when they are presented within real text).

Relationship to the tilt illusion

That so much of the bias data we report is consistent with repulsion of target orientation from contour orientation suggests that, under conditions of crowding, contours formed by the flanker and target can serve as an orientation context able to induce illusions of perceived target-orientation similar to the traditional simultaneous tilt illusion. Furthermore, Mareschal et al. (2010) have shown that, for a center-surround tilt illusion induced with stimuli presented in the periphery bias can switch from repulsive to assimilative with increasing eccentricity (approximately 8° for their stimulus set-up). Our observing increased repulsive bias at smaller eccentricities (4°) and a decrease in overall repulsive bias at greater eccentricities suggests that the tilt illusion and biases induced under crowding share a common mechanism. If crowding worked just like the tilt illusion we might have expected a uniform switch from repulsion to attraction. However we note that our stimuli differ in one critical way from those of Mareschal et al. (2010) and that is that shifting flanker location serves to increase both stimulus separation and contour orientation. Based on the tilt illusion, larger flanker offsets will produce more tilted contours that we would expect to generate more repulsion, but will also increase separation that makes one more likely to see assimilation. That increasing flanker offset could both increase and decrease repulsion, likely explains the idiosyncratic pattern of results we observed in Experiment 2.

Keywords: crowding, contour integration, peripheral vision

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Corresponding author: Steven C. Dakin.

Email: s.dakin@ucl.ac.uk.

Address: UCL Institute of Ophthalmology & NIHR Biomedical Research Centre at Moorfields Eye Hospital, London, UK.

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