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When crowding meets binocular rivalry: Challenges for object perception

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ABSTRACT

Both crowding and binocular rivalry impair object perception, but their influence on object perception has so far only been investigated in separate fields. Three experiments investigated the joint influences of crowding and rivalry on object perception (orientation discrimination). Experiment 1 investigated how crowding and rivalry influence orientation discrimination together. Experiment 2 tested whether rivalry between flankers affects crowding using an orientation discrimination task. Experiment 3 tested whether crowding affects the temporal dynamics of the rivalry between a target and a rival stimulus. In Experiment 1, judgments of target orientation were more impaired when crowding and rivalry were simultaneously induced than when they were separately induced and their effects were combined. In Experiment 2, judgments of target orientation were impaired even when flankers were undergoing rivalry, thus highlighting the importance of the presence of flankers. Experiment 3 showed that flankers presented in the neighborhood of a target undergoing rivalry shortened target dominance and prolonged target suppression. The augmented impairments of object perception found in Experiments 1 and 3 suggest that crowding and rivalry interact, presumably through signal suppression. The adverse effect of flankers shown in Experiment 2 suggests that inappropriate feature integration may have additionally contributed to this interaction.

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1. Introduction

In real life, we see objects cluttered among each other and as appearing more often in the peripheral than in the foveal region. Moreover, objects can often be out of focus: many objects are displaced in depth from the fixation point and thus become blurred when we accommodate to focus on them. These challenges make it difficult to identify objects (Arnold, Grove, & Wallis, 2007; Pelli & Tillman, 2008). Simultaneously, we have a biological limit such that the retinal area with the highest resolution is only about 1.5° (Loschky et al., 2005), and thus the images of most objects are projected onto the retinal area with a relatively low resolution. These problems confront us whenever we attempt to perceive a target object. These obstacles to human vision have been separately studied by utilizing interesting phenomena such as crowding (Levi, 2008; Whitney & Levi, 2011) and binocular rivalry (Blake, 1989; Blake & Logothetis, 2002).

To investigate object perception in the periphery with neighboring objects, previous studies relied on crowding. Crowding is a type of impairment in object identification, which occurs when

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a target object is presented in the periphery and is flanked by distractors (for review, see Levi, 2008 and Whitney & Levi, 2011). Crowding does not appear to take place due to the poor acuity in the periphery (e.g., He, Cavanagh, & Intriligator, 1996). In fact, the distance of a target from a flanker is more important than the eccentricity of the target location. Studies have revealed that the critical target-flanker distance requires the target to be half (0.5e), or less than half (~0.5e), the distance between the fixation point and the target object (Bouma, 1970; Pelli & Tillman, 2008). Crowding occurs, because the flankers decrease the target signal (Bi et al., 2009; Blake et al., 2006) or as a result of inappropriate feature integration (Chakravarthi & Cavanagh, 2009; Chung, Levi, & Legge, 2001; Freeman, Donner, & Heeger, 2011; Greenwood, Bex, & Dakin, 2009, 2012; Levi, Hariharan, & Klein, 2002; Pelli, Palomares, & Majaj, 2004). Based on the two-stage model (feature detection and integration) of object recognition (Parkes et al., 2001; Treisman & Gelade, 1980), crowding occurs because the detected features of a target object are inappropriately jumbled with those of neighboring objects. Thus, the information about the target is not lost but is rather averaged together with the information from the neighboring objects (Parkes et al., 2001).

The functional role of rivalry suppression has been suggested to deal with out-of-focus images and double images (Arnold, Grove, & Wallis, 2007; Norman, Norman, & Bilotta, 2000). Also, binocular

rivalry has been used to study how the visual system resolves an ambiguous situation of object perception (Blake & Logothetis, 2002). Binocular rivalry refers to the phenomenon in which perception alternates between two different images presented separately to an identical location of each eye (Levelt, 1965). The temporal dynamics of this alternation can depend on stimulus strength, which has often been manipulated by the contrast of stimuli (Levelt, 1965; Mueller & Blake, 1989).

Although investigations of these two phenomena have helped elucidate the characteristics of object perception in the past, such work was primarily conducted using each method and rarely sought to maximize the benefits that each one can provide. This is partly due to the regional focus of these investigations: crowding and rivalry have been investigated mainly in the periphery (Bouma, 1970; Levi, 2008; Pelli & Tillman, 2008) and the fovea (Blake, 2001), respectively. Unlike this separate investigation, the present study has combined the two methods and investigated the interaction between the two, thus enabling us to investigate object perception in more challenging situations. Specifically, we investigated how object perception is influenced by signal suppression (crowding and rivalry) and inappropriate feature integration (crowding).

Recently, Vickery et al. (2009) induced crowding and masking separately and simultaneously in order to investigate the extent to which observers correctly judged the orientation of a target. They found not only the typical masking and crowding effects but also an augmented effect, referred to as supercrowding effect, in which orientation judgments were much more adversely affected when the target was presented with a mask and flankers than when only the flankers were used. Moreover, this effect was observed even at the farthest target-flanker distance of $0.7e$, which exceeds the critical distance of $0.5e$ (Bouma, 1970; Pelli & Tillman, 2008). These results suggest that the mask added to the target area disproportionately increases the interfering effects of flankers on target identification compared to the effects of flankers or masks alone. Chakravarthi and Cavanagh (2009) also introduced both crowding and masking to investigate the locus of feature integration (i.e., the locus of recovery for a crowded target). They masked flankers with noise, metacontrast, and object substitution masks, presumably operating on different stages of visual processing. They found that, unlike noise and metacontrast masking, object substitution masking did not reduce the detrimental effect of crowding on orientation judgments, suggesting that feature integration occurs prior to the stage at which object substitution masking becomes effective.

As demonstrated in these studies, combining psychophysical methods (such as crowding and masking) allows us to observe the same phenomenon (e.g., object perception) under various conditions where our ability to perceive the target changes. When changes in object perception induced by one method meet those induced by the other, it becomes more likely to capture the complex phenomena that take place due to the interaction between the two. Thus, we expected that combining crowding and rivalry would allow us to observe their interaction and to probe the processing priorities in the visual processing stream.

Earlier, we discussed the mechanisms through which crowding and rivalry take place: signal reduction of the target and inappropriate feature integration for crowding, and suppressive interaction between stimuli for rivalry. These mechanisms can be understood through the ways in which object perception is challenged. First, perceiving objects can be difficult when the strength of an object is relatively weak (e.g., objects with low contrasts). Second, it can be difficult when external noise interferes with to-be-perceived objects. Presumably, both of these mechanisms give rise to crowding, and the first mechanism plays a major role in binocular rivalry (e.g., Levelt, 1965; Mueller & Blake, 1989). If both

crowding and binocular rivalry contribute jointly to impairing observers' object discrimination and to producing the type of severe impairments found in Vickery et al. (2009), this would indicate that these mechanisms jointly contribute to object discrimination performance and produce something more than the sum of the two (i.e., overadditivity). Further, if reducing the impact of one mechanism changes that of the other, this would suggest that both mechanisms interact with each other. Otherwise, they may operate independently and perhaps at different levels of processing (cf., Chakravarthi & Cavanagh, 2009).

Three experiments were conducted using sine-wave gratings as stimuli while the orientation of the target, rival-stimulus, and flankers varied. The first experiment investigated how a joint induction of crowding and binocular rivalry affects target orientation discrimination thresholds. The second experiment investigated if crowding still occurs with flankers undergoing rivalry. Experiment 3 investigated how the joint induction of crowding and binocular rivalry influences the temporal dynamics of target perception.

2. Experiment 1

Experiment 1 investigated the degree to which target perception is impaired by both crowding and binocular rivalry. We used an orientation discrimination task in which sine-wave gratings appeared as targets. During this task, target discrimination was impaired by the presentation of flankers, a rival stimulus, or both. If the orientation discrimination threshold of the target is increased more by the simultaneous presentation of flankers and a rival stimulus than by the sum of their separate presentation, this will indicate that the interaction between crowding and rivalry occurred.

2.1. Method

2.1.1. Observers

Four observers, including the first author, participated in this experiment. All had normal or corrected-to-normal visual acuity and were naïve to the purpose of the experiment, except for the first author. All aspects of the study were carried out in accordance with the regulations of Yonsei University. Written informed consent was obtained from each observer (except for the author) prior to participation.

2.1.2. Apparatus and stimuli

Stimuli were presented on two linearized 21-in. Samsung TW22WS LCD monitors at a resolution of 1680×1050 pixels using a refresh rate of 60 Hz. Stimuli for the left and right eyes were dichoptically presented on the two monitors using a conventional mirror stereoscope. A forehead-and-chin rest stabilized the observers' head movements. The viewing distance was 75 cm, making the size of a pixel 0.021° . Stimuli were generated using MATLAB and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). They were sine-wave gratings with a diameter of 1.24° and a spatial frequency of 3.23 cycles/deg. The mean luminance of these gratings and the background was 51 cd/m^2 .

There were three types of stimuli – target, flankers, and rival stimulus – and all were sine-wave gratings. The orientation of the target (Fig. 1A) was varied around the vertical orientation (0°) and was always presented to the observers' dominant eye 5 degrees away from the fovea (right visual field). The orientations of these gratings were varied in fixed steps (e.g., a 2° step: $-4, -2, 0, 2, 4$). During our preliminary experiment, the sizes of these steps were individually determined depending on the observer's ability for orientation discrimination. As a result, the maximum

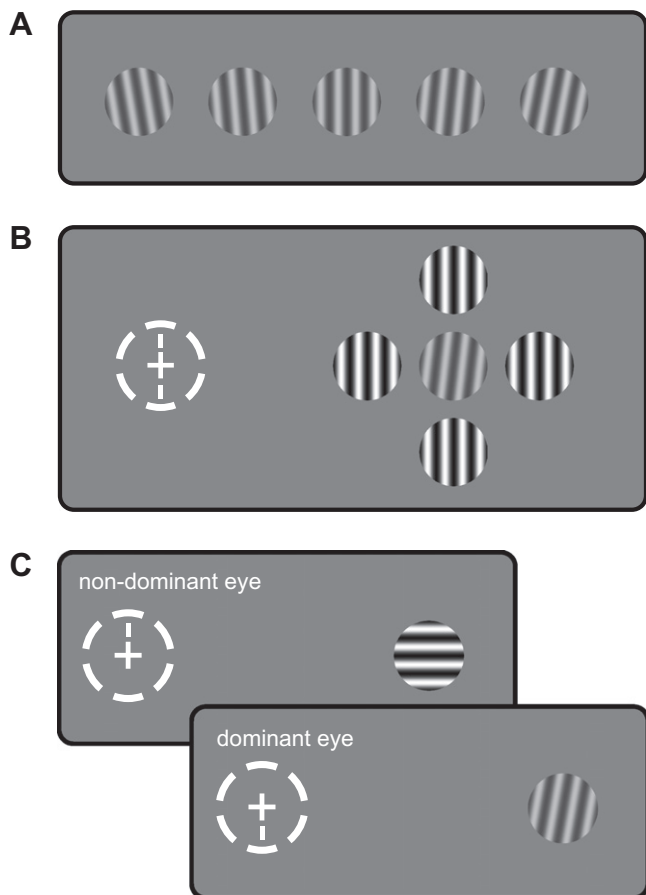


Fig. 1. (A) Five vertically oriented gratings were used for the targets. Observers were asked to discriminate the orientation of the target. (B) The flankers were placed at four locations 1.49° away from the center of the target and had a higher contrast than the target. (C) The target grating was presented to the dominant eye and the rival grating was presented to the corresponding location of the opposite eye.

increment was $\pm 7^\circ$ per step and the minimum increment was $\pm 1^\circ$ per step among the observers. The target had a 50% Michelson contrast. Unlike the target gratings, the flankers and rival gratings had a 99.78% Michelson contrast. As shown in Fig. 1B, the flankers were placed at four different locations—above, below, left, and right relative to the target position. The centers of these flankers were 1.49° distant from the target's center, which is within the range of the critical distance (Bouma, 1970). The rival stimulus was presented to the opposite eye, and its location corresponded to the target location in the dominant eye (i.e., 5° from the fovea). Note that in some conditions, flanker stimuli and the target were presented to different eyes. Nonetheless, the flankers appeared as if they had been presented close to the target grating because each flanker was presented in a location that corresponded to the respective flanker location of the other eye (i.e., the target eye). The orientation of the rival stimulus was always orthogonal to the target's orientation, thus inducing competition with the target for visual awareness.

We used a special fixation formation to align both eyes and to prevent them from moving (see Fig. 1C). A white fixation cross was presented in the center of each monitor screen, but the observers perceived only one fixation cross. Nonious lines were presented separately to each eye above and below each fixation cross. In addition, a fusion frame surrounding the fixation was added to help the information from the two eyes to fuse.

2.1.3. Design

Experiment 1 had eight within-subjects conditions. We had one baseline condition in which we measured the orientation discrimination thresholds without crowding and rivalry being induced. There were two crowding conditions for measuring the effect of crowding on orientation discrimination and one rivalry condition for measuring the effect of rivalry on orientation discrimination. Finally, there were four combined conditions for measuring the combined effects of crowding and rivalry on orientation discrimination.

In the baseline condition, only the target was presented to the dominant eye. In the two crowding conditions, the target was presented together with four flankers. The flankers in one condition had orientations that were approximately parallel to the target (referred to as same orientation flankers) while they had orientations perpendicular to the target (referred to as different orientation flankers). In the rivalry condition, we presented the target to the dominant eye and a rival stimulus to the opposite eye. In the combined condition, the target, the rival stimulus and the flankers were all presented together. Because the flankers could have two different orientations (the same or different) and two different eye locations (dominant or opposite), we had four combined conditions.

Each target orientation was presented 50 times. Thus, 250 trials were devoted to each condition, resulting in a total of 2000 trials (250 trials \times 8 conditions) per observer. The eight conditions were blocked and, except for the baseline condition, their order was randomized. The baseline condition was always given first. Note that observers were instructed to fix their eyes on the fixation cross, which remained in the center throughout the experiment.

2.1.4. Procedure

Observers began the task, with the fixation cross (and the flankers in the crowding trials) already shown on the screen. An observer's press of the space-bar initiated a trial. For the trials involving crowding, the flankers remained on the screen throughout the experiment. The target and the rival stimulus were shown for 3 s.¹ During the first sec, the contrasts of both the target and the rival stimulus gradually increased until they reached their pre-determined levels (i.e., 50% for the target and 99.78% for the rival stimulus). The arrival of these pre-determined contrasts was signaled by a beep, after which the observer began to respond to the target grating by pressing one of two arrow keys on a keyboard for the next sec. Observers pressed the left-arrow key for left-tilted targets and the right-arrow key for right-tilted targets. For the last sec, the contrasts of the target and the rival stimulus gradually decreased. These gradual changes in contrast were made to prevent an abrupt change in luminance from influencing the temporal dynamics of rivalry. After a response to the target, another space-bar press initiated the next trial.

2.1.5. Analysis

First, we plotted the proportions of "clockwise" responses against the orientations of the target and then fitted a cumulative Gaussian function to examine how individual data were shaped in different conditions. This psychometric function $\psi(x)$ was defined as follows:

$$\psi(x) = \gamma + (1 - \gamma - \lambda)F(x; \alpha, \beta)$$

Here, $F(x)$ is a cumulative Gaussian function in which α and β

¹ The presentation duration of 3 s might appear to be too short for the observers to fully engage rivalry. We used this short duration because crowding studies usually use short durations (e.g., 100 ms in Parkes et al. (2001); 250 ms in Yeotikar et al. (2011)). To assess how much time the observers needed to experience rivalry, we calculated a mean phase duration using the data from Experiment 3 in which the same four observers participated. The result was calculated as 1.53 s, certainly falling within the 3-s period.

are constants associated with the center and slope of the function. γ and λ also are constants that give the lower and upper bounds to the function, respectively. We used the Psignifit toolbox (Wichmann & Hill, 2001a, 2001b) to find individual psychometric functions and computed the point of subjective equality (PSE) and the standard deviation (SD) for each condition within each psychometric cumulative function.

The PSE indicates the orientation that observers perceived subjectively as the vertical orientation. As shown in the dashed lines in Fig. 2A, when $\psi(x)$ is equal to 0.5, the x value on the abscissa corresponding to this value is the PSE. The SD indicates the spread of the psychometric function. Fig. 2A shows the different patterns between the baseline and crowding conditions in the psychometric functions. These different patterns are reflected in the SDs. To illustrate the idea of the SD in this psychometric function, we expressed the SDs in normal distribution functions by differentiating the cumulative Gaussian functions $F(x)$. These new distribution functions are shown in Fig. 2B. The SD from these normal distributions was identical to the β from psychometric function $\psi(x)$ and was used to compare conditions. For example, Fig. 2A shows the observers' psychometric functions depending on the two conditions. In this figure, the grey curve was obtained in the baseline condition, and the black curve was obtained in the crowding condition with the flankers similarly oriented to the target. Clearly, the SD was larger when similarly oriented gratings were adjacent to the target than when no gratings were nearby the target.

We used a bootstrapping procedure to compute 95% confidence intervals and compared the magnitude of crowding and rivalry effects on orientation discrimination (Efron & Tibshirani, 1986). To test the combined effects of both crowding and rivalry specifically, we constructed a 95% confidence interval for the sum of the effects

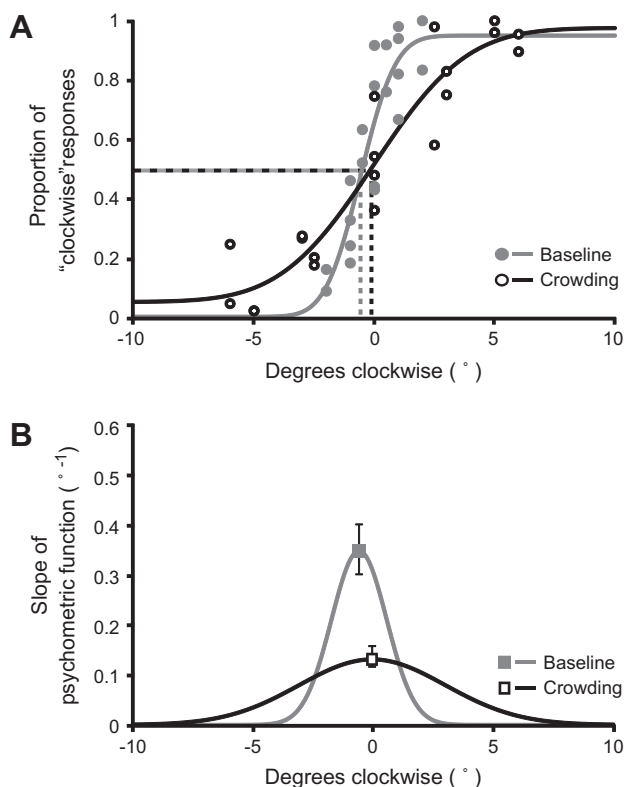


Fig. 2. (A) The proportions of "clockwise" responses are plotted against the orientations of the target. The gray and black lines indicate fitted values in the baseline and crowding conditions, respectively. (B) The standard deviations (SDs) of the functions shown in A.

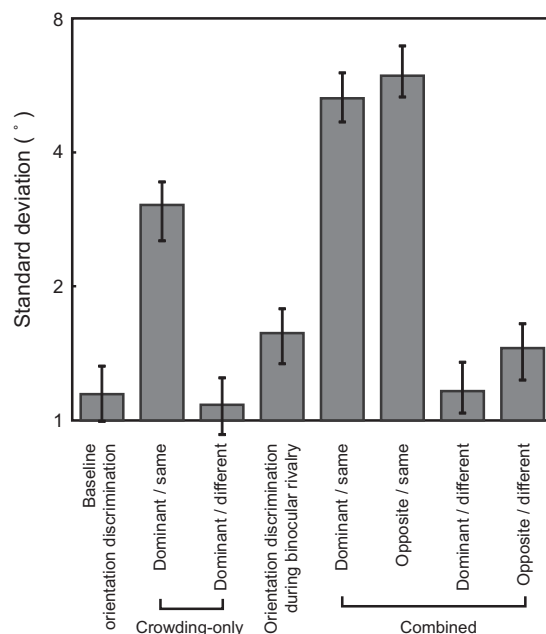


Fig. 3. The results of Experiment 1. The SDs are plotted depending on the conditions. Error bars indicate the 95% confidence intervals.

of crowding and rivalry. In testing crowding and rivalry effects, we considered non-overlapping confidence intervals between two conditions (e.g., the baseline condition and the crowding-only condition) to indicate that there was a significant difference.

2.2. Results and discussion

We initially analyzed the PSE. The observers' PSEs generally showed a consistently negative bias, indicating that they tended to perceive a left-tilted orientation as vertical. Nonetheless, these PSEs did not vary much across different conditions.

Fig. 3 shows SD results with the error bars representing 95% confidence intervals. Unlike the PSEs, these data significantly differed across the conditions² (Fig. 3). First, there was a significant effect of crowding only when the flankers had the same orientation. Specifically, the flankers with the same orientation increased the SD, but flankers with different orientations did not have this effect. These results suggest that only flankers with the same orientation produce crowding, consistent with previous studies (Andriessen & Bouma, 1976; Hariharan, Levi, & Klein, 2005; Wilkinson, Wilson, & Ellemberg, 1997; Yeotikar et al., 2011). Second, there was a small but significant effect of rivalry as shown in the different SDs between the baseline and rivalry conditions. This suggests that the rival stimulus reduced the strength of the target, resulting in poorer target orientation discrimination.

Despite the negative impact of both crowding and rivalry on orientation discrimination, it is worth noting that the negative impact of crowding was significantly greater than that of binocular rivalry (as seen when we compared the crowding-only condition that were induced by the same orientation flankers with the rivalry-only conditions). This highlights the negative impact of the flankers on target perception, which was further investigated in Experiment 2.

Given that both crowding and rivalry had adverse effects on ori-

² We used SD results to compare conditions because they can describe the entire psychometric function instead of just a portion of it. We redefined the orientation threshold as the orientation difference that was required to raise performance from 50% to 82%. Even in this case we found essentially the same pattern of results.

entation discrimination, we examined the combined effects of crowding and rivalry. Specifically, we investigated whether target discrimination was more negatively affected in the combined conditions than the sum of the crowding-only and the rivalry-only conditions. Only the same-flanker conditions were examined in this analysis because the different-flanker conditions did not significantly induce crowding (see Fig. 3). The 95% confidence interval constructed for the sum of the effects of crowding and rivalry ranged from 1.60 to 2.81. The combined/dominant/same and combined/opposite/same conditions showed the confidence intervals ranging from 3.50 to 4.88 and from 4.14 to 5.77, respectively. These results showed that the sum of the effects of crowding and rivalry was significantly smaller than the two combined conditions with the same orientation flankers, suggesting that target visibility was reduced disproportionately by the interaction between the same orientation flankers and the rival stimulus. It is possible that the target signal was suppressed by both the rival stimulus and the flankers initially, after which it was further interfered with by the flankers while integrating its features.

We also found no significant difference depending on the eye locations of the flankers. As long as the flankers were similarly oriented to the target, the augmented effect was observed regardless of the flankers' eye-of-origin. In other words, the same orientation flankers disrupted orientation discrimination for both the dominant and opposite eyes. This is consistent with previous findings in which flankers presented to the non-target eye also impaired target perception (Flom, Heath, & Takahashi, 1963; Kooi et al., 1994; Tripathy & Levi, 1994). These results suggest that crowding occurs during or after the visual information from the two eyes is combined (Flom, Heath, & Takahashi, 1963; Kooi et al., 1994; Tripathy & Levi, 1994).

3. Experiment 2

In Experiment 1, we found that the simultaneous induction of crowding and binocular rivalry impaired target orientation judgments more than the sum of the separate inductions of those two phenomena. This overadditivity suggests crowding and binocular rivalry affect orientation discrimination jointly, presumably by both reducing target signal strength and intermixing the feature information of the target with that of flankers. In Experiment 2, we sought to assess the impact of flankers on target perception. Specifically, we investigated whether the adverse impact of flankers on target perception would be weakened or remain the same when the strength of the flankers was reduced. This time, target orientation discrimination was examined again, but flankers underwent rivalry. Because a rival stimulus weakens the strength of the other eye's stimulus (Blake, 1989; Levelt, 1965), the strength of the flankers is expected to be reduced in this situation. This reduced strength of the flankers may either relieve or still produce crowding. Relieved crowding suggests that the signal strength of the flankers is important in crowding, whereas intact crowding suggests that the signal strength of the flankers is not critical for the occurrence of crowding.

3.1. Method

3.1.1. Observers

The same four observers and one additional observer participated in Experiment 2.

3.1.2. Apparatus and stimuli

The apparatus and stimuli were identical to those used in Experiment 1, except that the viewing distance and the diameter of the stimuli were altered. Each computer screen was 80 cm away from the observers' eyes, resulting in a pixel being 0.020° . All stim-

uli had a diameter of 1.65° and a spatial frequency of 3.23 cycles/deg.

3.1.3. Design

Experiment 2 had seven within-subjects conditions. We had one baseline condition in which we measured the orientation discrimination thresholds without crowding and rivalry. There were four crowding conditions for measuring the effect of crowding on orientation discrimination. Finally, there were two combined conditions for measuring the effect of rivalry on crowding as manifested in orientation discrimination.

In the baseline condition, only the target was presented to the dominant eye. In the four crowding conditions, the target was presented together with four flankers. The flankers had either the same (Fig. 4A) or different orientations, and were located in either the dominant eye or the opposite eye (Fig. 4B). Finally, in the two combined conditions, crowding and rivalry were induced simultaneously, as in Experiment 1. However, in this experiment, the flankers presented to the non-dominant eye were oriented orthogonally to those shown with the target to the dominant eye, thus inducing rivalry among the flankers. The same orientation flankers were presented to either the dominant eye (Fig. 4C) or the opposite eye.

As in Experiment 1, the seven conditions were performed in different sessions and, except for the baseline condition, their order was randomized. Each session had 250 trials (5 target orienta-

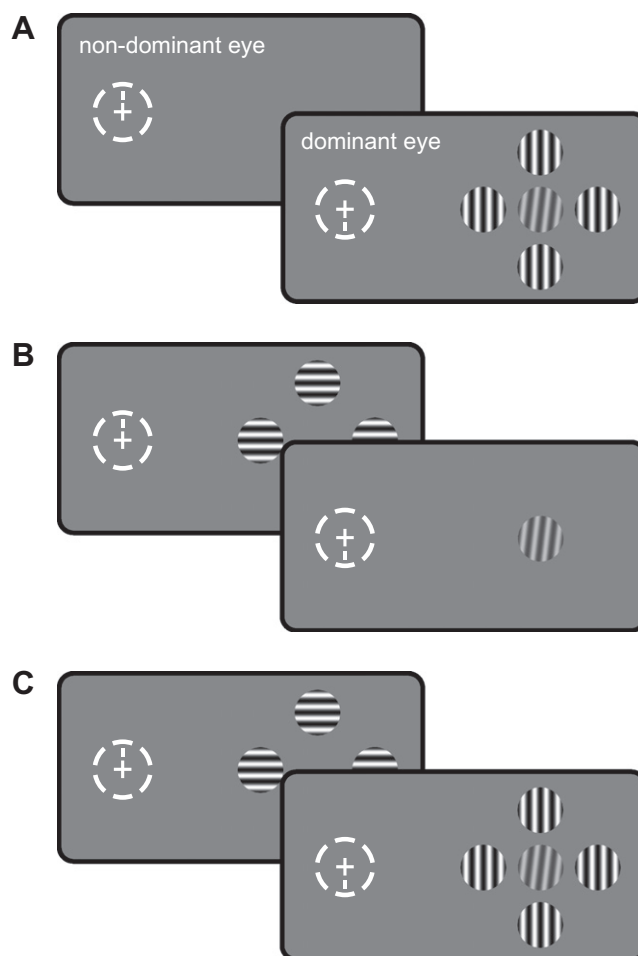


Fig. 4. Examples of the stimuli and the conditions used in Experiment 2. (A) The target and same orientation flankers were presented to the dominant eye. (B) The target and different orientation flankers were shown to the opposite eye. (C) The flankers undergoing rivalry (dominant/same + opposite/different) in the combined condition.

tions \times 50 repetitions). Thus, an observer underwent a total of 1750 trials (250 trials \times 7 conditions).

3.1.4. Procedure

The procedure was very similar to that of Experiment 1. The only difference was the duration of the target, which flashed for 100 ms with a beep sound, while observers fix their eyes on the fixation point. The target duration was made much shorter here because it did not undergo binocular rivalry. However, the flankers remained on the screen throughout the experiment.

3.1.5. Analysis

Data analysis was performed in the same manner used in Experiment 1.

3.2. Results and discussion

The PSEs mostly centered on 0 across conditions and did not significantly differ from each other. SD results are shown in Fig. 5. We examined whether crowding occurred in both the crowding and combined conditions by comparing their SDs with the SD in the baseline condition. The presence of the same (but not different) orientation flankers increased the SDs such that they were significantly larger than the SD in the baseline condition. This increase was observed regardless of the flankers' eye-of-origin (i.e., dominant or opposite), consistent with the result from Experiment 1 and with those from previous studies (Flom, Heath, & Takahashi, 1963; Kooi et al., 1994; Tripathy & Levi, 1994). This adverse effect produced by the same orientation flankers was also found in the combined conditions. The same orientation flankers presented to the target eye (dominant/same + opposite/different) and to the opposite eye (dominant/different + opposite/same) increased the SDs such that they were significantly larger in these combined conditions than in the baseline condition. Yet, the same flankers presented to the target eye did not significantly increase the SDs compared to the same flankers presented to the opposite eye. This pattern was observed regardless of whether crowding was induced independently or in conjunction with rivalry, suggesting that it is

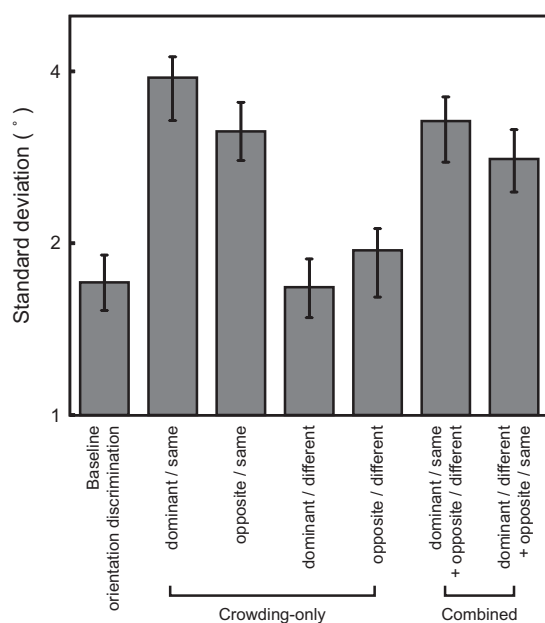


Fig. 5. The results of Experiment 2. The SDs are plotted depending on the conditions. Error bars indicate the 95% confidence intervals.

the presence of the same orientation flankers (not the flankers' eye-of-origin) that impairs target discrimination.

We then examined whether the flankers undergoing rivalry impaired target discrimination less than, or to a similar degree as, the flankers not undergoing rivalry. We compared the SDs in the combined conditions with those in the crowding conditions. The two combined conditions showed SDs comparable to the flankers with the same orientation in the crowding conditions, demonstrating that the same orientation flankers impaired target perception even when they were suppressed by the different orientation flankers.

These results are surprising, considering the relationship between the amount of suppression and stimulus strength in binocular rivalry. The fact that stimulus strength affects the amount of suppression for one eye (Levelt, 1965; Mueller & Blake, 1989) suggests that the amount of suppression should vary depending on the contrast of the flankers in this experiment. So far, both the same and the different flankers had the same contrast. Thus, we expected that the strength of the flankers should be similar for both types of orientations during rivalry, and that the perceived duration of the same orientation flankers should be similar to that of the different orientation flankers. More importantly, we expected that the perceived duration of the same orientation flankers should be shorter in these combined conditions than in the crowding conditions due to the suppressive interactions that occur during rivalry. Therefore, given the adverse effect of the flankers with the same orientation on target perception, the combined conditions (in which the same and different orientation flankers were competing) should show larger SDs than the different orientation crowding conditions, but smaller SDs than the same orientation crowding conditions. Contrary to these expectations, the SDs were similar among the combined and the same orientation crowding conditions, as if no interference had existed other than the flankers with the same orientation.

We examined these results further by varying the contrasts of the same and different flankers in the combined conditions and thus inducing changes in the dominant duration of the flankers for each eye (Levelt, 1965; Mueller & Blake, 1989). We generated two combined conditions for this test. The same orientation flankers were presented to the target eye and the different orientation flankers were presented to the opposite eye in both conditions, but their contrast combinations were different. In one condition, the same orientation flankers had a contrast of 50%, whereas the different orientation flankers had a contrast of 100%. In the other condition, the contrast of the same orientation flankers was 100%, and that of the different orientation flankers was 50%. Presumably, suppression should be greater for the same orientation flankers in the former condition and for the different orientation flankers in the latter condition. This is because stimuli with a higher contrast usually dominate those with a lower contrast (Levelt, 1965; Mueller & Blake, 1989). This differential suppression can lead to different durations of dominance. Specifically, the different orientation flankers may be perceived longer in the former condition, while the same orientation flankers may be perceived longer in the latter condition. Thus, we expected that the same flankers with a contrast of 100% would show a larger SD than those with a contrast of 50%.

We tested 4 among the 5 observers who had participated in Experiment 2 and found that the new combined conditions showed significantly larger SDs than the baseline condition. Interestingly, the extent to which crowding occurs did not significantly differ between the two new conditions despite the differences in contrast. This suggests that it is the presence of the same flankers (even at 50% contrast), not the strengths of the flankers, that impairs target perception. Not surprisingly, it has been shown that the presence of the flankers is important for the occurrence of

crowding. For example, crowding occurred as long as the contrast of the flankers was high enough to make the flankers visible (Levi & Carney, 2009; Wallis & Bex, 2011; Yeotikar et al., 2011). Moreover, Ho and Cheung (2011) found that even invisible flankers produced crowding.

Experiment 2 showed that crowding still occurred, even when the strength of the flankers was reduced by binocular rivalry and thus suppressive effect of the flankers on the target may have been weakened. This result suggests that binocular rivalry did not influence the occurrence of crowding. This further indicates that target signal reduction and inappropriate feature integration are separate mechanisms that take effect independently as the recovery of crowding differed depending on the low- and high-level masking (Chakravarthi & Cavanagh, 2009). Some investigators have emphasized the importance of inappropriate feature integration for producing crowding (Freeman, Donner, & Heeger, 2011; Greenwood, Bex, & Dakin, 2012, 2009; Levi, 2008; Pelli & Tillman, 2008). We postulate that even when perceived at reduced strengths, the presence of the flankers interferes with the feature integration process of the target through which the features of the target and the flankers are jumbled, consequently making target discrimination difficult. In Experiment 3, we manipulated the ways in which the flankers were shown and investigated the temporal dynamics of binocular rivalry.

4. Experiment 3

Experiment 2 showed that the presence of the flankers is important for impairing target perception. In this experiment we investigated if the appearance of flankers could change the temporal dynamics of the duration of target dominance. As in Experiment 1, we induced crowding and rivalry simultaneously but examined perceived durations of a target and a rival stimulus. Imagine that flankers gradually appear close to a target currently undergoing rivalry with a rival stimulus. The target and the rival stimulus would be constantly competing to gain access to visual awareness. At the same time, target perception would be suppressed and interfered with due to the appearance of the flankers. These situations would increase the likelihood that the target becomes suppressed (if dominant) and stays suppressed (if suppressed). We tested these possibilities by measuring phase durations while observers were viewing the target and the rival stimulus. We calculated mean phase durations (MPDs) for the target-dominant and target-suppressed (i.e., rival-stimulus dominant) conditions. Presumably, the flankers impairing target visibility also shorten the duration of target perception.

4.1. Method

4.1.1. Observers

Eleven observers including the five observers who had participated in Experiment 2 took part in this experiment.

4.1.2. Apparatus and stimuli

Apparatus and stimuli were identical to those in Experiment 2, except that the diameter of the stimuli (targets, rival stimuli, and flankers) was 1.65° and thus the spatial frequency was 2.42 cycles/deg. Targets were always vertically oriented, and rival gratings were always horizontally oriented. Four flankers were vertical gratings and thus always had the same orientation as the target grating. The centers of the flankers subtended 1.98° of the visual angle to the center of the target from a viewing distance of 80 cm. All gratings had a Michelson contrast of 99.78%.

4.1.3. Design

Fig. 6 displays three different conditions: baseline rivalry condition (baseline condition, Fig. 6A); target dominant condition (dominant condition, Fig. 6B); and the target suppressed condition (suppressed condition, Fig. 6C). The baseline condition was a typical binocular rivalry condition in which observers viewed a target and a rival stimulus with each eye. In both the dominant and suppressed conditions, flankers were always presented to the target-viewing eye. In the dominant condition, flankers were presented while observers perceived the target—that is, the target was dominant. In the suppressed condition, flankers were presented while observers perceived the rival stimulus—that is, the target was suppressed.

The baseline condition allowed us to calculate the MPD of the perception of each stimulus type (i.e., the target and the rival-stimulus), which is a measurement of how long each stimulus type was perceived, on average. This MPD was calculated for each observer and served as a means to determine the time to present the flankers in the dominant and suppressed conditions. Specifically, we derived a flanker-delay time based on the MPD. This flanker delay was defined as one-third of the MPD and was obtained separately for the target and the rival stimulus in each observer. We introduced this flanker delay to ensure that the phase of target or rival-stimulus perception was in progress when the flankers appeared.

4.1.4. Procedure

Observers fixed their eyes on the central fixation cross while the target and the rival stimulus were shown to each eye. Both types of stimuli were presented for 90 s. Observers were instructed to keep the up- or the right-arrow key pressed while they were perceiving

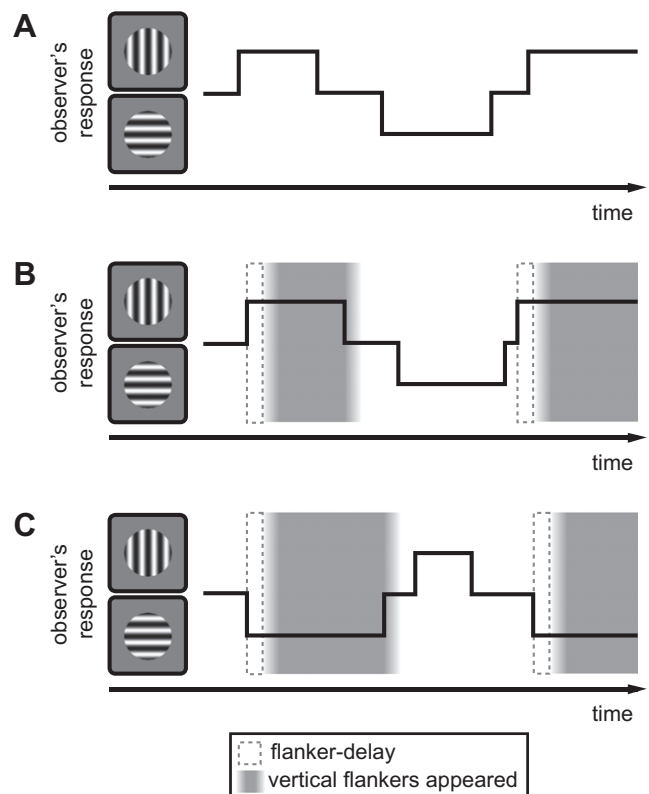


Fig. 6. Stimuli and the three conditions used in Experiment 3. The vertical grating is the target and the horizontal grating is the rival stimulus. The dotted rectangles represent flanker-delays and the gray areas indicate the durations of the flankers' appearances. (A) The baseline condition. (B) The dominant condition. (C) The suppressed condition.

the vertically oriented target or the horizontally oriented rival-stimulus, respectively. When they perceived a mixture of both types of stimuli, they were asked to release the keys. This procedure was repeated three times per condition. Immediately after the baseline condition, the flanker-delays were calculated and used for the dominant and suppressed conditions. Thus, all observers started with the baseline condition and proceeded with either the dominant or the suppressed condition. The order of these two conditions was counterbalanced across observers.

For the dominant condition, observers indicated that they started to perceive the target by pressing the up-arrow key. Then, four vertical flankers gradually appeared over 250 ms, starting at the target flanker-delay time. When observers started to perceive a rival stimulus or a mixture of the two types of stimuli (and thus pressed the right-arrow key or released the key, respectively), the four flankers gradually disappeared over 250 ms. In the suppressed condition, observers indicated their perception of the rival-stimulus. This triggered the gradual appearance of the flankers (over 250 ms) at the rival-stimulus flanker-delay time. When observers started to change their percepts, the flankers gradually disappeared over 250 ms. The gradual appearance and disappearance of the flankers were introduced to minimize disturbances in the temporal dynamics of rivalry.

4.2. Results and discussion

Prior to statistical analysis, we normalized the phase durations to control individual differences and thus we can also examine the distributions of the phase durations (e.g., Kang & Blake, 2010; Kovacs et al., 1996). For normalization, the phase duration was divided by the MPD calculated from all trials within an observer. Fig. 7A shows the normalized MPDs of the target and the rival stimulus in each condition, and Fig. 7B shows MPDs before normalization. We performed a two-way repeated measures analysis of variance (ANOVA) on the type of rivalry (baseline, dominant, and suppressed) and stimulus type (target and rival stimulus). We report here the normalized MPD results using the Huynh-Feldt corrected p values³. Whereas no significant effect was found for the type of rivalry, $F(2,20) = 0.74$, $p = 0.49$, the stimulus type showed that the MPD was significantly shorter for the target than for the rival stimulus, $F(1,10) = 7.46$, $p < 0.05$. In addition, the difference between the target and the rival stimulus became larger as the type of rivalry moved from the baseline, to the dominant and suppressed conditions (see, Fig. 7A). This observation was corroborated by a significant interaction between the type of rivalry and the stimulus type, $F(2,20) = 4.73$, $p < 0.05$, suggesting that the presence of the same orientation flankers negatively influenced target visibility differentially across the conditions. We also performed two separate repeated measures ANOVAs for each stimulus type. Whereas the rival-stimulus MPDs did not significantly differ, $F(2,20) = 0.51$, $p = 0.53$, the target MPDs did significantly differ across the rivalry conditions, $F(2,20) = 9.88$, $p < 0.01$. Moreover, the comparison between the dominant and suppressed conditions for the target and the rival stimulus revealed that the target MPD was significantly shorter for the suppressed than for the dominant trials, $t(10) = 3.28$, $p < 0.01$, whereas the rival-stimulus MPD was not significantly different, $t(10) = 0.85$, $p = 0.42$. These results suggest that the same orientation flankers reduced the visibility of the target but not that of the rival stimulus. Fukuda and Blake (1992) found the same pattern of results when they surrounded the target with an annulus concentric with the target in rivalry.

³ We also analyzed MPDs without normalization and found essentially the same results.

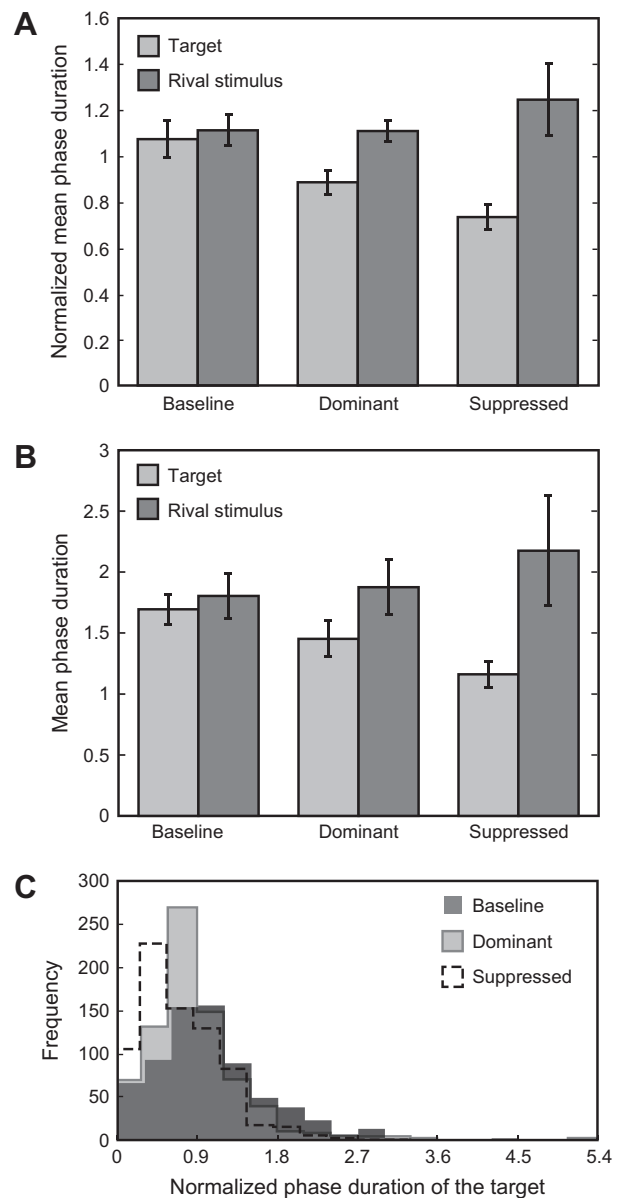


Fig. 7. The results of Experiment 3. (A) The normalized mean phase durations (MPDs) are plotted depending on the conditions. (B) The MPDs before normalization. (C) The histograms of binned MPD frequencies for the target observed in the baseline, dominant, and suppressed conditions. Error bars indicate standard errors of the mean.

We examined this target duration effect further by binning the phase durations and comparing the frequencies of these bins in the three rivalry conditions. Fig. 7C shows a histogram of phase duration frequencies plotted according to the normalized phase durations of the target. In this figure, the frequency bars representing each rivalry condition are superimposed on top of each other. In the dominant condition, the frequency increased between 0.3 and 0.9 but decreased thereafter compared to the baseline condition. In the suppressed condition, the frequency increased between 0 and 0.6 and then decreased relative to the baseline condition. Although both the dominant and suppressed conditions showed similar frequencies beyond the duration of 0.9, the suppressed condition had a higher number of short durations than the dominant condition, particularly in the short durations of 0–0.6.

This frequency analysis of the target provides a clear picture of how the flankers influenced the duration of target perception while

each type of rivalry was underway. We found that the decrease in the target MPD was driven by the higher frequencies of shorter durations. This frequency pattern was more pronounced in the suppressed condition than in the dominant condition.

In summary, the appearance of the same orientation flankers suppressed target perception. Based on this result, we can postulate the following: (a) when the target was dominant, the appearance of the flankers suppressed the target signal such that it was easier for the target to be suppressed by the rival stimulus and be perceived for only a short period; (b) when the target was suppressed, the strength of the target was already weak and hence the appearance of the flankers allowed the target to remain suppressed, consequently prolonging the duration of rival-stimulus dominance. Evidently, the double suppression of the target by both the rival stimulus and the flankers often limited target dominance to very short durations. In addition, the appearance of visible flankers may have been a negative influence on target perception, possibly through an inappropriate mixture of target-flanker features (as shown in Experiment 2).

5. General discussion

The current study investigated object perception in challenging situations. For example, a target object is cluttered with other distracting objects and multiple objects compete for visual awareness. Both crowding and binocular rivalry were incorporated in our investigation to create situations like these examples. Crowding occurs due to a reduction in target strength and to inappropriate feature integration, and rivalry occurs due to competition by stimulus strength (Blake, 1989; Levi, 2008; Mueller & Blake, 1989; Whitney & Levi, 2011). As in other previous studies (Chakravarthi & Cavanagh, 2009; Vickery et al., 2009), we combined two perceptual phenomena (crowding and binocular rivalry) and investigated the joint contribution of the two to target identification. In Experiment 1, we were interested in observing any emergence of a joint contribution effect akin to supercrowding (Vickery et al., 2009). Further, we investigated if flankers undergoing rivalry could relieve or still produce crowding (in Experiment 2), in turn, testing whether reduced stimulus strength decreases susceptibility to interference generated by the flankers. Finally, in Experiment 3, we investigated the joint contribution of crowding and rivalry in the context of the temporal dynamics of the perceived durations of objects, particularly focusing on the duration of target dominance.

In Experiment 1, when object perception was disrupted simultaneously by both crowding and binocular rivalry, it was worse than with the simple addition of the two effects. In Experiment 2, rivalry between flankers did not influence the degree of the crowding effect. In Experiment 3, flankers gradually appearing nearby the target influenced the temporal dynamics of binocular rivalry.

Experiments 1 and 3 suggest that crowding and rivalry interacted with each other. This is supported by the overadditivity shown in the results of Experiment 1 and by the shortened durations of target dominance (particularly in the suppressed condition) in Experiment 3. We think that the simultaneous induction of crowding and rivalry significantly weakened the target strength due to the double suppression produced by the flankers and the rival stimulus (Bi et al., 2009; Blake, 1989; Freeman, Donner, & Heeger, 2011; Levelt, 1965). When the effects of crowding and rivalry are met through the same mechanism (i.e., reduced target strength), the result appeared to be augmented.

Moreover, the presence of the flankers may have made target identification even more difficult (in Experiment 1) and might have frequently shortened conscious perception of the target (in

Experiment 3). These possibilities are strengthened by the finding that crowding still occurred even when the strength of the flankers was reduced (Experiment 2). Some studies have shown that crowding occurred as long as flankers were visible (Levi & Carney, 2009; Pelli, Palomares, & Majaj, 2004; Wallis & Bex, 2011; Yeotikar et al., 2011) and even when they were invisible (Ho & Cheung, 2011). These underline the importance of the physical presence of flankers for producing the crowding effect, regardless of actual perceptual awareness of them. Therefore, we postulate that inappropriate integration of target and flanker features is also reflected in our results, suggesting that the two accounts of crowding—that is, reduced target strength by flankers and inappropriate integration of target-flanker features are orthogonal to each other and perhaps are applied for different levels of processing.

All three experiments consistently showed that the flankers oriented similarly to the target produced significant crowding effects. This is in line with previous findings in which a target and flankers with similar visual properties produced a greater degree of crowding (Andriessen & Bouma, 1976; Hariharan, Levi, & Klein, 2005; Wilkinson, Wilson, & Elleberg, 1997; Yeotikar et al., 2011). Moreover, these similarly oriented flankers impaired target discrimination when presented to both the target-eye and the opposite-eye (Experiments 1 and 2). Previous studies have demonstrated that crowding was observed regardless of the flankers' eye-of-origin (Flom, Heath, & Takahashi, 1963; Kooi et al., 1994; Tripathy & Levi, 1994), indicating that crowding occurs after the integration of information from the two eyes. Based on this idea, the interaction we found between crowding and rivalry could have begun from the moment the two eyes were united, possibly as early as V1, where binocular cells are observed (Hubel & Wiesel, 1968; Poggio & Fischer, 1977). Another damaging effect of crowding—inappropriate feature integration—may have occurred rather later, possibly between V1 and the lateral occipital cortex. Chakravarthi and Cavanagh (2009) have suggested that feature integration occurs prior to the locus of object substitution masking and that the neural locus of this particular masking was found to be in the lateral occipital cortex (Carlson, Rauschenberger, & Verstraten, 2007). Freeman, Donner, and Heeger (2011) also found that activity in V1 was correlated with the visual word form area in the occipitotemporal cortex of humans, and that this correlated activity turned out to be important for producing the effect of crowding for letter recognition.

A large number of studies have suggested that both crowding and rivalry occur over multiple areas of the brain (for an overview see Blake & Logothetis, 2002; Levi, 2008; Whitney & Levi, 2011) depending on the processes required by a task and given stimuli. For example, Blake et al. (2006) found that an orientation-specific adaptation effect was substantially reduced during both crowding and rivalry, suggesting that crowding and rivalry occur as early as V1, in which this adaptation occurs (Movshon & Lennie, 1979). However, the fact that the receptive field size in V4 (Motter, 2002) approximately matches Bouma's law (0.5e, Bouma, 1970; Pelli & Tillman, 2008) suggests that area V4 is a valid candidate for the locus of crowding. For rivalry, the discovery that the strength required to suppress rival stimuli increases as a function of the complexity of stimuli (Nguyen, Freeman, & Alais, 2003) indicates that the depth of suppression increases along the visual pathways as higher areas process more complex stimuli (Felleman & Van Essen, 1991; Ungerleider & Mishkin, 1982). For crowding, Anderson et al. (2012) found that repetition suppression in fMRI responses followed crowded percepts from V1 to V4, suggesting that crowding is also a multi-stage process. Thus, the interactions we found might have involved the brain regions that process the specific type of stimuli (i.e., differently oriented gratings). Orientation selectivity has been found in areas from V1 to V3 in monkeys (Vanduffel et al., 2002) and from V1 to V4v in humans (Kamitani &

Tong, 2005). Therefore, it is difficult to pinpoint the neural locus or loci of the interactions we uncovered. Consequently, we can only offer reasonable speculations about their locations because both crowding and rivalry involve multiple areas from V1 to V4.

In summary, we have found that object perception deteriorates disproportionately when two challenging situations (crowding and rivalry) are combined. Both crowding and rivalry impaired object perception by creating signal reduction in an object. Furthermore, crowding additionally impaired object perception by generating an inappropriate integration of features. In addition, we discovered that signal reduction in the flankers did not improve target perception in crowding. This suggests both that crowding is primarily based on feature integration (Levi, 2008; Pelli & Tillman, 2008) and that it exhibits two orthogonal functions for flankers in target perception.

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