

Global stimulus configuration modulates crowding

Toni P. Saarela

Laboratory of Psychophysics, Brain Mind Institute,
Ecole Polytechnique Fédérale de Lausanne (EPFL),
Lausanne, Switzerland



Bilge Sayim

Laboratory of Psychophysics, Brain Mind Institute,
Ecole Polytechnique Fédérale de Lausanne (EPFL),
Lausanne, Switzerland



Gerald Westheimer

Department of Molecular and Cell Biology,
University of California, Berkeley, CA, USA



Michael H. Herzog

Laboratory of Psychophysics, Brain Mind Institute,
Ecole Polytechnique Fédérale de Lausanne (EPFL),
Lausanne, Switzerland



In crowding, neighboring elements impair the perception of a peripherally presented target. Crowding is often regarded to be a consequence of spatial pooling of information that leads to the perception of textural wholes. We studied the effects of stimulus configuration on crowding using Gabor stimuli. In accordance with previous studies, contrast and orientation discrimination of a Gabor target were impaired in the presence of flanking Gabors of equal length. The stimulus configuration was then changed (1) by making the flankers either shorter or longer than the target or (2) by constructing each flanker from two or three small Gabors. These simple configural changes greatly reduced or even abolished crowding, even though the orientation, spatial frequency, and phase of the stimuli were unchanged. The results challenge simple pooling explanations for crowding. We propose that crowding is weak whenever the target stands out from the stimulus array and strong when the target groups with the flanking elements to form a coherent texture.

Keywords: crowding, perceptual organization, spatial vision, detection/discrimination

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Introduction

Recently, there has been a surge of interest in crowding in human vision (e.g., Levi, 2008; Pelli, Cavanagh, Desimone, Tjan & Treisman, 2007). In crowding, flanking stimuli impair the observer's ability to make judgments about a target stimulus (Bouma, 1970; Pelli, Palomares, & Majaj, 2004). Crowding is most famously observed in letter identification (Bouma, 1970; Estes, 1972; Flom, Weymouth, & Kahneman, 1963), but it also impairs the discrimination of basic stimulus attributes such as orientation and contrast (Andriessen & Bouma, 1976; Parkes, Lund, Angelucci, Solomon, & Morgan, 2001; Westheimer, Shimamura, & McKee, 1976; Wilkinson, Wilson, & Ellemberg, 1997).

A prominent view is that in crowding, information about the target is not completely lost but is pooled or integrated with the information from the contextual elements (Parkes et al., 2001; Pelli et al., 2004). Accordingly, crowding has been described as 'excessive feature integration' (Pelli et al., 2004) and 'texture perception when we do not wish it to occur' (Parkes et al., 2001). In

terms of the underlying causes, crowding is thus seen as distinct from other perceptual phenomena such as masking (Levi, Hariharan, & Klein, 2002; Pelli et al., 2004) and surround suppression (Petrov, Popple, & McKee, 2007) where similar interferences occur. In masking and surround suppression, information from the target is thought to be irretrievably lost (Parkes et al., 2001; Pelli et al., 2004; Petrov et al., 2007). Masking occurs when the target and the contextual stimulus (called the mask) stimulate neural mechanisms responding to the same spatial location in the visual field and a process such as divisive inhibition (Foley, 1994; Heeger, 1992) reduces the incremental responses to the target. In surround suppression, the target and the contextual stimulus stimulate neural mechanisms responding to adjacent locations in the visual field, and the responses to the target are suppressed by neural inhibition that operates 'over space' (Cavanaugh, Bair, & Movshon, 2002; Kapadia, Westheimer, & Gilbert, 2000).

In the crowding literature, various hypotheses have been put forward to explain the pooling or integration of information. Crowding has been suggested to reflect the limited spatial resolution of visual attention (Intriligator &

Cavanagh, 2001), ‘hard-wired’ feature integration mechanisms (Pelli et al., 2004), and the operation of spatial pooling mechanisms signaling the textural grain of the visual scene (Parkes et al., 2001; Wilkinson et al., 1997). According to the spatial pooling hypothesis of crowding, when many similar elements are presented in close proximity, the visual system processes them as a coherent texture instead of as individual elements. This view suggests that neural mechanisms pool information from nearby locations in the visual field to represent the textural properties of the stimulus (Parkes et al., 2001; Wilkinson et al., 1997). This grouping into a textural whole comes at the expense of articulation of individual elements.

But which comes first: are the textural wholes based on the pooling of individual elements, or do the wholes determine which elements are pooled? In a recent report, Malania, Herzog, and Westheimer (2007) showed that the deterioration of foveal vernier discrimination caused by flanking stimuli can be reversed when the target is not perceived as ‘belonging’ to the flanker array. Our purpose here was to test how stimulus configuration affects crowding and to see whether the effects are compatible with the pooling approach to crowding. Following Wilkinson et al. (1997), we used Gabor elements as stimuli. We measured changes in orientation and contrast discrimination that resulted when the flankers were perceptually decoupled from the target pattern. We kept constant the orientation, spatial phase, and spatial frequency of the flankers while changing the global configuration of the stimulus. We show that, when a target Gabor is flanked on both sides by an array of distracting Gabors, changes in the configuration of the flanking Gabors lead to improvements in performance that are not readily explained by simple spatial pooling. Rather, any change in the configuration of the stimulus that makes the target ‘stand out’ from among the flankers leads to better performance, even in conditions where a pooling account of crowding would predict a deterioration in performance.

Methods

Observers

Eight observers (21–30 years, two females) participated in the experiments: the first author and seven observers who were naive to the purposes of the experiments. Each observer had normal or corrected-to-normal vision, reaching a visual acuity of 1.0 or better in at least one eye (corresponding to 20/20), measured with the Freiburg Visual Acuity Test (Bach, 1996). The experiments were approved by the local ethical committee and the observers signed an informed consent before participating in the experiments.

Equipment

Stimuli were presented on a Philips 201B4 monitor driven by a RadeOn 9200 SE graphics card. The display was linearized through look-up tables and had an effective luminance resolution of 8 bits. The screen was refreshed at 100 Hz and had a spatial resolution of 1024×768 pixels (subtending 22.1×16.6 degrees of visual angle). Mean luminance was 45.0 cd/m^2 .

Stimuli

The stimuli used were similar to those used by Wilkinson et al. (1997), consisting of arrays of vertical Gabor patches. The luminance profile of a single patch is given by

$$G(x, y) = L \times [1 + c \times \exp(-(x-x_0)^2/\sigma_x^2 - (y-y_0)^2/\sigma_y^2) \times \sin(2\pi f(x-x_0))], \quad (1)$$

where L is the mean luminance of the screen, c is the contrast, and f is the spatial frequency of a Gabor centered at the point (x_0, y_0) ; σ_x and σ_y are the space constants for the Gaussian envelope. Spatial frequency of the carrier was 3.3 cycles per degree (cpd) of visual angle, and the horizontal space constant (σ_x) was 0.19 degrees. The vertical space constant (σ_y) of the target was always 0.57 degrees and varied for the flankers between experimental conditions (see below).

The target was the central one in a row of fifteen Gabor patches. The target appeared at an eccentricity of 5.7 degrees (1.9 degrees above and 5.4 degrees to the right of fixation). The horizontal center-to-center spacing between the Gabors was 0.57 degrees. In the conditions testing the effect of flanker length (LENGTH condition), the vertical space constant (σ_y) of the flanking Gabors was varied in steps of 0.19 degrees from 0.19 to 1.14 degrees (see examples in Figures 1a, 1c, and 1d). In the conditions testing the effect of the finer structure of the flankers (ROWS condition), each flanker consisted either of a pair or a triplet of Gabors, with a σ_y of 0.19 degrees (Figures 1e and 1f). A pair of Gabors was presented with one Gabor 0.38 degrees above and the other 0.38 degrees below the midline of the stimulus. In a triplet, one Gabor was presented on the midline, and the other two 0.57 degrees above and below the midline. Because changing the length of a Gabor also changes its total contrast energy, we ran two variations of each condition. In the first, the *equal contrast condition*, the carrier contrast of all flankers was 0.40 Michelson contrast. In the second, the *equal contrast energy condition*, the contrast of the flankers was scaled to keep their contrast energy constant relative to a Gabor with $\sigma_y = 0.57$ degrees and carrier contrast of 0.40. Contrast energy of a Gabor was calculated as the integral of the squared contrast values over the

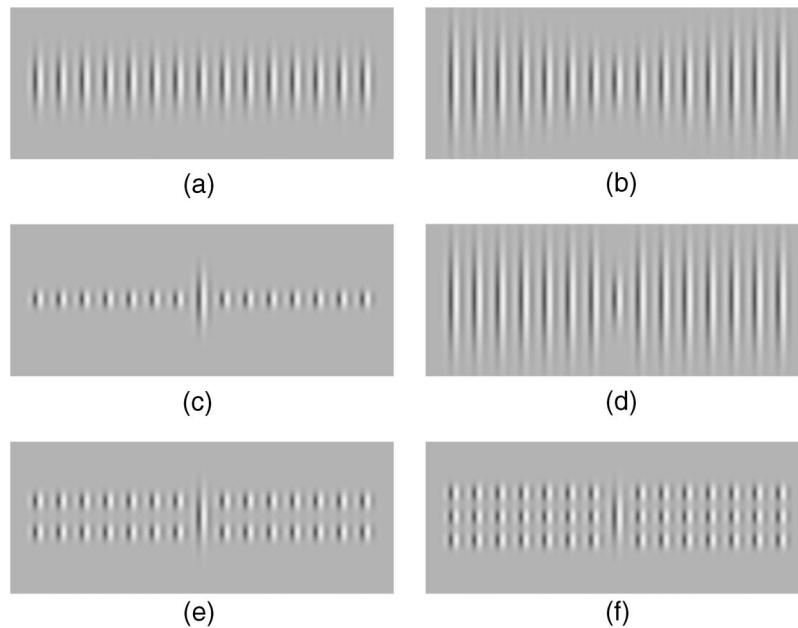


Figure 1. Examples of stimuli used in the experiments. (a) The target was the middle element of an array of 15 Gabor patches. Here, the flanking elements are equal in length to the target. (b) Stimulus used in the control experiment for positional uncertainty. The Gabor length increases from the central target towards the outermost Gabors. (c, d) Examples of the shortest and longest flanker lengths used in the LENGTH conditions. (e, f) Flanker configurations in the ROWS conditions. Contrast of the stimuli is exaggerated in these examples.

Gabor pattern. The Michelson contrast of the shorter flankers was thus scaled up, and the contrast of the longer flankers was scaled down. An exception was the condition where each flanker consisted of a triplet of Gabors. The triplet already had the same contrast energy as a single Gabor with $\sigma_y = 0.57$, so no scaling was needed.

In additional control experiments, we cued the target location in two ways. First, the vertical space constant of the Gabors was linearly increased from $\sigma_y = 0.57$ (the target) to $\sigma_y = 1.14$ (the outermost flanker) degrees to emphasize the target position (Figure 1b). Second, the target position in the equal flanker length condition (Figure 1a) was cued by two short (0.4 degrees), black vertical line segments presented immediately above and below the target. These lines appeared 250 ms before the stimulus onset and were present until the end of the stimulus presentation.

Procedure

The experiments were run in a dimly illuminated room, with the observer seated 100 cm from the monitor. The data for each observer were gathered in several sessions, one session lasting about 1–1.5 hours. The observers received training in the tasks before the actual experiments.

Contrast discrimination

Contrast discrimination thresholds were measured using a 2IFC task. The observer fixated a central fixation

spot and started the experiment by a button press. After a 250-ms blank period, two 100-ms stimulus intervals were presented, separated by a 750-ms blank period. Target carrier contrast was 0.40 in one interval (selected randomly for each trial) and $0.40 + \Delta c$ in the other. The increment Δc was controlled by an adaptive procedure (Taylor & Creelman, 1967). The observer's task was to indicate with a button press the interval in which the target contrast was higher. Auditory feedback was provided after incorrect responses. The response initiated the next trial. The fixation spot was always visible, and the observers were instructed to hold their fixation in the center throughout the experiment. One block consisted of 80 trials, and only one flanker condition was tested in a given block (that is, conditions were not mixed). The order of the blocks was randomized for each observer.

Orientation discrimination

Orientation discrimination thresholds were measured with a binary task, a trial consisting of a single 100-ms stimulus presentation (preceded by a 250-ms blank period). The target carrier had a contrast of 0.40, and the target was tilted either clockwise or counterclockwise with respect to vertical. The amount of tilt was again controlled by an adaptive procedure. The observer's task was to indicate whether the target was tilted clockwise or counterclockwise. Again, auditory feedback was given after incorrect responses, and one block consisted of 80 trials.

Data analysis

The data from each block were saved for off-line analysis. A psychometric function (a cumulative normal) was fitted to the data using a maximum likelihood fitting procedure to extract the 75% threshold. The individual thresholds reported are averages of two such estimates and the mean thresholds are averages across observers.

Target conspicuousness ratings

To measure the extent to which the target groups with or stands out from among the flankers, we used a rating task. A set of four naive observers participated in the experiment (different from those who had participated in the discrimination experiments except for DW who also participated in one control experiment). The observers were shown, in a random order, the same stimuli as in the discrimination experiments (except for the control stimulus where the

target was cued with two lines), in the same location but with an unlimited viewing time. The target was vertical and its contrast was equal to the flanker contrast. The observers rated the target conspicuousness on a scale from 0 to 10. They were instructed to give a rating of 0 when the target grouped with the flankers so as to form one coherent pattern with them, a rating of 10 when the target was very conspicuous and seemed to clearly stand out from among the flankers, and to use the numbers in between as seemed appropriate. Each observer rated each stimulus twice, and the two ratings were averaged.

Results

Contrast discrimination

The data from the LENGTH condition are shown in Figure 2. Contrast discrimination thresholds are plotted as

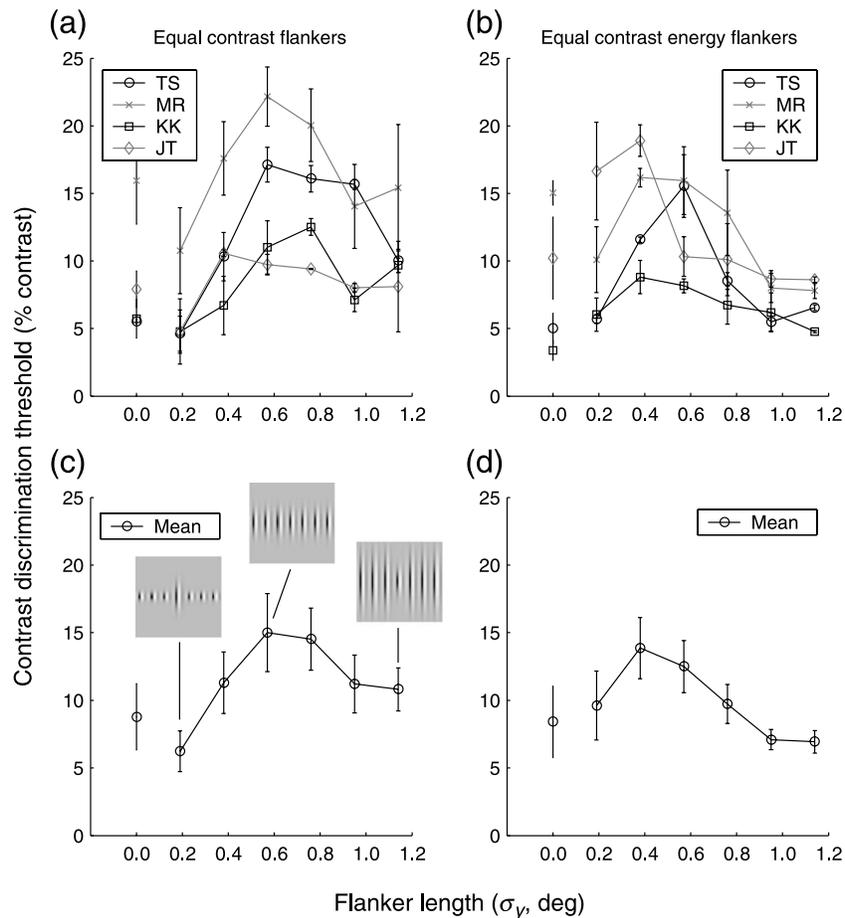


Figure 2. Contrast discrimination as a function of flanker length. The 75% discrimination thresholds are plotted for individual observers (a, b) and as average results (c, d). The abscissa shows the flanker length, defined as the vertical space constant of the Gabor (σ_y). Data in (a) and (c) are from the condition with equal contrast flankers, data in (b) and (d) are from the condition where the contrast of the flankers was scaled to keep the contrast energy constant when the length was changed. The leftmost points (flanker length = 0.0) show the thresholds for the control condition, measured with no flanking elements. The insets show cropped examples of the stimuli, see full versions in Figure 1. Error bars show $\pm SEM$.

a function of flanker length. The left panels show the equal contrast condition (flanker contrast always 0.40, same as the target pedestal). The right panels show the data from the equal energy condition (flanker contrast adjusted to compensate for the changes in contrast energy due to changes in size). The isolated data points on the left (flanker length = 0) always show the discrimination thresholds in the absence of flankers.

Although there is some individual variation, all the observers show an inverted u-shape curve when the thresholds are plotted against flanker length. In the average results in the equal contrast condition (Figure 2c), the greatest threshold elevation occurred when the flanker length was equal to the target length ($\sigma_y = 0.57$). When the flankers were made either shorter or longer, performance improved approximately to control level. With the equal energy flankers (Figure 2d), the peak threshold elevation shifted to shorter flankers. Still, with the shortest and longest flankers, performance was about as good as in the target-only condition.

In Figure 3, the data from the ROWS condition are plotted both for individual observers (Figure 3a) and as average thresholds (Figure 3b). Again, one row of equal-length flankers raised the thresholds compared to the control condition (the second and first bar from the left, respectively, in Figure 3b). However, when each of the flankers consisted of either a pair or a triplet of small Gabors, thresholds were at or close to the control thresholds. The same recovery in performance was apparent in both the equal contrast and in the equal contrast energy conditions. The effect is clearly seen in the average results, and from the individual data, it is apparent that three of the four observers showed the same pattern of results. Results from one observer (MR) do not show such clear differences between conditions.

Orientation discrimination

Orientation discrimination data from the LENGTH condition are shown in Figure 4. The control level (discrimination without the flankers) is again shown by the leftmost points (flanker length = 0). For all observers, threshold elevation was greatest with the equal-length flankers ($\sigma_y = 0.57$), in both the equal contrast (Figure 4a) and equal contrast energy conditions (Figure 4b). The same can be seen in the average thresholds for both conditions (Figures 4c and 4d). With the shortest and longest flankers, thresholds were at or close to the control level.

As in contrast discrimination, dividing the flankers into rows reduced their threshold-raising effect (the ROWS condition, Figure 5). One row of equal-length flankers substantially raised the thresholds compared to the control condition, but this effect was reduced when the flankers consisted of pairs of short Gabors. Compensating for contrast energy did not greatly change the effect. When

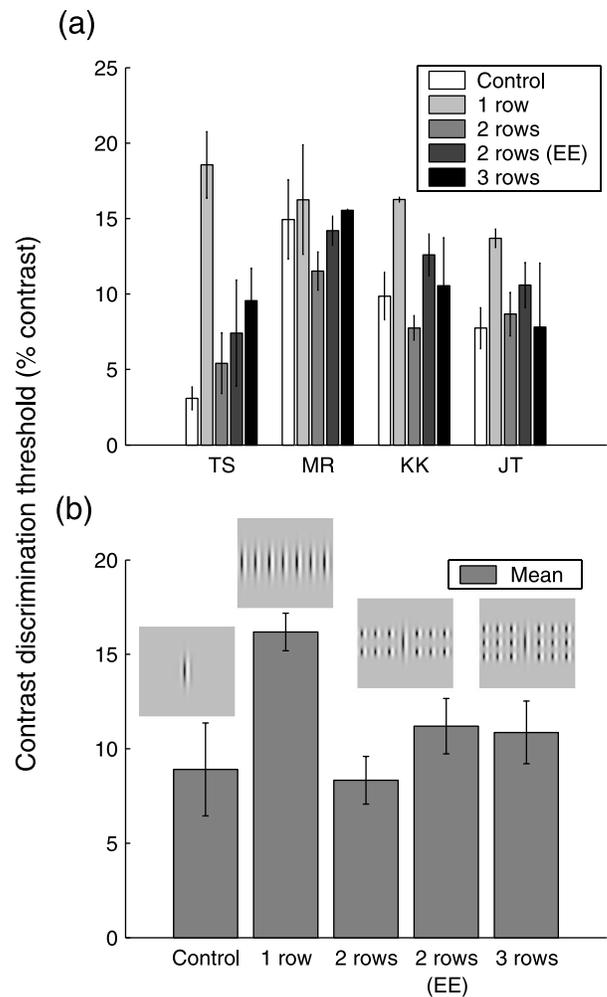


Figure 3. Contrast discrimination in the ROWS condition. The 75% discrimination thresholds are shown for the individual observers (a) and as average results (b). The control condition was measured with no flanking elements. In the ‘1 row’ condition, flankers were equal in length to the target. In the ‘2 rows’ condition, each flanker consisted of a pair of Gabors (see Figure 1e), ‘EE’ indicates the equal contrast energy condition. ‘3 rows’ condition: each flanker consisted of a triplet of Gabors (see Figure 1f). The insets show cropped examples of the stimuli, see full versions in Figure 1. Error bars show $\pm SEM$.

the flankers consisted of triplets of Gabors, the results were mixed. In the average results, the ‘three rows’ condition was between the ‘one row’ and ‘two rows’ conditions. When looking at the individual results, it can be seen that there were two observers who showed a clear reduction in thresholds in this condition (observers MR and KK), and two observers who did not (TS and JT).

Positional uncertainty

Control experiments were run to test the role of positional uncertainty in the results reported above.

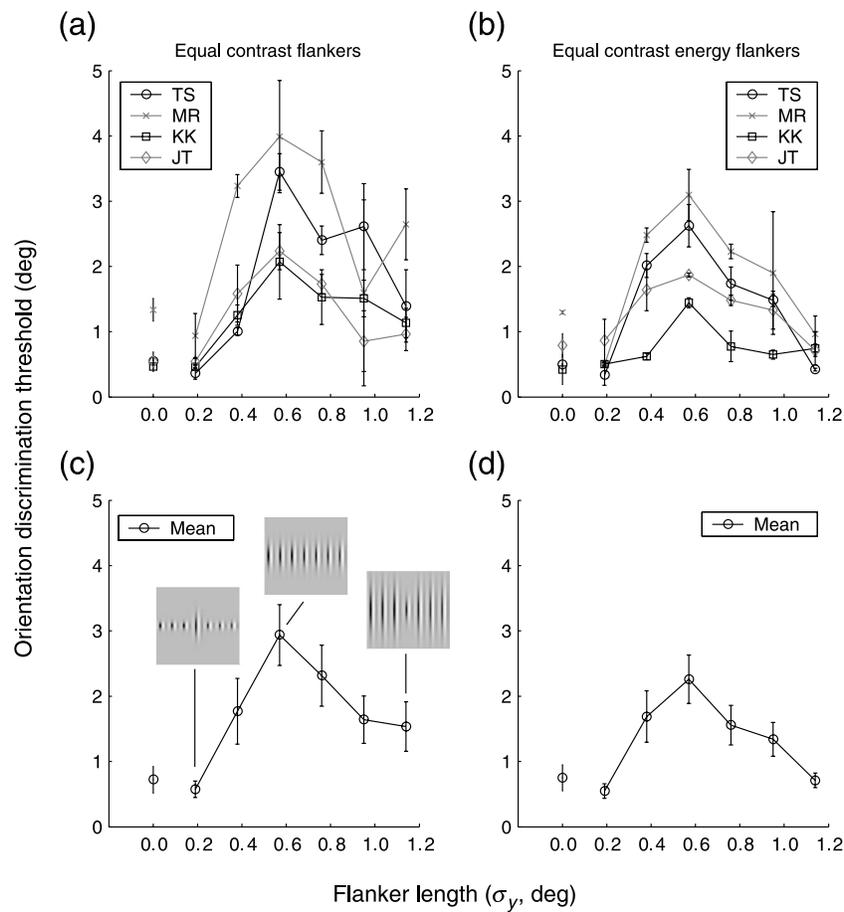


Figure 4. Orientation discrimination as a function of flanker length. The 75% discrimination thresholds are plotted for individual observers (a, b) and as average results (c, d). Conventions as in Figure 2.

There might be uncertainty about the target position within the Gabor array when the flankers are equal in length to the target. This uncertainty would be reduced when, for example, the length of the flankers is changed, leading to improved performance. We tested this hypothesis by cueing the target location in two ways. First, we used an ‘implicit cue’ in the Gabor array itself. The flanker length increased from the middle towards the outermost elements, giving a clear cue for the target location (Figure 1b). The results from the control experiment are shown in Figures 6a (contrast discrimination) and 6b (orientation discrimination). The additional cue did not improve performance in either case, and the thresholds were as high as with the equal-length flankers.

Second, we added short vertical lines immediately above and below the target in the equal-length condition to indicate the target location. The results in Figures 7a (contrast discrimination) and 7b (orientation discrimination) reveal no improvement in thresholds in the presence of the cue, confirming an earlier result by Wilkinson et al. (1997). The crowding effects we observed do not seem to be caused by positional uncertainty.

Target conspicuousness ratings

Figure 8 shows the results from the target conspicuousness rating experiment. The rating scale used was from 0 (target forms a coherent group with the flankers) to 10 (target clearly stands out). The average ratings across observers are plotted against the average contrast (Figure 8a) and orientation (Figure 8b) discrimination thresholds. The ratings and discrimination thresholds are negatively correlated. The stimuli that received high conspicuousness ratings produced low thresholds, and the stimuli that received low ratings produced high thresholds. Thus, the judgments about conspicuous targets were easier to make than judgments about grouped targets. The correlations between the ratings and thresholds are -0.91 for contrast discrimination and -0.81 for orientation discrimination. The lines show the best linear fits to the data.

Discussion

The present results provide strong evidence that peripheral crowding is strongest when the target element

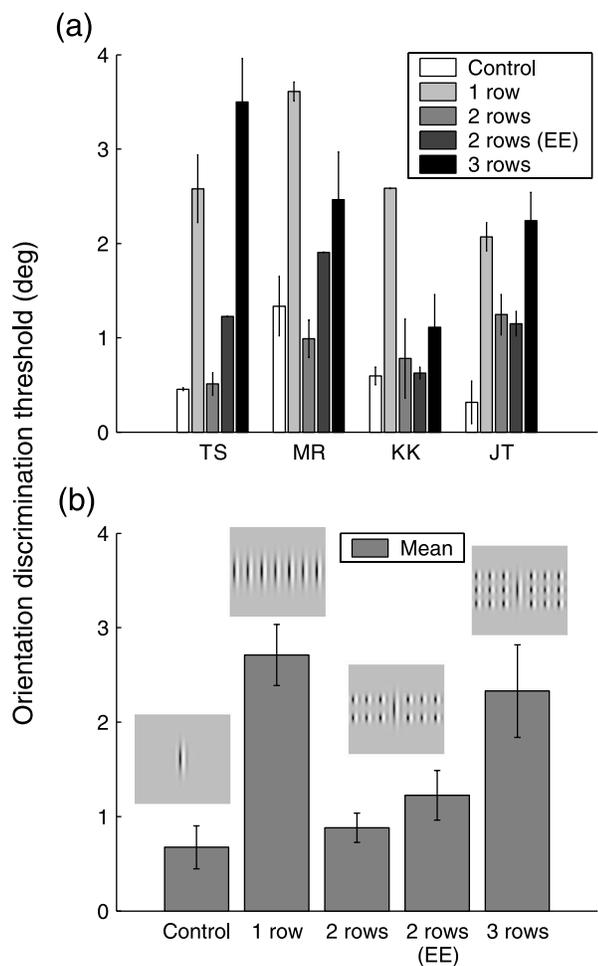


Figure 5. Orientation discrimination in the ROWS condition. The 75% discrimination thresholds are shown for the individual observers (a) and as average results (b). Conventions as in Figure 3.

‘groups’ with the flankers to form a coherent texture and is greatly reduced when the target ‘stands out’ from among the flankers. These effects cannot be attributed to changes in contrast energy or to uncertainty about the target location. The results therefore challenge the simplest explanations for crowding that are based on limited spatial resolution, be it due to (1) pooling, (2) feature integration, or (3) limitations in attentional resolution. Of special interest to us is spatial pooling, because our study was very similar to a study by Wilkinson et al. (1997), which presented pooling as an explanation for crowding.

The present results show that in contrast discrimination as well as in orientation discrimination, the greatest threshold elevation occurs when the flankers are equal in length to the target (Figures 2 and 4). When the flankers are made either shorter or longer, performance improves, approaching the control level. The fact that *shorter* flankers lead to improved performance could easily be explained with a simple pooling mechanism: the amount

of task-irrelevant stimulus energy that is pooled is reduced, and thus the signal-to-noise ratio is increased. However, following the same reasoning, *longer* flankers should lead to even worse (or at least not better) performance, because now the amount of task-irrelevant energy pooled is *increased*. This clearly is not the case: increasing the flanker length actually reduces thresholds almost to the control level (Figures 2 and 4). Also, the pattern of results does not significantly change when the contrast energy is equalized across flankers of different lengths. The peak threshold elevation is only slightly shifted towards shorter flankers in contrast discrimination (Figure 2d) and occurs with equal-length target and flankers in orientation discrimination (Figure 4d).

The crowding effect is also reduced when the flankers are constructed from pairs or triplets of smaller Gabors (the ROWS conditions, Figures 3 and 5). In spite of some individual differences when the flankers consist of triplets of Gabors (Figure 5), the general pattern of results implies that changing the flanker structure reduces the effect.

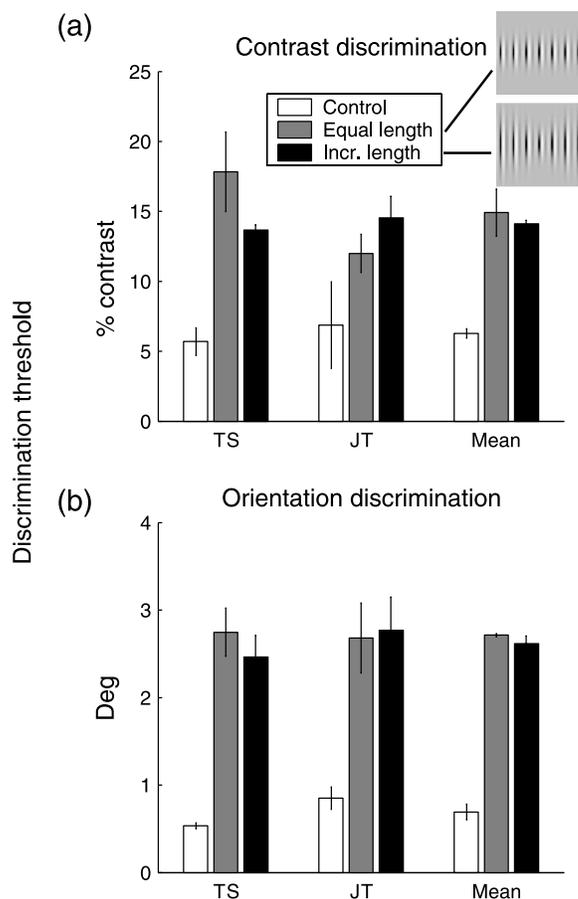


Figure 6. Experiment testing the role of positional uncertainty I. The position of the target was cued by the linear increase in flanker length from the middle towards the edges. The 75% discrimination thresholds are shown for contrast (a) and orientation (b) discrimination. The insets show cropped examples of the stimuli, see full versions in Figure 1. Error bars show $\pm SEM$.

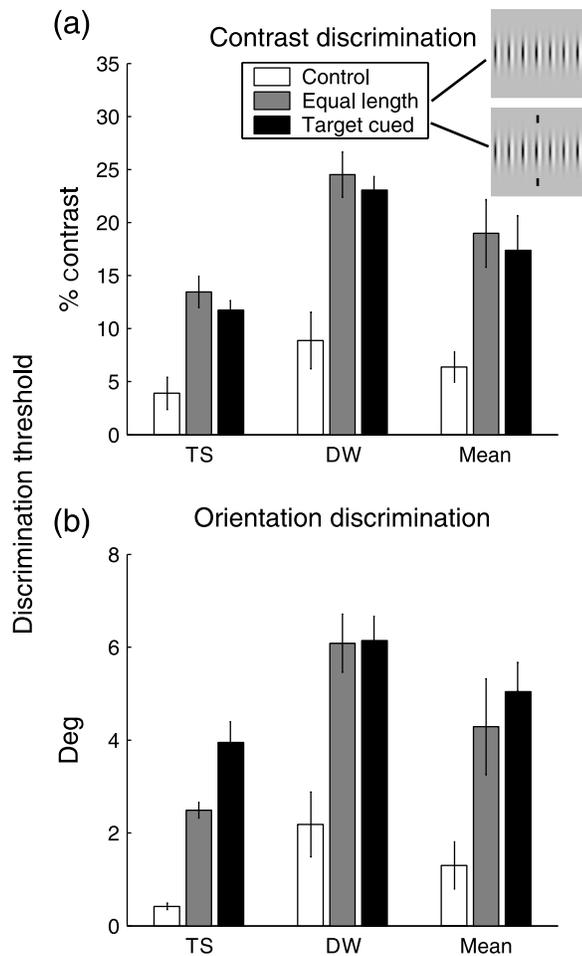


Figure 7. Experiment testing the role of positional uncertainty II. The position of the target was cued by two short vertical line segments presented immediately below and above the target. The 75% discrimination thresholds are shown for contrast (a) and orientation (b) discrimination. The insets show cropped examples of the stimuli, see full versions in Figure 1. Error bars show $\pm SEM$.

While size tuning (e.g., end-stopping) could play a role in the modulation of crowding when changing the flanker length, it cannot account for this result as the Gabor pairs and triplets occupied approximately the same area as the flankers that are equal in length to the target.

Changing the length of grating stimuli, as was done in our experiments, also changes their orientation content. Very small (in our case, short) stimuli are more broadband in their orientation content as compared to the larger (longer) stimuli. It could be argued, therefore, that the reduced effect with the long flankers was due to their narrower orientation bandwidth. However, this is not a likely explanation for our results. First, with the longest flankers, we observed practically no crowding at all. It is difficult to conceive how a change in orientation bandwidth could lead to a total lack of crowding among iso-oriented stimuli. Second, the shortest flankers we used, which were also the most broadband, did not induce crowding even in the equal contrast energy condition

where their contrast was scaled up. On the other hand, equating the contrast energy of Gabors of different lengths by changing their Michelson contrasts introduces a new potential segmentation cue between the target and the flankers. In principle, this could highlight the target and reduce crowding. However, it has been shown that contrast does not have such effect on crowding: crowding strength increases monotonically with flanker contrast (Chung, Levi, & Legge, 2001; Felisberti, Solomon, & Morgan, 2005). Finally, uncertainty about the target location cannot explain the observed modulation of crowding. The control experiments (Figures 6 and 7) show that performance does not improve when the target location is cued when there is no abrupt change between the target and the flankers in the stimulus array. We therefore argue that the LENGTH and ROWS manipulations do not reduce crowding by reducing positional uncertainty but by changing how well the target coheres with the flankers.

This proposition is supported by the target conspicuousness ratings. The strength of crowding varies inversely with the conspicuousness of the target (Figure 8):

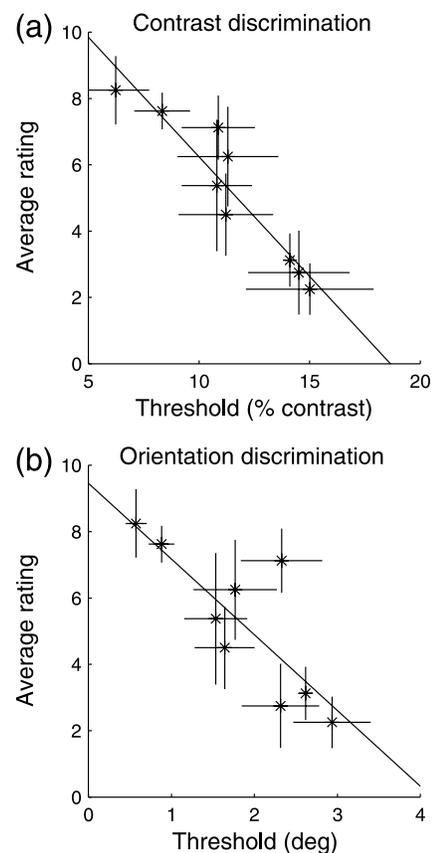


Figure 8. Target conspicuousness as a function of contrast (a) and orientation (b) discrimination thresholds. Target conspicuousness was rated on a scale from 0 (target groups with the flankers) to 10 (target is very conspicuous and stands out from among the flankers). The lines show the best linear fits to the data. Error bars show $\pm SEM$.

discrimination of target attributes (contrast or orientation) is easy when the target is perceptually very conspicuous and difficult when the target is perceptually coherent with the flankers. Thus, summarizing the results from the LENGTH and ROWS conditions in light of the rating data, it is apparent that the effect of the flankers is reduced whenever they are made more dissimilar from the target so that the target ‘stands out’ from among the flankers. When the target is similar to the flankers, and they form a coherent texture, the target seems to ‘lose its identity’, making judgments about it more difficult.

The present results argue against simple pooling as the underlying cause of crowding. Pooling models could explain reduced crowding effects in experiments where the target and flankers are indeed very different from each other—disks differing in size (Engel, 1974), lines or Gabors of orthogonal orientation (Andriessen & Bouma, 1976; Wilkinson et al., 1997), and letters flanked by different shapes (Estes, 1972; Nazir, 1992) or by letters of different colors or of opposite contrast polarity (Kooi, Toet, Tripathy, & Levi, 1994)—because dissimilar stimuli are likely processed by largely separate neuronal populations, the outputs of which are not necessarily pooled by the same mechanisms. However, our results indicate that the strength of crowding can be modulated by the spatial layout of the stimulus even when orientation, spatial phase, and spatial frequency are kept constant. On the other hand, it has been suggested that increasing target salience (or conspicuousness) does not always reduce crowding (Felisberti et al., 2005): crowding can occur with an intermediate (e.g., 45 deg) orientation difference between a target and 2 distractors (Solomon, Felisberti, & Morgan, 2004) although comparable orientation differences cause the target to ‘pop out’ from among 4 or 15 distractors (Felisberti et al., 2005). It would be interesting to test the effect of these intermediate orientation differences on crowding in larger stimulus arrays where possibly stronger segregation could occur.

Some recent reports have questioned pooling as well, suggesting explanations based on attentional resolution (Petrov & Popple, 2007) and orientation-dependent lateral interactions (Solomon et al., 2004) instead. Previous studies have also shown that crowding is reduced when the flankers group together (Banks, Larson, & Prinzmetal, 1979; Banks & White, 1984; Livne & Sagi, 2007; Renninger & Verghese, 2007). In our experiments, the flankers themselves were always aligned and identical to each other; they were always grouped. The crucial aspect is whether the *target* is grouped with the flankers. When the target is similar to the flankers, and thus perceptually grouped with them, crowding is strong. When the target is distinct from the flankers, crowding is reduced.

Configuration and grouping can also affect the speed and accuracy in search tasks (Banks & Prinzmetal, 1976; Duncan & Humphreys, 1989), and in foveal vision, the impairing effect of surround elements is reduced when the central target is made more ‘perceptually distinct’ by a

difference in luminance or color (Sayim, Westheimer, & Herzog, 2008; Saylor & Olzak, 2006) or in length (Malania et al., 2007). Our results extend these findings to peripheral vision and crowding with tightly spaced stimuli.

Summary and conclusions

In terms of perceptual organization, the present results show that the strength of crowding is tightly linked to the conspicuousness of the target. The more clearly the target stands out from among the flankers, the weaker the crowding. Strong crowding occurs when the target is perceptually grouped with the flankers so that they form a coherent pattern together. In this sense, crowding can be seen as a form of texture perception (cf. Parkes et al., 2001; Wilkinson et al., 1997). On a neural level of description, we argue that simple spatial pooling cannot explain the changes in crowding we observed. In terms of the underlying mechanisms, it is possible that (1) a common mechanism is responsible for perceptual grouping and crowding or (2) perceptual grouping and crowding are produced by different mechanisms and the effects of grouping or segmentation can overcome or prevent crowding.

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Corresponding author: Toni P. Saarela.

Email: toni.saarela@epfl.ch.

Address: EPFL SV BMI LPSY, Station 19, CH-1015, Lausanne, Switzerland.

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