Illusory contour formation survives crowding

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Flanked objects are difficult to identify using peripheral vision due to visual crowding, which limits conscious access to target identity. Nonetheless, certain types of visual information have been shown to survive crowding. Such resilience to crowding provides valuable information about the underlying neural mechanism of crowding. Here we ask whether illusory contour formation survives crowding of the inducers. We manipulated the presence of illusory contours through the (mis)alignment of the four inducers of a Kanizsa square. In the inducer-aligned condition, the observers judged the perceived shape (thin vs. fat) of the illusory Kanizsa square, manipulated by small rotations of the inducers. In the inducer-misaligned condition, three of the four inducers (all except the upper-left) were rotated 90°. The observers judged the orientation of the upper-left inducer. Crowding of the inducers worsened observers' performance significantly only in the inducer-misaligned condition. Our findings suggest that information for illusory contour formation survives crowding of the inducers. Crowding happens at a stage where the low-level featural information is integrated for inducer orientation discrimination, but not at a stage where the same information is used for illusory contour formation.

Keywords: crowding, illusory contour, peripheral vision, Kanizsa

Citation: Lau, J. S. F. & Cheung, S.-H. (2012). Illusory contour formation survives crowding. *Journal of Vision*, *12*(6):15, 1–12, http://www.journalofvision.org/content/12/6/15, doi: 10.1167/12.6.15.

Introduction

The human visual system is capable of robust and effortless object recognition in foveal vision. In contrast, an object in a cluttered environment becomes incredibly difficult to recognize using peripheral vision (Bouma, 1970). This is visual crowding. The current study examines the interaction between crowding and another visual phenomenon, Kanizsa's illusion.

Certain types of information about a crowded object can still be processed while the object remains unrecognizable. For instance, a crowded object can be detected, despite being unidentified (Levi & Carney, 2011; Levi, Hariharan, & Klein, 2002; Pelli, Palomares, & Majaj, 2004). Previous findings on whether crowding weakens early visual adaptation of orientation signals have been inconclusive (Bi, Cai, Zhou, & Fang, 2009; Blake, Tadin, Sobel, Raissian, & Chong, 2006; He, Cavanagh, & Intriligator, 1996; Ho & Cheung, 2011). Nevertheless, threshold elevation aftereffects from a crowded adaptor were consistently observed. Similarly, crowded motion adaptors were found to produce a significant motion aftereffect (Aghdaee, 2005; Blake et al., 2006).

Research on adaptation to a crowded signal had been extended to include the illusory contour as the adaptor (Montaser-Kouhsari & Rajimehr, 2005; Rajimehr, Montaser-Kouhsari, & Afraz, 2003). Rajimehr, Montaser-Kouhsari, and Afraz (2003) used abutting phase-shifted line gratings to induce the percept of an illusory contour. Adaptation to a horizontal or a vertical illusory contour reduced the performance of identifying a subsequently shown test pattern with an illusory contour of the same orientation to chance level. Rajimehr et al. (2003) found that such an adaptation effect persisted even when the illusory contour was crowded by similar patterns with an illusory contour.

Crowded visual information is available for processing not only in detection and adaptation, but also in high-level preference judgment. Kouider, Berthet, and Faivre (2011) found that participants were more likely to judge a foveally presented ambiguous object as pleasant after being adapted to a crowded happy face than a crowded angry face presented in peripheral vision. The emotional expressions of the crowded face images influenced their participants' preference judgment. In another study, Fischer and Whitney (2011) found that emotional (disgust) expression of a crowded face, which was surrounded by six other faces, affected the perceived average emotion of the whole group of seven faces. These findings suggest that the human visual system can access high-level visual information such as emotion, although crowding impairs the awareness of the stimulus identity.

doi: 10.1167/12.6.15 Received July 29, 2011; published June 12, 2012 ISSN 1534-7362 © 2012 ARVO

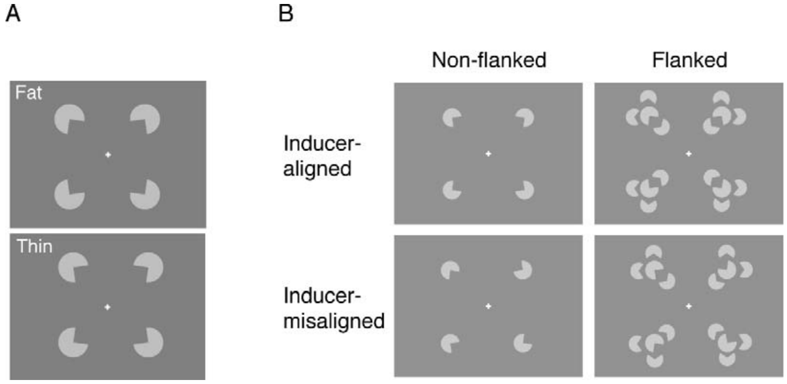

Figure 1. (a) Two Kanizsa squares are shown here. Four Pac-man inducers are oriented and positioned to imply the four corners of a square. Each inducer is rotated by a small angle to induce the percept of curved sides. In this illustration, the left and right sides (illusory contours) curve outward (top) or inward (bottom) to create a percept of a *fat* or *thin* square-like shape, respectively. (b) Typical stimulus configuration for the four conditions (inducer alignment × presence of flankers). Upper left: A typical Kanizsa square can be perceived when inducers are aligned. Upper right: A Kanizsa square-like shape with three flankers surrounding each of the four inducers. Lower left and lower right: Three of the inducers, except the upper-left corner of the Kanizsa shape, are rotated 90° clockwise so that no illusory contours can be formed. (Angle of rotation used in the figure is larger than that in the actual experiments for illustration purpose.)

Current theories of crowding often suggest that object-level information of the crowded target is lost, due to either an erroneous integration of featural information (Pelli et al., 2004) or an insufficient resolution of spatial attention (He et al., 1996). On the contrary, Fischer and Whitney (2011) argued that object-level (specifically face-level) information is preserved despite crowding, as shown in their study of perceived average emotion. Illusory shapes can be considered a special class of objects, which are perceived when inducers are appropriately positioned. Here we ask if object-level information of an illusory percept survives crowding of the illusion inducers. We use the Kanizsa square to address this question.

An illusory Kanizsa square is formed by four Pac-men, the inducers, that indicate its four corners (Figure 1a). The Pac-men induce an illusory percept of a square surface with perceived brightness different from the background. Can the illusory percept be formed even without conscious awareness of the inducers? Harris, Schwarzkopf, Song, Bahrami, and Rees (2011) asked their participants to differentiate between a left- vs. right-pointing Kanizsa triangle when the inducers were masked dichoptically by continuous flash suppression (CFS) (Tsuchiya & Koch, 2005; Shimaoka & Kaneko, 2011). Participants were at chance level when the inducers were rendered invisible using CFS. Crowding is another method often used to manipulate visual awareness (Blake et al., 2006; He et al., 1996). While both crowding and dichoptic masking have been used to manipulate visual awareness (Blake et al., 2006), the two can have separately measurable effects on object perception (Ho & Cheung, 2011). We used a perceived shape discrimination task to test whether a Kanizsa illusion could still arise despite crowding of the inducers.

In our shape discrimination task, we asked our observers to judge whether the perceived Kanizsa square was a *thin* or a *fat* one. The thin vs. fat distinction was created by small rotations of the inducers, such that the two vertical sides of the illusory square would be perceived as curving inward (thin square) or outward (fat square) (Figure 1a). We measured the minimum luminance contrast of the inducers for the observers to perform the illusory shape discrimination task, with or without other Pac-men as flankers. Such effects of crowding the inducers on illusory shape discrimination were compared with conditions where illusory contours could not be formed. Presence of illusory contours was manipulated by rotating three of the four inducers 90° clockwise. The inducer-aligned and inducer-misaligned conditions are illustrated in Figure 1b. In the absence of an illusory shape percept, we asked our observers to indicate whether the upper-left inducer rotated clockwise or counter-clockwise in the inducer-misaligned conditions. Crowding strength was compared between the inducer-aligned and inducer-misaligned conditions.

As mentioned above, Montaser-Kouhsari studied crowding effect on illusory contours induced by abutting phase-shifted line gratings (Montaser-Kouhsari & Rajimehr, 2005; Rajimehr et al., 2003). Our current study differed from the previous studies in two important aspects. First, we studied crowding of the inducers instead of crowding of the illusory contour. Along with other studies of adaptation to a crowded signal, Rajimehr et al. (2003) studied whether a crowded, and thus *unidentifiable*, illusory contour could result in an adaptation effect. Here we asked if an *identifiable* illusory contour could be perceived, despite the crowding of the inducers. Second, we used a discrimination task rather than an adaptation paradigm. As shown in previous studies, adaptation to a signal and conscious identification of it could happen in different cortical loci along the visual processing stream. Would crowding of the inducers happen after the illusory contour was available for adaptation or even after conscious perception of it? To anticipate our findings, the Kanizsa illusory shape could still be perceived despite crowding of the inducers.

General methods

Observers

Seven adults[1] (aged 19 to 31 years) with normal or corrected-to-normal vision performed these experiments binocularly. Two observers were the authors. Two were other members of the same laboratory unaware of the details of the experiments. The others were naïve observers. We allowed adequate practice for the observers to familiarize themselves with the psychophysical tasks. Informed consent was obtained from each observer before data collection.

Stimuli

Stimuli were Kanizsa illusory contour inducers, the Pac-men. The angle of the missing sector in each inducer was 90°. The size of the inducers ranged from 0.9° to 2.5° across experiments. Four inducers were presented at equidistance from the fixation cross, which was 0.25° in size. In the flanked conditions, each inducer was flanked by two to three other Pac-men. Two flankers were on the outer side and one on the inner side of the target (see Figure 1b). The center of the inner flanker was near the radial line between the target center and the fixation cross. The outer two were on the two sides of that radial line. The flankers faced towards the target with the missing sector such that the flankers could get close enough to produce measurable crowding effects without overlapping.

Stimuli were programmed and generated on an Apple Mac Pro computer using MATLAB with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). Stimuli were presented on a 17-inch, gamma-corrected Dell Monitor (1024 × 768 at 85 Hz). Background luminance was 39.4 cd/m^2. Viewing distance varied from 53 to 150 cm across different experiments.

Tasks

Illusory shape discrimination task

In the *inducer-aligned* conditions, the four inducers were aligned such that a Kanizsa illusory rectangle could be perceived. The observer's task was to discriminate whether the perceived illusory rectangle was *fat* or *thin*. The perceived shape was manipulated by a small rotation (5°) of the inducers. For instance, with a clockwise rotation of 5° for the upper-left and lower-right inducers, and a counter-clockwise rotation of 5° for the lower-left and upper-right inducers, the two vertical sides of the illusory rectangle would be perceived as curving outward (top of Figure 1a), leading to an illusory percept of a fat rectangle. Similarly, an illusory percept of a thin rectangle could be induced by the same amount of inducer rotation in the opposite direction (bottom of Figure 1a). Observers were asked to report whether they perceived a fat or a thin illusory rectangle in a two-alternative-forced-choice (2AFC) paradigm.

Inducer orientation discrimination task

In the *inducer-misaligned* conditions, three inducers (all except the upper-left inducer) were rotated 90° clockwise. Therefore, no Kanizsa illusory shape could be perceived. Each inducer was then rotated by a small angle (5°) as in the inducer-aligned conditions. Observers were asked to report whether the upper-left inducer was rotated clockwise or counter-clockwise in a 2AFC paradigm.

Contrast threshold measurement and threshold elevation

The minimum luminance contrast of the inducers required for performing either the illusory shape discrimination task or the inducer orientation discrimination task at a certain criterion (see below for the specific criterion levels used in different experiments) was estimated by the method of constant stimuli in Experiments 1A and 1B, and by QUEST (Watson & Pelli, 1983) in Experiments 2, 3, and 4. Threshold elevation, as the ratio of the contrast threshold in the flanked condition to that in the non-flanked condition, was calculated to estimate crowding strength. Crowding would be indicated by a >0 log threshold elevation (i.e., >1 threshold elevation).

Experiments 1A and 1B: effect of inducer alignment

Harris et al. (2011) showed that visual awareness of the Pac-man inducers, manipulated by continuous flash

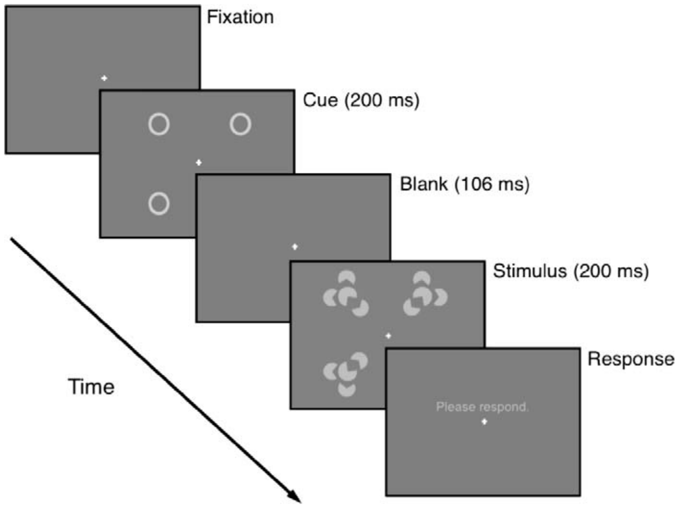

Figure 2. Presentation sequence of a typical trial in Experiment 1A. After observers indicate that they have fixated at the center of the screen by pressing a key, four circular position cues are displayed for 200 ms. The stimulus screen is shown for 200 ms after a fixation-only screen for 106 ms.

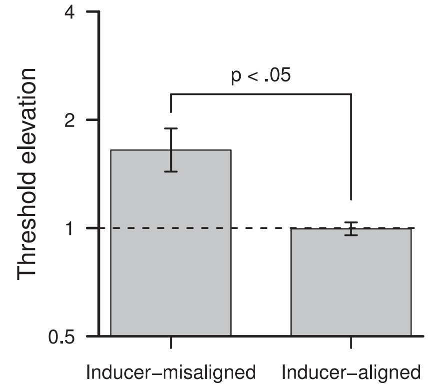

Figure 3. Results from Experiment 1A. Mean threshold elevation across all participants is plotted for the inducer-misaligned and the inducer-aligned conditions in log scale. The horizontal dash line indicates the level when threshold elevation equals one, which means that the presence of flankers does not affect performance. Error bars show ±1 *SEM*. The threshold elevation in the inducer-misaligned condition is larger than that in the inducer-aligned condition in Experiment 1A.

suppression, was needed for the Kanizsa illusory shape to be perceived. Here we asked if the Kanizsa illusory shape could still be perceived even when the inducer identity (orientation) was crowded out of visual awareness.

Experiment 1A

Observers

Five observers participated.

Stimuli and procedures

Inducers were 0.9° in diameter, presented at 2.5° away from the fixation. Three flankers were presented around each inducer in the flanked condition (see Figure 1b). Flankers were 0.8° in diameter. The center-to-center distance between the flankers and each inducer was 0.78°. Weber contrast of the flankers was set to be the same as the inducers. To preclude the flankers from being used as references for discriminating the inducer rotation, each flanker jittered by a random amount according to a multivariate normal distribution (variance of horizontal and vertical jittering = 0.0025°; covariance = 0°). The maximum amount of jittering was set at 1.5 times the standard deviation. The whole set of stimuli also jittered by a random amount according to a multivariate normal distribution with a variance of 0.01° for both directions and a covariance of 0°. This whole-set jittering was constrained to be no larger than 2 times the standard deviation of the multivariate normal distribution. The stimuli were rendered on a computer display at 150 cm viewing distance.

Figure 2 illustrates the presentation sequence of a typical trial in Experiment 1A. Observers fixated on the fixation cross and triggered the trial with a key press on the computer keyboard. Four circular position cues (0.9° in diameter) were shown briefly (200 ms) to indicate the locations of the inducers. After a blank screen of 106 ms, the stimulus screen was displayed for 200 ms. Weber contrast of the position cues was set at 0.5.

Inducer-aligned and inducer-misaligned trials were run in separate blocks. Each block consisted of 300 trials at five target contrast levels. The method of constant stimuli was used to estimate the contrast threshold for 82.5% correct criterion. Each contrast threshold was estimated from four to six blocks of trials.

Results

Figure 3a shows the results from Experiment 1A. The average log threshold elevations in the inducer-misaligned and the inducer-aligned conditions were 0.22 ± 0.06 and –0.00 ± 0.02 (mean ± *SEM*) respectively. A paired t-test indicated that the log threshold elevation in the inducer-misaligned condition was significantly larger than that in the inducer-aligned condition [$t(4) = 2.87$, $p < 0.05$]. One-sample t-test indicated that the log threshold elevation in the

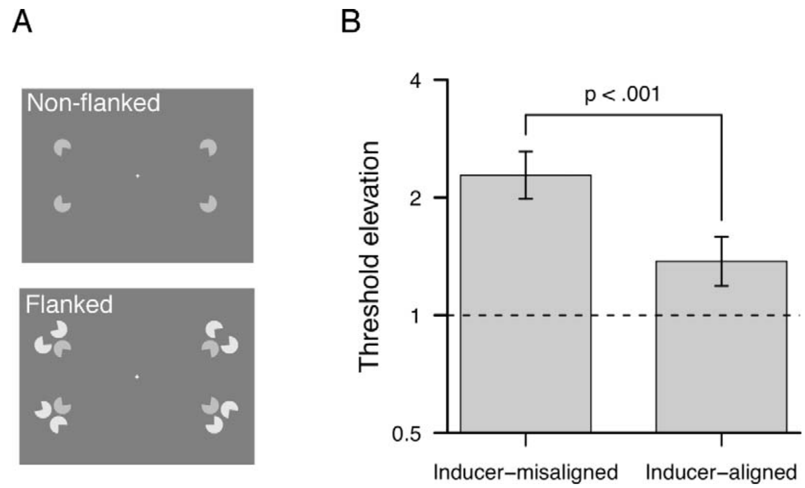

Figure 4. (a) Stimulus configuration of the inducer-aligned condition in Experiment 1B. Top: An illusory rectangle can be perceived when inducers are aligned. Bottom: A Kanizsa rectangle shape with two outer flankers next to each of the four inducers. For the inducer-misaligned condition (not shown here), three of the inducers, all except the upper-left corner of the Kanizsa shape, are rotated 90° clockwise such that no illusory contours can be formed. (b) Results from Experiment 1B. Mean threshold elevation across all participants is plotted for the inducer-misaligned and the inducer-aligned conditions in log scale. The horizontal dash line indicates the level when threshold elevation equals to one, which means that the presence of flankers does not affect performance. Error bars show ±1 *SEM*. The threshold elevation in the inducer-misaligned condition is larger than that in the inducer-aligned condition in Experiment 1B.

inducer-misaligned condition was significantly different from zero [$t(4) = 3.61$, $p < 0.05$], while that in the inducer-aligned condition was not [$t(4) = -0.12$, $p = 0.91$].

Experiment 1B

In Experiment 1A, we found that performance in the illusory shape discrimination task was more resilient to crowding of the inducers than performance in the inducer orientation discrimination task. Some might argue that the results in Experiment 1A were due to the specific spatial arrangement of the flankers. For example, the inner flankers could form an illusory shape with the four inducers in the inducer-aligned condition. Such "local" illusory shapes could make the flanked condition relatively easier for the inducer-aligned condition than for the inducer-misaligned condition. Others could also argue that crowding would be relatively weak at 2.5° eccentricity. Therefore, in Experiment 1B, we tried to replicate our initial findings with the removal of the inner flanker. Furthermore, we presented the target at 4° eccentricity, where crowding should be stronger.

Observers

Five observers participated.

Stimuli and procedures

Inducers were 1.2° in diameter, presented at 4° away from fixation. The aspect ratio of the illusory rectangle was 1.8 (see Figure 4a). The center-to-center distance between the flankers (1.2° in diameter) and each inducer was 1.9°. Figure 4a illustrates the configuration of the new stimuli. Contrast of the flankers was fixed at 0.5. Flankers were rotated by an amount randomly drawn from a uniform distribution of values ranging from −15° to +15°. No positional jittering was used. Stimuli were rendered on a computer display at 114 cm viewing distance. The circular cues were removed and the exposure duration of the stimulus screen was reduced to 150 ms. The method of constant stimuli, with five to seven contrast levels, was used to estimate each contrast threshold.

Results

Figure 4b shows the results from Experiment 1B. The average log threshold elevations in the inducer-misaligned and the inducer-aligned conditions were 0.36 ± 0.06 and 0.14 ± 0.06 (mean ± *SEM*) respectively. A paired *t*-test indicated that the log threshold elevation in the inducer-misaligned condition was significantly larger than that in the inducer-aligned condition [$t(4) = 10.47$, $p < 0.001$]. One-sample *t*-test indicated that the log threshold elevation in the inducer-misaligned condition was significantly different from zero [$t(4) = 5.91$, $p < 0.01$], while that in the

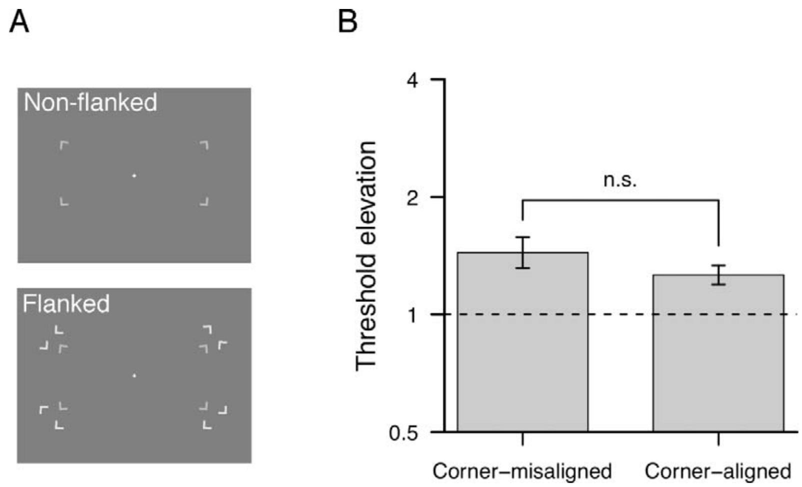

Figure 5. (a) Stimulus configuration of the corner-aligned condition in Experiment 2. Top: Pac-man inducers are replaced by four rectangle corners. Bottom: Rectangle corners with two outer flankers next to each of the four corners. For the corner-misaligned condition (not shown here), three of the inducers, all except the upper-left corner, are rotated 90° clockwise. (b) Results from Experiment 2. Mean threshold elevation across all participants is plotted for the corner-misaligned and the corner-aligned conditions in log scale. The horizontal dash line indicates the level when threshold elevation equals one, which means that the presence of flankers does not affect performance. Error bars show ±1 *SEM*. No significant difference in threshold elevation is found between the two conditions.

inducer-aligned condition was not [$t(4) = 2.19$, $p = 0.09$].

Discussion of Experiments 1A and 1B

In Experiments 1A and 1B, we found that crowding of the inducers had little or no effect on performance in the illusory shape discrimination task (inducer-aligned condition). One might interpret that the inducer-aligned condition could have invoked a multifeature global shape mechanism in the absence of illusory contour formation. The mere presence of the Pac-men at their respective locations could be linked to form a multifeature object representation, which had been shown to be resilient to crowding (Fischer & Whitney, 2011). In Experiment 2, we further tested whether the formation of an illusory contour was a necessary condition for such resilience to crowding to occur.

Experiment 2: was it due to the representation of a global shape with multiple features?

Was the formation of illusory contours a necessary condition for the observed resilience to crowding of the inducers? Our observers could have perceived the stimulus in the inducer-aligned condition as a multi-feature object. Integration of information from the four features (the four inducers) could have happened without the percept of an illusory surface and made the task easier. To test such an explanation, we ran Experiment 1B again with corners of a rectangle as the stimuli instead of the Pac-men (Figure 5a). Presumably, the percept of illusory contours would be absent or very weak with the rectangle corners. Nonetheless, the observer could still adopt a strategy that made use of multiple features in the corner-aligned condition. If the use of multiple features was sufficient to remedy the effects of crowding on each feature even in the absence of illusory shape percept, crowding of the individual features should not influence shape discrimination performance in the corner-aligned condition. On the other hand, if illusory shape percept was a necessary condition, significant crowding should still take place in the corner-aligned condition.

Observers

Five observers participated.

Stimuli and procedures

Stimulus settings were identical to those in Experiment 1B except that the Pac-man inducers were replaced by rectangle corners (Figure 5a). Each side of the corner was 0.6° long, resembling the 90° edge of the Pac-man inducers (i.e., the Pac-man mouth) used in Experiment 1B.

Corner-aligned and corner-misaligned trials were run in separate blocks. In each block, two interleaved

QUEST staircases (criterion = 0.825, $\beta = 3.5$; Watson & Pelli, 1983) were run to estimate the contrast thresholds in the non-flanked and flanked conditions. Each staircase consisted of 30 trials. Each final contrast threshold estimate was based on two to four QUEST runs.

Results

Figure 5b shows the results from Experiment 2. The average log threshold elevations in the corner-misaligned and the corner-aligned conditions were 0.16 ± 0.04 and 0.10 ± 0.02 (mean ± *SEM*) respectively. A paired *t*-test indicated that the log threshold elevation in the corner-misaligned condition was not significantly different from that in the corner-aligned condition [$t(4) = 1.48$, $p = 0.21$]. One-sample *t*-test indicated that the log threshold elevation in both the corner-misaligned [$t(4) = 3.96$, $p < 0.05$] and the corner-aligned [$t(4) = 4.13$, $p < 0.05$] conditions were significantly greater than zero. In other words, crowding was observed in both conditions.

Discussion of Experiment 2

Crowding of the individual features made it more difficult to discriminate the shape of the multi-feature object when the illusory contour percept was absent. Results from the three experiments reported so far indicate that the illusory contour percept is indeed necessary for resilience to crowding of the individual inducers.

One might question whether the detrimental effects of the flankers in the stimulus (inducer or corner)-misaligned condition were indeed due to crowding. Flankers could make a peripheral task more difficult through mechanisms other than crowding. In the next two experiments, we tested whether the observed effects of flankers in the inducer orientation discrimination task would exhibit some known properties of crowding (Whitney & Levi, 2011).

Experiment 3: discrimination vs. detection

Could the observed effects of the flankers in previous experiments be due to lateral masking? One characteristic distinction between lateral masking and crowding is that masking makes a signal harder to be detected while crowding does not (Pelli et al., 2004). In Experiment 3, we compared observers' performance in our inducer orientation discrimination task to that in an inducer detection task. Strong effects of flankers on the detection task would be observed if lateral masking, but not crowding, was at work.

Observers

Four observers participated.

Stimuli and procedures

Stimulus settings were similar to those in the inducer-misaligned condition of Experiment 1A. Different from Experiment 1A, flanker contrast was fixed at 0.5 (same as Experiment 1B) for both the detection and the discrimination tasks.

Inducer detection task

Observers performed a two-interval-forces-choice (2IFC) detection task. Each interval followed a mask-stimulus-mask presentation sequence. Both pre- and post-masks were static Gaussian noise fields ($\sigma = 0.1 \times$ background luminance). The mask and stimulus were displayed for 59 ms and 200 ms, respectively. The two intervals were separated by 506 ms. The observer's task was to report whether the inducers appeared during the first or the second interval.

Inducer orientation discrimination task

The stimulus sequence was similar to that in Experiment 1A, except that the circular position cues were not displayed. Instead, the same pre- and post-masks as in the detection task were used in the discrimination task to make the two tasks more comparable to each other.

Detection and discrimination trials were run in separate blocks. In each block, two interleaved QUEST staircases (criterion = 0.9, $\beta = 3.5$; Watson & Pelli, 1983) were run to estimate the contrast thresholds in the non-flanked and the flanked conditions. Each staircase consisted of 30 trials. Each observer completed three blocks for each task.

Results

Figure 6 shows the results from Experiment 3. The average log threshold elevations in the discrimination and the detection tasks were 0.26 ± 0.03 and –0.17 ± 0.05 (mean ± *SEM*), respectively. A paired *t*-test indicated that the log threshold elevation in the discrimination task was significantly larger than in the detection task [$t(3) = 5.86$, $p < 0.05$]. One-sample *t*-test

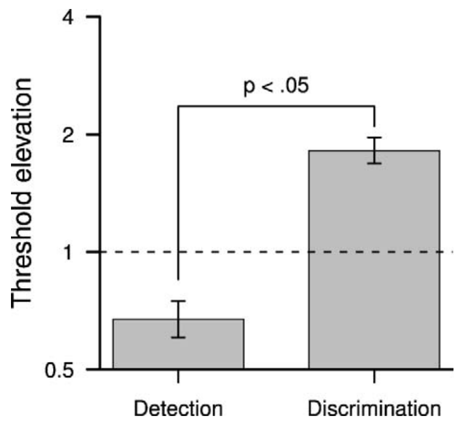

Figure 6. Results from Experiment 3. Mean threshold elevation across all participants is plotted for the detection and the discrimination tasks in log scale. The horizontal dash line indicates the level when threshold elevation equals one, which means that the presence of flankers does not affect performance. Error bars show ±1 *SEM*. Threshold elevation is significantly larger than one in the discrimination task but significantly smaller than one in the detection task. Flanking impairs the inducer discrimination performance but improves detection performance.

indicated that the log threshold elevation in the discrimination task was significantly larger than zero [$t(3) = 7.72$, $p < 0.01$], while that in the detection task was significantly *smaller* than zero [$t(3) = -3.76$, $p < 0.05$].

Discussion of Experiment 3

The presence of flankers impaired the observers' performance only in the discrimination task but not in the detection task. Results from Experiment 3 suggested that lateral masking was unlikely to be the mechanism behind the detrimental effects of the flankers observed in previous experiments.

Interestingly, the presence of flankers enhanced target detection, consistent with previous findings (Levi & Carney, 2011). It was suggested that such facilitation effects of flankers on target detection could be due to the excitatory effects of nearby neurons through lateral connections (Polat & Sagi, 1993). The flankers could also help detection through reducing the uncertainty of the spatial location of the target signal (Levi et al., 2002; Petrov, Verghese, & McKee, 2006).

Experiment 4: Bouma's rule

In his classic study on crowding, Bouma (1970) discovered that the critical target-flanker spacing at which flankers ceased to influence the target was proportional to the eccentricity of the target. Bouma further postulated that the critical spacing should equal about half eccentricity. We measured the critical spacing as a function of target eccentricity to test such prediction according to Bouma's rule.

Observers

Two observers participated.

Stimuli and procedures

Stimulus settings were similar to Experiment 3. In addition to the 2.5° eccentricity used in Experiments 1A and 3, eccentricities of 4.5° and 7° were also included. Eccentricities were manipulated by varying the viewing distance between the observer and the display. Viewing distance ranged from 150 cm (2.5° eccentricity) to 83 cm (4.5° eccentricity) to 53 cm (7° eccentricity). The physical size of the stimuli remained unchanged across the three eccentricity conditions. The diameter of each inducer subtended a visual angle of 0.9° at 2.5° eccentricity, 1.6° at 4.5° eccentricity, and 2.5° at 7° eccentricity. Unlike the inducer orientation discrimination task in Experiment 3, no pre- and post-masks were used. Observers triggered the trial with a key press and the stimulus screen was presented for 200 ms after a 200 ms delay.

Only the inducer-misaligned and flanked condition was included in this experiment. At each eccentricity, six target-flanker spacings, measured by center-to-center distances, were used. Trials at different eccentricities were run in separate blocks. In each block, three interleaved QUEST staircases (criterion = 0.825, $\beta = 3.5$; Watson & Pelli, 1983) were run to estimate the contrast thresholds for three different center-to-center distances. Each staircase consisted of 30 trials. Each final contrast threshold estimate was based on two to four QUEST runs.

Log contrast threshold as a function of target-flanker spacing at each eccentricity was fitted with the following two-line function:

$$f(x) = a + bx, \quad \text{if } x < c$$

$$f(x) = a + bc, \quad \text{if } x \geq c$$

where x was the target-flanker spacing, a was the y-intercept, b was the slope of the decreasing part of the function, and c was the critical spacing. The two-line function was fitted to the data by minimizing the squared weighted errors using the Nelder-Mead simplex algorithm. The squared residuals were weighted by the reciprocal of the estimated standard deviation of each of the log contrast threshold estimates.

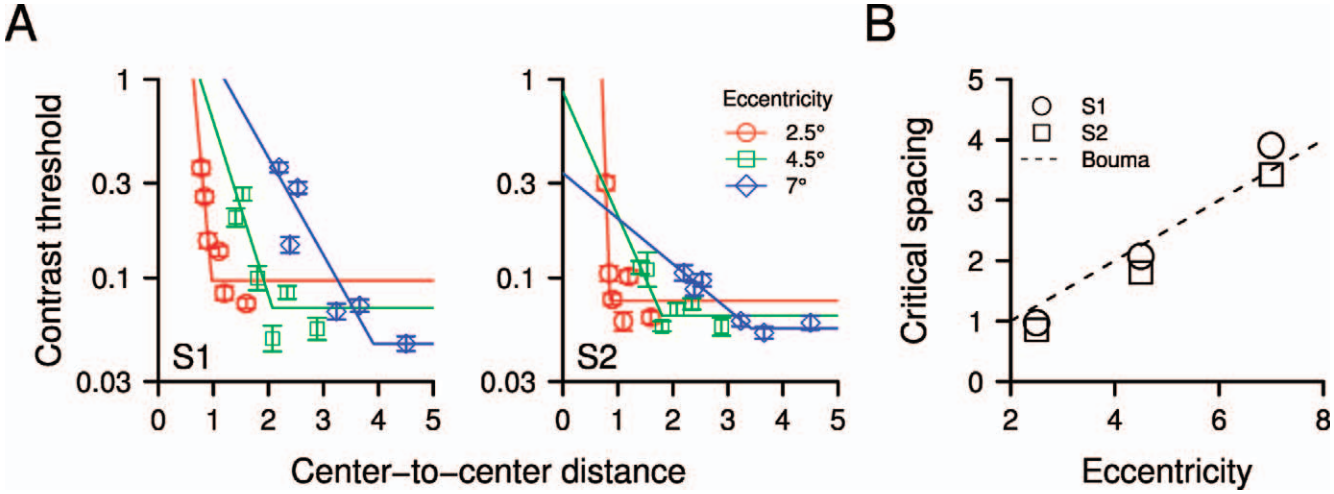

Figure 7. Results from Experiment 4. (a) Contrast threshold is plotted against the center-to-center distance between target and flankers for two observers in log scale. Contrast threshold was measured with target presented at 2.5° (red circle), 4.5° (green square), and 7.0° (blue diamond) eccentricities from the fixation. The turning point of the fitted function indicates the critical spacing in each set of data. (b) The estimated critical spacings from Figure 7a are replotted against eccentricity. Open circles and open squares indicate the critical spacings measured from observers S1 and S2 respectively. The dash line represents the relationship between critical spacing and eccentricity as suggested by Bouma's rule. The collected data is consistent with Bouma's rule.

Results

Figure 7 shows the results from Experiment 4. The estimated critical spacings at eccentricities 2.5°, 4.5°, and 7° were 0.97°, 2.07°, and 3.91° for observer S1 and 0.85°, 1.80°, and 3.43° for observer S2, respectively (Figure 7a). Figure 7b shows the critical spacing as a function of eccentricity for the two observers. The relationship as predicted according to Bouma's rule was also plotted as a dash line for comparison. Our data was very consistent with Bouma's observation (1970) that the critical spacing was about half target eccentricity.

Discussion of Experiment 4

Results from Experiment 4 were highly consistent with the predictions according to Bouma's rule. Experiments 3 and 4 have shown that the detrimental effects of the flankers observed in our inducer orientation discrimination task exhibit two diagnostic characteristics of crowding (Whitney & Levi, 2011): (a) The presence of flankers impairs performance only in a discrimination task but not in a detection task; (b) The ratio of critical spacing to target eccentricity is about 0.5.

General discussion

To summarize our findings across the five experiments reported here, we found that (A) crowding of the inducers led to significant threshold elevation only in inducer orientation discrimination, but not in illusory shape discrimination (Experiments 1A and 1B). (B) Such resilience to crowding of the inducers in illusory shape discrimination was due to the presence of illusory contours instead of mere global shape information (Experiment 2). (C) The crowding task we used exhibited two diagnostic properties of crowding (Experiments 3 and 4; Whitney & Levi, 2011).

One possible interpretation of the resilience to crowding of the inducers in illusory shape discrimination is that crowding operates at a relatively high level where conscious access to the inducer orientation information is blocked due to the presence of flankers. Meanwhile, the inducer orientation information remains accessible to the visual process that is responsible for illusory contour formation. In other words, the inducer orientation information is passed along two different paths, one for conscious report of the individual inducer orientation and the other for illusory contour formation. This is similar to the attention resolution account of crowding suggested by He, Cavanagh, and Intriligator (1996). He et al. argued that crowding was a result of the limited spatial resolution of visual attention. Crowded information of the target is available to the visual system, but the process of attention fails to select only the information (features) of the target. However, more recent studies have shown that the effects of flankers could have started quite early (Blake et al., 2006; Ho & Cheung, 2011). Whether crowding operates at a high level gating conscious access is still questionable.

A related interpretation is that the cortical locus of illusory contour formation comes before that of crowding. Illusory contours may have already formed before the inducer orientation information is crowded out. Single cell recording studies on monkeys showed that some V1 and V2 neurons were responsive to illusory contours (Grosof, Shapley, & Hawken, 1993; von der Heydt, Peterhans, & Baumgartner, 1984). Subsequently, multiple areas including V1 and V2 along the human visual pathway were shown to process or represent illusory contour information (ffytche & Zeki, 1996; Montaser-Kouhsari, Landy, Heeger, & Larsson, 2007; Seghier et al., 2000). More recently, Wu, He, Bushara, Zeng, Liu, and Zhang (2011) studied how different visual areas would respond to Kanizsa squares with small or large gaps among the inducers. They argued that the *local* illusory contour completion became more prominent when the gaps were large, while the *global* illusory shape representation became more prominent when the gaps were small. Consistent with their hypothesis, human V1 was more active in the large-gap condition than in the small-gap condition, with human LOC showing the opposite direction. However, Wu et al.'s (2011) findings did not address the temporal aspect of cortical responses to test whether the observed V1 responses to illusory contour were a result of feedback from other visual areas (Murray, Wylie, Higgins, Javitt, Schroeder, and Foxe, 2002; Shpaner, Murray, & Foxe, 2009; Stanley & Rubin, 2003). Lee and Nguyen (2001) observed the temporal properties of monkey V1 and V2 neuronal responses to illusory contours and found that V2 responded earlier to the illusory contours than V1. Combining data from electrophysiology and functional magnetic resonance imaging (fMRI), Murray et al. (2002) suggested that the cortical responses in V1 and V2 were due to feedback from the lateral occipital complex (LOC), where the response to illusory contours seemed to have started. If illusory contours were formed before crowding, that would place crowding at a cortical locus after LOC in the visual processing stream. Nonetheless, our stimuli were more similar to Wu et al.'s (2011) large-gap stimuli than the small-gap ones, V1 could also play an important role in our task.

Recent studies have suggested visual areas earlier than LOC as the cortical locus of crowding. Chakravarthi and Cavanagh (2009) used three kinds of masks to render the flankers invisible and studied the corresponding impact on crowding strength. They found significant recovery from crowding when the flankers were masked by noise and metacontrast, but not by object substitution. Considering that noise masking and object substitution happen in V1 and LOC, respectively, Chakravarthi and Cavanagh concluded that crowding should have happened between V1 and LOC. Other studies have suggested V2/V3 (Bi et al., 2009) and V4 (Liu, Jiang, Sun, & He, 2009) as the potential candidates for the cortical locus of crowding. In a recent study, Freeman, Donner, and Heeger (2011) found that flanked stimuli resulted in smaller cortical responses in V2, V3, and V4. More importantly, they argued that crowding disrupted the feature integration process in object identification and led to a lowered intrinsic covariation of neuronal activities between V1 and the visual word form area (VWFA). Their findings are consistent with the view that crowding may not happen at any particular cortical area. Instead, crowding makes it difficult for the whole network of visual areas to come up a stable interpretation of the flanked stimulus.

The discrepancy about whether crowding operates at a high level gating consciousness or whether crowding happens before or after LOC assumes that crowding happens in a single locus. Nonetheless, some have suggested that crowding can be a multi-stage phenomenon in which crowding happens at more than one stage along the visual processing stream (Whitney & Levi, 2011). The faulty feature integration account of crowding states that crowding is a result of erroneous integration of low-level features of nearby objects (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001; Pelli et al., 2004). It is possible that crowding happens at a stage where the low-level features are integrated to form the inducers in one cortical area. Meanwhile, the features are used directly to form illusory contour in another cortical area.

Conclusion

Whitney and Levi (2011) listed four categories of information that could survive crowding. The four categories were the detection of a feature, adaptation aftereffects, averaged/pooled signal from the target and the flankers, and partial identity information of the target. Here we show that information for illusory contour formation can be the fifth category. Crowding happens at the stage where the low-level featural information is integrated for inducer orientation discrimination, but not at the stage where the same information is used for illusory contour formation.

Acknowledgments

This research was supported by a grant from the Hong Kong Research Grants Council (HKU741808H) to SHC. We thank Cristy Ho and two anonymous reviewers for helpful comments on earlier drafts.

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Footnote

[1]Not all observers participated in every experiment.

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