

# Crowding, visual awareness, and their respective neural loci

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In peripheral vision, object identification can be impeded when a target object is flanked by other objects. This phenomenon of crowding has been attributed to basic processes associated with image encoding by the visual system, but the neural origin of crowding is not known. Determining whether crowding depends on subjective awareness of the flankers can provide information on the neural origin of crowding. However, recent studies that manipulated flanker awareness have yielded conflicting results. In the current study, we suppressed flanker awareness with two methods: interocular suppression (IOS) and adaptation-induced blindness (AIB). We tested two different types of stimuli: gratings and letters. With IOS, we found that the magnitude of crowding increased as the number of physical flankers increased, even when the observers did not report seeing any of the flankers. In contrast, when flanker awareness was manipulated with AIB, the magnitude of crowding increased with the number of perceived flankers. Our results show that whether crowding is contingent on awareness of the flankers depends on the method used to suppress awareness. In addition, our results imply that the locus of crowding is upstream from the neural locus of IOS and close to or downstream from that of AIB. Neurophysiology and neuroimaging studies jointly implicate mid-to-high level visual processing stages for IOS, while direct evidence regarding the neural locus of AIB is limited. The most consistent interpretation of our empirical findings is to place the neural locus of crowding at an early cortical site, such as V1 or V2.

## Introduction

In peripheral vision, object recognition in a cluttered scene is difficult. This phenomenon, known as crowding, is thought to be a key factor limiting peripheral form vision (Levi, 2008) and is thought to provide an important avenue toward a basic understanding of visual processing associated with object recognition (Balas, Nakano, & Rosenholtz, 2009; Freeman & Simoncelli, 2011; Nandy & Tjan, 2012; Pelli & Tillman, 2008; Whitney & Levi, 2011). Although the underlying mechanism of crowding is not well understood, it is commonly suggested that crowding is due to a breakdown in feature integration necessary for object perception. This faulty feature integration theory suggests that the detection of simple visual features is not impeded in clutter (Chung, Levi, & Legge, 2001; He, Cavanagh, & Intriligator, 1996; Levi, 2008; Levi, Hariharan, & Klein, 2002; Nandy & Tjan, 2007; Pelli, Palomares, & Majaj, 2004); rather, clutter prevents the detected features from being properly integrated (Levi et al., 2002; Nandy & Tjan, 2007; Pelli et al., 2004). A natural question to ask with respect to this theory is, what are the features that the visual system detects but fails to integrate? Knowing the neural locus/loci of crowding will provide the answer. In general, the locus of crowding will inform us on the mechanism of crowding.

One approach to identify the locus/loci of crowding is to study the relationship between awareness and crowding. Such an approach can be effective if the underlying mechanism of a given manipulation of visual awareness is known. In the context of a crowding experiment, visual awareness of the target or the flankers can be manipulated. Table 1 summarizes

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Studies	Stimuli	Awareness	Awareness manipulation	Measurements	Findings	Locus of crowding
He, Cavanagh, & Intriligator, 1996	Gabors	Target	Crowding	Adaptation to orientation	Orientation-specific adaptation is not affected by crowding.	After V1
Rajimehr, Vaziri-Pashkam, Afraz, & Esteky, 2004	Dots	Target	Crowding	Adaptation to apparent motion	Selective adaptation to apparent motion is not affected by crowding.	After V5
Aghdaee, 2005	Spiral grating	Target	Crowding	Adaptation to spiral motion	Adaptation to spiral motion is not affected by crowding.	After V5/MT
Moutoussis & Zeki, 2006	Moving gratings	Target	Crowding	BOLD signal	Crowded stimuli enhance neural signals in V3A, V5, and parietal cortex.	-
Veenemans, Cavanagh, & Chakravarthi, 2009	Letters	Flankers	Pre- and postmasks	Letter identification	Impaired target identification even when the flankers are made invisible by masking.	-
Cham & Cheung, 2009	Gabors	flankers and target	Continuous flash suppression	Adaptation to invisible target orientation	Adaptation to target orientation is reduced when invisible flankers are presented.	-
Wallis & Bex, 2011	Letters	Flankers	Adaptation-induced blindness	Letter identification	Less crowding when the flankers are invisible.	After V1
Ho & Cheung, 2011	Gratings	Flankers	Continuous flash suppression	Adaptation to orientation	Contrast threshold of orientation discrimination of a grating is elevated even when flankers are not visible.	V1

Table 1. Studies on the effects of visual awareness on crowding and the inferred loci of crowding.

several representative studies that manipulated awareness to infer the neural locus of crowding.

Crowding reduces awareness of target stimuli such as static gratings (He et al., 1996), moving dots (Rajimehr, Vaziri-Pashkam, Afraz, & Esteky, 2004), spiral gratings (Aghdaee, 2005) and moving gratings (Moutoussis & Zeki, 2006). He et al. (1996) showed that target orientation made invisible by crowding was still able to induce an orientation-specific contrast threshold elevation for a subsequent test Gabor, suggesting that crowding takes place after V1, where orientation information is processed. Rajimehr et al. (2004) showed that direction-selective adaptation to random-dot motion occurred even when the adapting stimulus was made invisible by crowding. They concluded that crowding occurred after the locus of motion processing, such as V5/MT. Similarly, the rotation selective adaptation to spiral motion also occurred even when it was made invisible by crowding, suggesting that crowding may occur after the locus of spiral motion, such as V5/MT (Aghdaee, 2005). Moutoussis and Zeki (2006) found that a moving grating that was removed from awareness by crowding evoked neural activity in V3/V5 and the parietal cortex. Their finding suggested that the locus of crowding was after these cortical areas in the feedforward visual hierarchy.

Several studies have also investigated the effects of flanker awareness on crowding (Chakravarthi & Cavanagh, 2009; Cham & Cheung, 2009; Ho & Cheung, 2011; Veenemans, Cavanagh, & Chakravarthi, 2009; Wallis & Bex, 2011), with conflicting results. Wallis and Bex (2011) showed that flanker awareness was necessary to elicit crowding. They found that letter flankers made invisible through adaptation-induced blindness (AIB) did not interfere with the target letter in a letter-identification task. They concluded that crowding requires awareness of flankers, and the locus of crowding would be after the neural locus of adaptation-induced blindness. Other studies showed that flanker awareness is not necessary for crowding. Making flankers invisible with pre- and postmasks (Veenemans et al., 2009), interocular suppression (a.k.a., continuous flash suppression; Cham & Cheung, 2009; Ho & Cheung, 2011) or noise and metacontrast masking (Chakravarthi & Cavanagh, 2009) led to crowding. For example, Ho & Cheung (2011) showed that Gabor flankers rendered invisible by interocular suppression (IOS) interact with target Gabors. They concluded that crowding occurs regardless of awareness, and the neural locus of crowding should therefore be situated before the neural locus of these awareness manipulations.

Various methods have been used to produce invisible flankers in crowding experiments, including interocular suppression (Blake & Fox, 1974; Tsuchiya & Koch, 2005; Wolfe, 1984) and adaptation-induced blindness

(Motoyoshi & Hayakawa, 2010). With interocular suppression (IOS), two different stimuli are presented to each eye, and compete for awareness. If one stimulus is much more salient than the other, because it has a higher contrast or is flashing, then the more salient stimulus can continuously suppress the weaker stimulus. In the case of high-contrast continuous flash suppression, numerous physiological and neuroimaging studies have implicated lower level visual areas as the probable locus of the suppression (Haynes, Deichmann, & Rees, 2005; Leopold & Logothetis, 1996; Logothetis & Schall, 1989; Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001; Wunderlich, Schneider, & Kastner, 2005). With adaptation-induced blindness (AIB), adapting to a drifting vertical grating (mask) at a temporal frequency of 10 Hz has been found to make a stimulus invisible when it was presented at the same location as the drifting mask (Motoyoshi & Hayakawa, 2010). Unfortunately, little is known about the neural basis of AIB.

Why did studies yield conflicting results on the relationship between crowding and visual awareness? Different methods for suppressing awareness (e.g., AIB vs. IOS) may rely on different neural substrates with different cortical loci. Differences in stimuli (e.g., Gabor vs. letters, narrowband vs. broadband) may also explain the discrepancy, as different stimuli may require distinct stages of processing and recruit different neural machinery. In the current study, we used two different methods to make flankers invisible: AIB and IOS. We also tested two different types of stimuli: narrowband Gabor patches and broadband letters. We first tested whether Gabor flankers rendered invisible by IOS (Experiment 1) or AIB (Experiment 2) would induce crowding. We then tested crowding with invisible letter flankers, induced with IOS (Experiment 3). To preview, we found that flankers made invisible with IOS continue to cause crowding, whereas flankers made invisible with AIB do not. These results suggest that visual awareness is not a necessary factor for crowding, and that the locus/loci of crowding are at the later stage from that of IOS (i.e., up-stream from that of IOS) and prior to that of AIB (i.e. down-stream from that of AIB). Incidentally, our findings also place the neural loci of AIB to be up-stream from those of IOS.

## Methods

### Experiment 1

#### Observers

Four healthy volunteers, including the first author, participated in Experiment 1. For this and other experiments, all observers, excluding the first author,

were naive to the purpose of the experiments. All observers had normal color vision and normal or corrected-to-normal visual acuity. The study was carried out in accordance with the regulations of the Institutional Review Board of the University of Southern California.

### Stimuli

Gaussian-windowed sinusoidal gratings (Gabors) were used as targets and flankers. For the Gabors, the Gaussian window had a standard deviation of  $0.35^\circ$ . The spatial frequency of the grating was 2.85 cycles/ $^\circ$ . The peak Weber contrast of the Gabors was 60%. The target was presented at an eccentricity of  $5^\circ$  below fixation, and the center-to-center spacing between the target and flankers was  $1.25^\circ$ .

Four Gaussian-windowed flickering radial square-wave gratings were used as interocular suppressors to render the flankers invisible. The suppressors were at 100% contrast and alternated between clockwise and counterclockwise rotation (angular velocity =  $144^\circ/\text{s}$ ) while alternating between shrinking and expanding ( $0.25^\circ/\text{s}$ ) at 1 Hz. This type of suppressor has been shown to minimize motion and orientation aftereffects (Blake, Tadin, Sobel, Raissian, & Chong, 2006). Their size ( $\sigma = 0.5^\circ$ ) was slightly larger than the flankers' in order to fully mask the flankers and minimize any mixed percepts (Blake, 2001). These suppressors were presented to the dominant eye of an observer, which was determined by the Porta test (Roth, Lora, & Heilman, 2002): observers extended a hand and aligned the thumb to a distant object with both eyes opened. By closing one eye at a time, the dominant eye was identified as the one that retained the alignment.

The stimuli were created in MATLAB (MathWorks, version 2007a) using Psychophysics Toolbox 3 (Brainard, 1997; Pelli, 1997). They were presented on a Dell P1230 19" monitor (resolution  $1024 \times 768$  at 100 Hz) driven by a MacBook computer (OSX version 10.5.8) via a passive video attenuator (Pelli & Zhang, 1991) to provide 11 bits of linearly spaced contrast levels achieved using custom-built calibration and contrast-control software implemented in MATLAB (<https://github.com/usc-tlab/LinearFineContrast.git>). Only the green channel of the monitor was used.

The observer's head was held fixed with a chin-and-head rest to maintain a viewing distance of 70 cm. At this viewing distance, a pixel subtended approximately  $0.031^\circ$  of visual angle. Background luminance of the display was  $25.7 \text{ cd/m}^2$ . Observers viewed the left- and right-halves of the screen through a mirror stereoscope. Two small fixation crosses were presented to the left- and right-halves of the screen to aid binocular fusion. Upper and lower nonius lines were also displayed to allow for self-monitoring of vergence.

### Procedures

Figure 1 shows the timing and stimuli for Experiment 1. One target and up to four flankers were presented in an observer's peripheral visual field. An observer fixated on the fixation mark, and the target was presented at  $5^\circ$  in the lower visual field. Both the target and flankers were shown to an observer's nondominant eye, and four suppressors, at 100% contrast, were presented to the observer's dominant eye regardless of the actual number of flankers. The primary task of the observer was to discriminate the orientation of a target—clockwise (CW) versus counterclockwise (CCW) relative to  $45^\circ$ , and respond with a key press. In addition, the observer reported the total number of Gabors perceived, from which we calculated the number of perceived flankers.<sup>1</sup>

As mentioned earlier, there could be one to four flankers for any given trial in Experiment 1. These flanking conditions were randomly presented within each experimental block, and each flanker condition was presented five times in each block. Therefore, each block consisted of 20 trials. Four blocks were performed in one run, and each observer completed five runs. In other words, each observer completed 100 trials for each condition, or a total of 400 trials for this experiment. Table 2 summarizes the number of trials tested for each flanker condition, and for each experiment in this study. The observer was required to take a break (minimum 5 minutes) between each run. The entire experiment was completed in a single session of approximately two hours.

The flankers, which were of a lower contrast (60%), were removed from visual awareness with continuous flash suppression (see Stimuli). Observers were unaware of the flankers in 82% of the trials (see Appendix, Figure A1). We also measured accuracy in a target-only condition before the main experiment to quantify the effect due to the suppressors alone (80 trials per observer). The target, flankers, and suppressors were presented simultaneously for a duration of 100 ms. The orientations of the flankers were independently jittered within  $\pm 2$  times the observer's angular threshold about  $45^\circ$ , which was obtained prior to the main experiment.

### Premeasure: Orientation threshold

Individual observers' orientation-discrimination thresholds for the Gabor stimuli were obtained prior to Experiments 1 and 2. Specifically, we presented a single Gabor target at one of these orientation offsets,  $\pm 1^\circ$ ,  $\pm 1.8^\circ$ ,  $\pm 3.1^\circ$ ,  $\pm 5.6^\circ$ , and  $\pm 10^\circ$ , from  $45^\circ$  at an eccentricity of  $5^\circ$  below the fixation point. Observers had to discriminate the tilted direction of the target (CW or CCW relative to  $45^\circ$ ). The orientation-discrimination threshold corresponded to a discrimination accuracy of 75% correct.

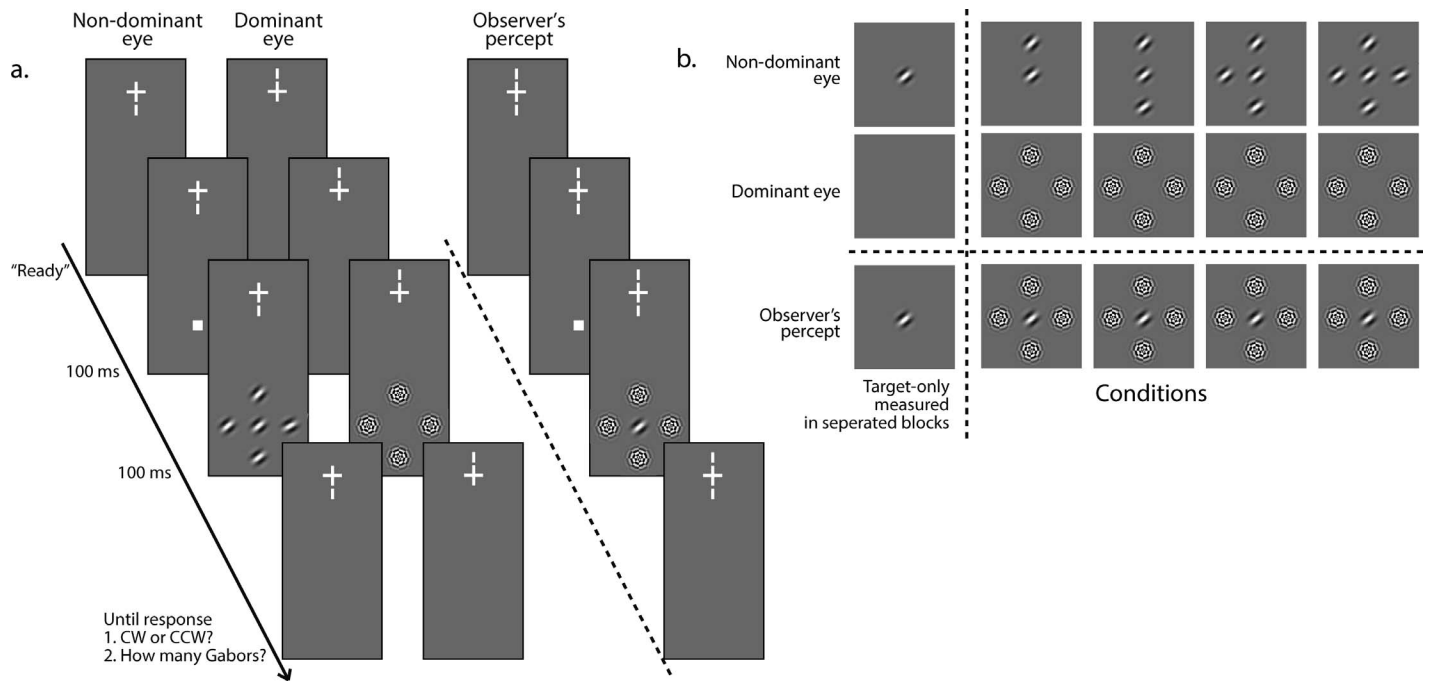


Figure 1. (a) A sample trial of Experiment 1. The left and middle series of images were presented to the nondominant and dominant eyes, respectively. The right series of images indicates an observer’s percept. A fixation point and a nonius line were shown to each eye. A small square appeared 100 ms prior to the stimulus to indicate the eccentric location of the target (5° below from the fixation point). Observers had to maintain fixation on the cross and a constant vergence state indicated by the alignment of the nonius lines. 100 ms after the small square disappeared, a target, flankers, and suppressors were presented for 100 ms simultaneously. The observer was asked to report the orientation of the target (CW or CCW from 45°) and the number of Gabors seen. (b) Conditions used in Experiment 1. The first row indicates the stimuli that were presented to the nondominant eye, the second row indicates the stimuli that were presented to the dominant eye, and the third row indicates an observer’s percept. The left-most column indicates a target-only condition, which was measured in separate blocks. The four flanking conditions were with one to four flankers and (always) four suppressors. It should be noted that an observer’s percept of these four conditions was usually the same: 82% of total trials were fully suppressed trials (Figure A1).

## Experiment 2

### Observers

Six normally sighted volunteers, including the first author, participated in Experiment 2. Among the six observers, two (including the first author) also participated in Experiment 1.

### Stimuli

The Gabor target and flankers were the same as in Experiment 1, except that observers viewed them with

	Number of presented flankers				
	0	1	2	3	4
Experiment 1	80	100	100	100	100
Experiment 2	64	64	64	64	192
Experiment 3	72	72	72	72	72

Table 2. Number of trials for each flanker condition tested for each observer in each experiment.

both eyes. AIB, as opposed to IOS, was used to suppress visual awareness of the flankers. During adaptation, four adaptors were presented at the flanker locations. The adaptors were the same Gabor patches as the flankers, and the orientation of adaptors was randomly selected within  $\pm 4$  times an individual observer’s orientation discrimination threshold with respect to 45° and was replaced every 100 ms.

### Procedures

Figure 2 shows the timing and stimuli for Experiment 2. Observers fixated at a fixation cross. The main task was identical to that of Experiment 1. There could be zero to four flankers. For conditions with zero to three flankers, each condition was presented for four trials per block; the four-flanker condition was presented for 12 trials per block. Each block consisted of 28 trials. Eight blocks were performed in one session, and each observer completed two sessions, one session per day. Thus, a total of 448 trials were performed by

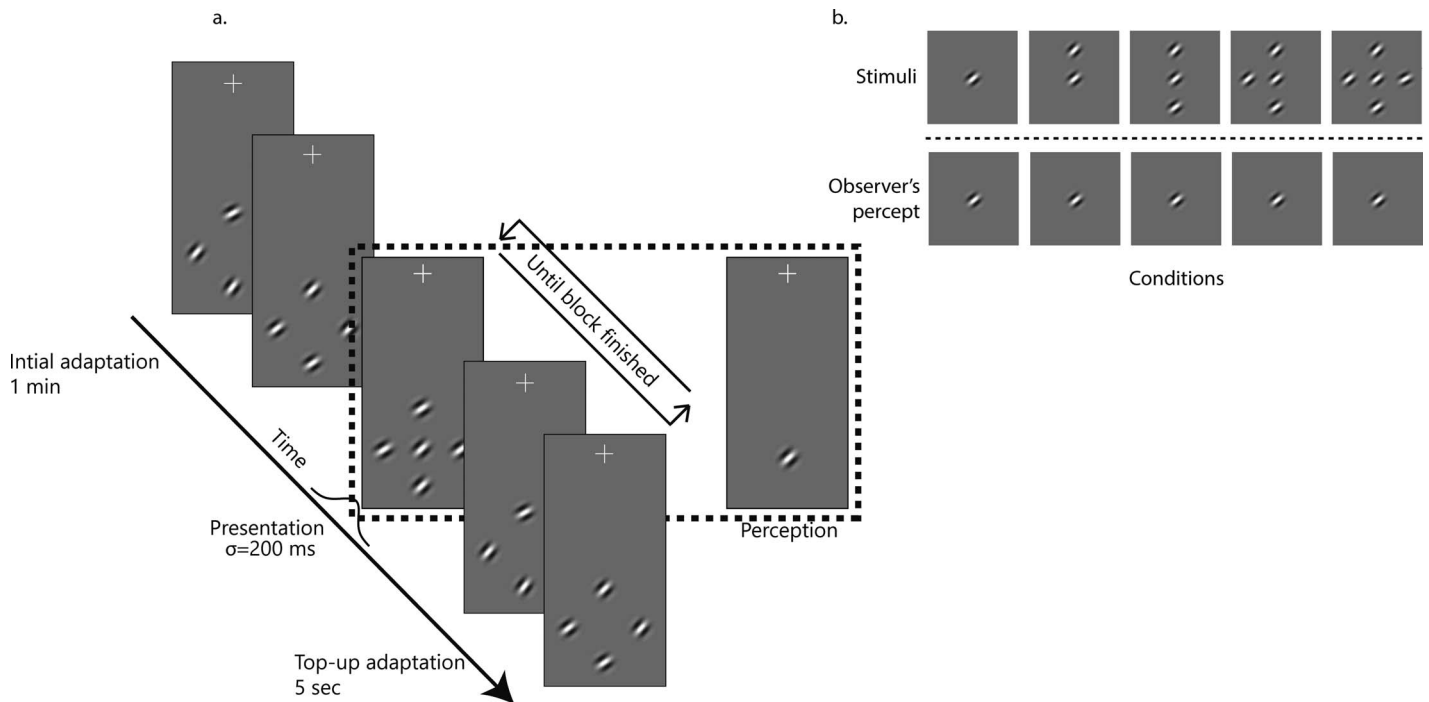


Figure 2. (a) A sample trial of Experiment 2. Eccentricity and center-to-center distance between a target and flankers were the same as for Experiment 1. During adaptation, the adaptors were presented dynamically at the same position as the flankers to induce “blindness” to the flankers. The orientations of adaptors were randomly selected from within  $\pm 4$  times of an individual observer’s orientation threshold relative to  $45^\circ$  and changed every 100 ms. Following adaptation, target and flankers were smoothly ramped on and off following a Gaussian time course with  $\sigma = 200$  ms. After that, observers had to report the orientation of the target (CW or CCW) relative to  $45^\circ$  and the total number of Gabors seen. Each block of 28 trials began with a 1 min initial adaptation, and each trial started with a 5 s top-up adaptation. (b) Conditions used in Experiment 2. The first row depicts the five flanking conditions; the second row depicts an observer’s dominant percept.

each observer. Before the first trial of each block, there was a 1 min adaptation. In addition, a 5 s top-up adaptation was shown before each subsequent trial. Following the top-up adaptation, the target and flankers were simultaneously and smoothly ramped on and off according to a Gaussian temporal profile with a standard deviation of 200 ms, following Wallis & Bex (2011). Adaptors were presented again during the response period to maximize adaptation effects. The 5-s top-up adaptation for the next trial commenced immediately after the observer had responded. As in Experiment 1, observers responded to the perceived orientation (clockwise or counterclockwise relative to  $45^\circ$ ) of the target, as well as the number of perceived Gabors.

### Experiment 3

#### Observers

Four normally sighted volunteers, including the first author, participated in Experiment 3. One observer (the first author) participated in both Experiment 1 and 2, and another participated in Experiment 2.

#### Stimuli

Gaussian-windowed Sloan letters (H, K, N, V, and Z) were used in Experiment 3. The Gaussian window had a standard deviation of  $0.2^\circ$ . Letter size was  $0.6^\circ$  and the letter separation was  $1^\circ$ . Circular gratings were used as suppressors. Unlike the letter flankers, the suppressors were devoid of any sharp edges. This allowed an observer to more easily detect incomplete suppression. The suppressor alternated between shrinking and expanding ( $0.25^\circ/\text{s}$ ) at 1 Hz. Other attributes of the stimuli were identical to those used in Experiment 1.

#### Procedures

Figure 3 shows the timing and stimuli for Experiment 3. The procedures were similar to those of Experiment 1. Each flanking condition, with number of letter flankers ranging from zero to four, was presented for six trials per block. A block consisted of 30 trials. Four blocks were performed in one run, and each observer completed three runs over one or two days. In other words, each observer was tested for a total of 360 trials. Before each run, an observer adjusted the

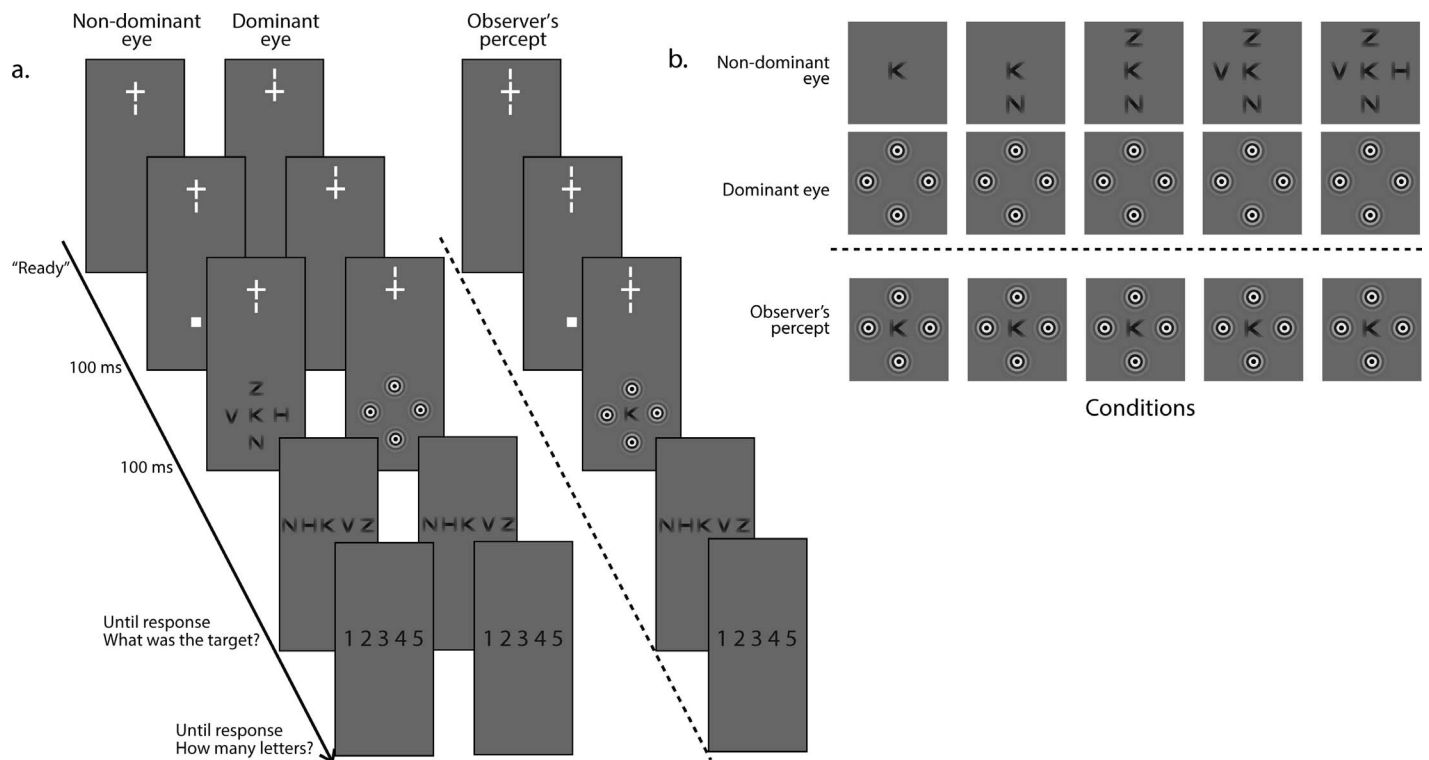


Figure 3. (a) A sample trial of Experiment 3. The left and middle series of images were presented to the nondominant and dominant eyes, respectively. The right series of images indicates an observer's percept. A fixation point and nonius lines were shown to each eye. A small square appeared 100 ms prior to the stimulus to indicate the location of the target ( $5^\circ$  below from the fixation point). Observers had to maintain fixation and vergence state (keeping the nonius lines aligned). 100 ms after the small square disappeared, the target, flankers and suppressors were presented simultaneously for 100 ms. The observer was asked to report the identity of the target and the number of letters seen on screen. (b) Conditions used in Experiment 3. The first row depicts the stimuli associated with the five flanking conditions that were presented to the nondominant eye, the second row depicts the suppressors that were presented to the dominant eye, and the third row indicates an observer's dominant percept.

contrast of the letter target and flankers with a key press such that the flankers became invisible in the presence of the continuous flash suppressors. The contrasts of the target and flankers were always the same. The purpose of this procedure was to find an effective contrast that was high enough for the target to be identifiable for the letter identification task while at the same time not so high that the flankers were not suppressed by the suppressors. If the contrasts of target and flankers were too low, then the flankers would be suppressed effectively; however, at the same time, the target letter would not be identified well. The average selected (Weber) contrast ranged from 0.62 to 1. The primary task of the observers was to identify the target letter by responding with a mouse click on a response screen. The secondary task was to report the total number of letters (target and flankers) perceived.

## Data analysis

We wanted to assess separately the effects of the number of presented and perceived flankers on object

identification performance. However, these two effects are inevitably related to each other because it seems more likely for a participant to miss a presented flanker than to hallucinate a nonexistent flanker. The conventional approach is to hold one effect constant by considering only a subset of trials. For example, to assess if the number of perceived flankers had an effect on performance, Wallis & Bex (2011) used only those trials in which all flankers were presented. This approach is inefficient because it throws away a considerable number of trials under conditions in which one, two, or three flankers were presented.

To fully utilize the data set for each experiment, two mixed-effect logistic regression models were fitted to the data using the lme4.0 package in R (Bates, Mächler, Bolker, & Walker, 2015; R Core Team, 2013). One model was used to examine the effect of the physical number of flankers, and the other to identify the effect of the perceived number of flankers. Each of these models treats the effect of interest as a fixed effect on the slope of the linear model and the effect of no interest as a random effect

on that slope. For example, when we assessed the effect of the number of physically presented flankers on performance, we considered this effect as a slope of the linear model separately for trials in which the participant reported seeing zero, one, two, three, or four flankers. The slopes due to the number of presented flankers are allowed to vary randomly across these five types of trials. We tested against the null hypothesis that these slopes were not significantly different from zero. More specially, in terms of mixed effect models, the model for testing the effect of physical flankers consisted of a fixed effect for the number of flankers presented, and two random effects: by-observer random intercepts and by-perceived-number-of-flankers random slope. We specified this model in R as

```
Physical_model
= glmer(correct ~ presented + (0 + presented|perceived)
  +(1|observer), data = full_data, family
  = binomial(link = "logit"))
```

That is, the linear predictor of the generalized linear model with a logit link function is

$$\eta = (C_i + \beta_1)X_j + \beta_0 + S_k$$

where the  $\beta$ s are the parameter estimates of the fixed effects,  $i, j, k$  index the perceived number of flankers, the presented number of flankers, and the observer, respectively; and  $C, S$  are Gaussian random variables drawn from different distributions, representing the random effects due to the number of perceived flankers and observers, respectively.

Similarly, the model for testing the effect of perceived flankers consisted of a fixed effect for the number of perceived flankers, and two random effects: by-observer random intercepts, and by-presented-number-of-flankers random slope:

```
Perceptual_model
= glmer(correct ~ perceived + (0 + perceived|presented)
  +(1|observer), data = full_data, family
  = binomial(link = "logit"))
```

These mixed effect models are statistically superior to approaches that require the selection of a subset of trials for a given analysis (Baayen, Davidson, & Bates, 2008), such as using only trials with four presented flankers to test for the effect of perceived flankers, as was done in earlier studies (e.g., Wallis & Bex, 2011). For completeness, we also carried out analyses using these earlier methods and showed that the method of analysis did not affect our main conclusion (see Appendix, Figures A2 through A4).

## Results

The purpose of Experiment 1 was to test whether flankers made invisible with interocular suppression (IOS) could lead to crowding. If orientation discrimination is impeded by the invisible flankers, we may conclude that the orientation features of the target and flankers are compulsorily overintegrated, causing crowding, before the stage where IOS impedes flanker visibility. Conversely, if performance of the orientation discrimination task is affected only by the number of subjectively visible flankers, we may conclude that crowding occurs downstream from the locus of IOS.

We found that the accuracy of orientation discrimination decreased significantly with increasing number of physical flankers (Figure 4a; slope:  $\beta = -0.23$ ,  $SE = 0.06$ ,  $z = -4.11$ ,  $p = 3.96e-5$ ), similar to a finding by Pöder (2008). In contrast, we did not find any significant effect due to the perceived number of flankers (Figure 4b; slope:  $\beta = -0.1$ ,  $SE = 0.12$ ,  $z = -0.93$ ,  $p = 0.35$ ). Our finding is that physically presented flankers, regardless of visual awareness, cause crowding, and suggest that crowding occurs upstream from the neural locus of interocular suppression. This pattern of findings is consistent with that of Ho and Cheung (2011) and extends the earlier study by varying the number of flankers.

When we used a different method (AIB) to manipulate flanker visibility, the results were very different. We found that both the presented (physical) and perceived numbers of flankers had a significant effect on target orientation discrimination ( $z = -2.37$ ,  $p = 0.0179$ , Figure 5a;  $z = -5.49$ ,  $p = 4.04e-8$ , Figure 5b; respectively), but the perceived number of flankers had a much stronger effect (slope:  $\beta = -0.08$ ,  $SE = 0.04$  for physical, vs.  $\beta = -0.19$ ,  $SE = 0.03$  for perceived). Regarding the effect of flanker awareness, we replicated the result of Wallis and Bex (2011). Namely, performance (and crowding) depends on the number of perceived flankers. However, whereas Wallis and Bex did not observe any significant effect of the physical number of flankers only, we did. This difference is likely due to the differences in how we tested these effects (Wallis & Bex did not use  $p$  value to test for significance, but instead, bootstrapped the area under their receiver operating characteristic curves for predicting correct/incorrect responses). Indeed, when we applied our analysis to their data, we found that both the number of presented flankers ( $p = 0.0162$ ) and the number of perceived flankers ( $p < 2e-16$ ) had a significant impact on performance (see Appendix, Figure A5). In other words, despite the different stimulus types (letters in Wallis & Bex, Gabors in the current study), the perceived number of flankers had a strong effect on crowding when visual awareness was manipulated with adaptation-induced blindness.



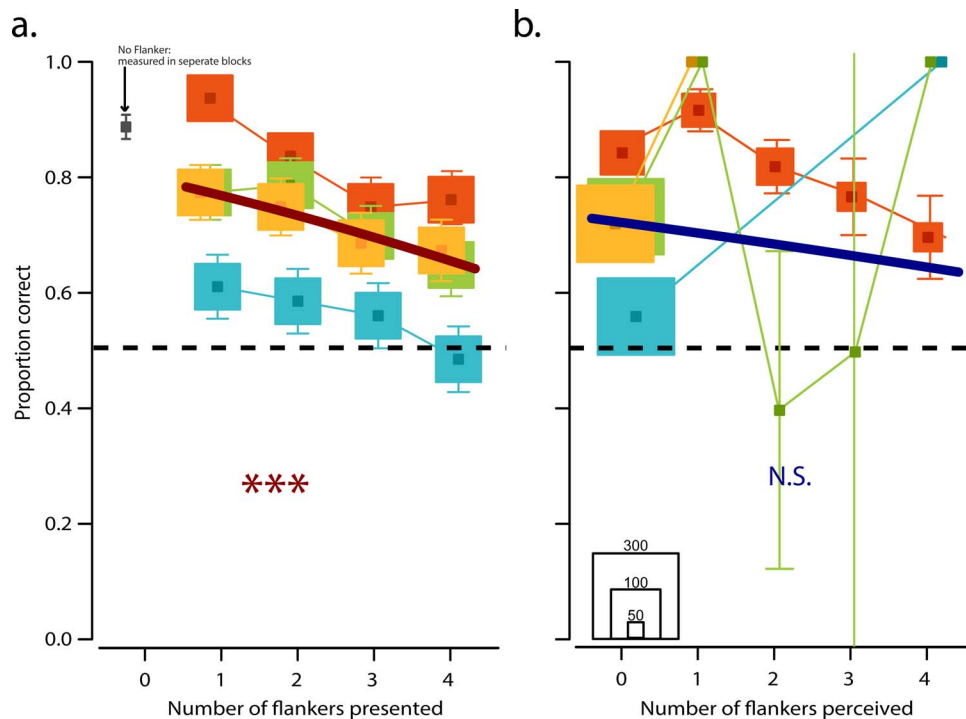


Figure 4. Results of Experiment 1. (a) Accuracy of orientation discrimination as a function of the number of presented flankers. Accuracy decreases with increasing number of presented flankers (thick maroon line,  $p = 3.96e-5$ ). (b) Accuracy of orientation discrimination as a function of the number of perceived flankers. Accuracy does not change significantly with increasing numbers of perceived flankers (thick blue line,  $p = 0.35$ ). The dotted lines indicate chance performance. Different observers' data are represented with different colors. Size of the square symbols shows the number of trials of a given condition for a given observer. Error bars represent standard error.

In Experiment 3, we returned to IOS and tested if, as for AIB, the pattern of results observed with Gabors (narrow in spatial-frequency bandwidth) generalized to letters (broadband). We found that it did. Figure 6 shows the results of Experiment 3. Similar to Experiment 1, we found that letter-identification accuracy decreased with the number of presented (physical) flankers (slope:  $\beta = -0.54$ ,  $SE = 0.08$ ,  $z = -6.97$ ,  $p = 3.08e-12$ , Figure 6a) but was not significantly modulated by the perceived number of flankers (slope:  $\beta = -0.32$ ,  $SE = 0.38$ ,  $z = -0.86$ ,  $p = 0.35$ , Figure 6b). We acknowledge, however, that there was substantial individual observers' variability in the number of perceived flankers, apparently more so than in the two previous experiments. Also, given that there were very few trials in which observers reported perceiving any flankers, a linear fit to the data might not be informative. We shall return to this in the Discussion.

## Discussion

We found that flankers rendered invisible with interocular suppression (IOS) continued to crowd a

target and impede target identification. The number of presented flankers, regardless of whether an observer is aware of them, monotonically affects target identification accuracy. This result appears to be independent of the stimulus type (narrowband Gabors in Experiment 1 or broadband letters in Experiment 3). In contrast, when flankers were made unperceivable by adaptation-induced blindness (AIB), target-discrimination performance depended on the number of perceived flankers, rather than the number of presented flankers. This was the case for Gabors, as shown in Experiment 2 and for letters, as shown in Wallis & Bex (2011). Therefore, it is the method used to manipulate visual awareness that determines whether invisible flankers have any effect on crowding.

These results resolve the apparent conflict in findings between Ho & Cheung (2011) and Wallis and Bex (2011), and attribute their opposing conclusions to the difference in methods used to manipulate visual awareness—Ho & Cheung used IOS, whereas Wallis & Bex used AIB. Whereas these two studies also differed in the stimuli they used, our results show that stimulus class is unlikely to be a factor.

Unlike in Wallis & Bex (2011), we did find a small but significant effect of the number of presented

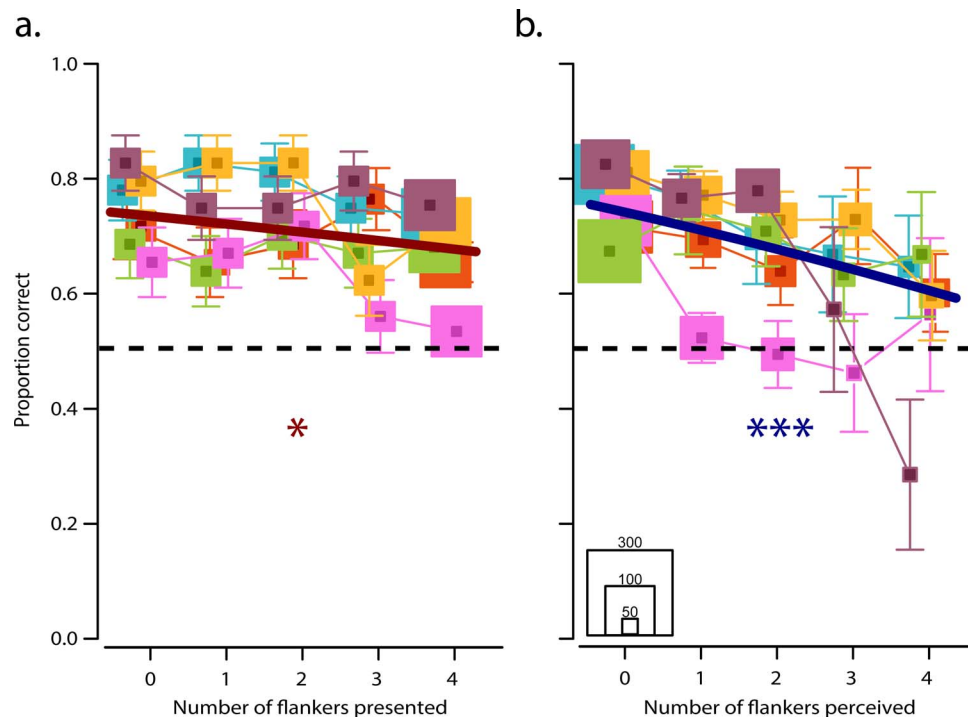


Figure 5. Results of Experiment 2. (a) Accuracy of orientation discrimination as a function of the number of presented flankers. Accuracy decreases with increasing number of presented flankers, but the effect size was small (thick maroon line, slope:  $\beta = -0.08$ ,  $SE = 0.04$ ,  $z = -2.37$ ,  $p = 0.0179$ ). Note that, by design, there were more four-flanker trials than other trial types—see Methods. (b) Accuracy of orientation discrimination as a function of the number of perceived flankers. Accuracy again decreases with increasing number of flankers perceived, but with a much larger effect size (thick blue line,  $\beta = -0.19$ ,  $SE = 0.03$ ,  $z = -5.49$ ,  $p = 4.04e-8$ ). The dotted lines indicate chance performance. Different observers' data are represented with different colors. Size of the square symbols shows the number of trials in a given condition for a given observer. Error bars represent standard error.

flankers on crowding (when controlling for visibility). We attribute this to the more sensitive mixed-effect logistic model that we used. Specifically, we modeled the factor of no interest (e.g., the number of presented flankers in the perceived-number-of-flanker model) as a random effect and thereby increased the sensitivity to the factor of interest (i.e., the number of perceived flanker in the parenthesis example above). We must note that the number of perceived flankers is bounded by the number of presented flankers. There is, therefore, a fundamental limit on any experiment's ability to tease these two apart. We were further limited by our ability to generate sufficient variance in the number of flankers perceived with interocular suppression—the suppression was so strong that in most cases the number of perceived flankers was zero. Therefore, it is entirely possible that our method of using IOS is not the most effective one in examining the effect of perceived flankers in Experiments 1 and 3. Note, however, the suppression was not as effective for one observer in Experiment 1, who demonstrated a downward trend for proportion correct as a function of the number of perceived flankers (Figure 4b), implying that it is likely that we might observe an effect of

perceived flankers if we can render IOS less effective. We also acknowledge that a linear fit to the data in Figures 4b and 6b might not be the most appropriate analysis, but since we used a linear fit to examine the effect of the number of presented flankers, and that the linear fit models the data of presented flankers well, for parsimonious reason, we used the same analysis for the number of perceived flankers. Focusing our attention on the effects due to the number of physically presented flankers avoids these limitations, revealing a distinct, clear result: The number of presented flankers, regardless of awareness, always has an effect on crowding with a strength dependent on how awareness is manipulated.

### Neural loci of crowding, IOS and AIB

Our findings imply that the primary neural locus of crowding is downstream from that of AIB but upstream from that of IOS, if we are to assume that there is a primary locus of crowding and that it does not change across these experiments. By using the same stimuli (Experiment 1 vs. Experiment 2), we have removed stimulus class as a potential confound that is

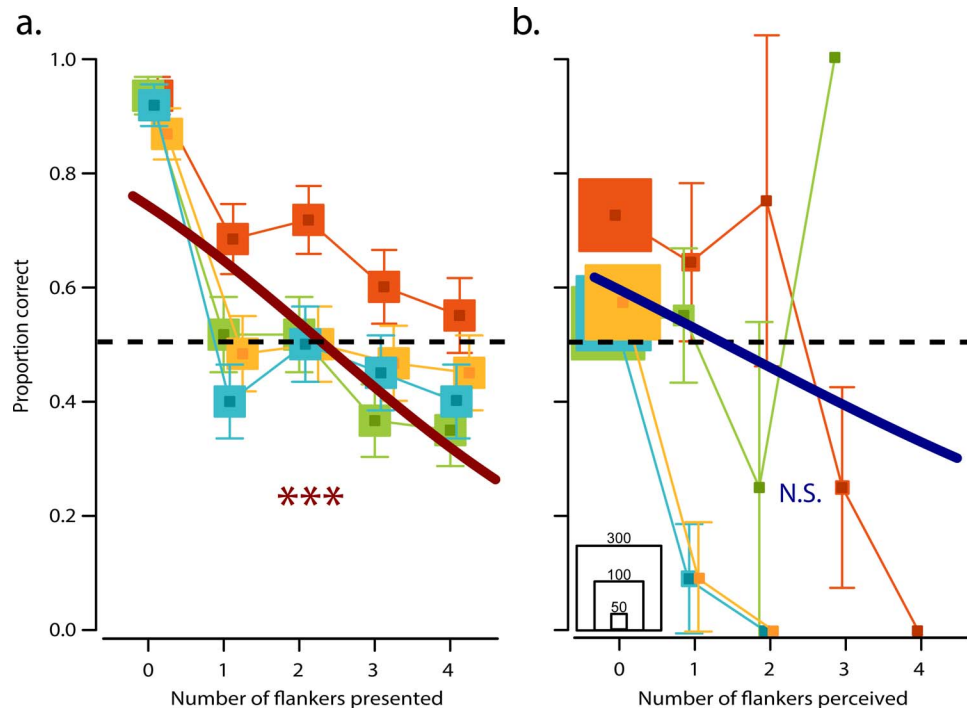


Figure 6. Results of Experiment 3. (a) Accuracy of orientation discrimination as a function of the number of presented flankers. Accuracy decreases with increasing number of presented flankers (thick maroon line,  $p = 3.08 \times 10^{-12}$ ). (b) Accuracy of orientation discrimination as a function of the number of perceived flankers. Accuracy decreased numerically with increasing number of flankers perceived, but the effect is not statistically significant (thick blue line,  $p = 0.35$ ). The dotted lines indicate chance performance. Different observers' data are represented with different colors. Size of the square symbols shows the number of trials of a given condition for a given observer. Error bars represent standard error.

present in the current literature. These results force a re-evaluation of some of the earlier conclusions regarding the loci of crowding, IOS and AIB. Indeed, the neural loci of IOS and AIB are not as clear as once thought.

The neural locus of IOS is unlikely to be in V1 or V2. Whereas IOS was found to reduce the neural activity associated with a target stimulus in V1 (Sengpiel, Baddeley, Freeman, Harrad, & Blakemore, 1998; Sengpiel, Blakemore, & Harrad, 1995; Sengpiel & Blakemore, 1994), the subjective awareness of the target stimulus did not correlate with firing rates, LFP power, or fMRI BOLD response in V1 (Maier et al., 2008; Wilke, Logothetis, & Leopold, 2006). Rather, a strong correlation between the subjective percept under IOS and neural activity was only found in higher visual areas, such as V3a and LOC (Fang & He, 2005; Hesselmann & Malach, 2011). Likewise, in binocular rivalry, a form of interocular suppression, a subjectively suppressed stimulus was found to still evoke neural activity in about 80% of the cells in V1/V2, 60% of cells in V4/MT, and 10% of cells in IT (Leopold & Logothetis, 1996; Logothetis & Schall, 1989; Sheinberg & Logothetis, 1997). In behavioral studies, the lower level features of a stimulus, such as spatial frequency

(Blake & Fox, 1974; Blake et al., 2006), orientation (Wade & Wenderoth, 1978), and color (White, Petry, Riggs, & Miller, 1978) are found to be less affected by binocular rivalry. Taken together, these results suggest that while IOS has a measurable impact on the neural response to a target stimulus in the early stages of visual processing, such as V1 and V2, its impact in these early stages is insufficient to affect a target's percept.

The current study found that flankers subjectively suppressed by IOS continue to cause crowding. Hence, the primary locus of crowding is unlikely to be in the high-level visual areas. Recent studies that found crowding-related fMRI response suppression as early as V1 (Chen et al., 2014; Kwon, Bao, Millin, & Tjan, 2014; Millin, Arman, Chung, & Tjan, 2014) further support this conclusion.

In contrast to IOS, there have been few studies regarding the neural origin of adaptation-induced blindness (AIB). Motoyoshi and Hayakawa (2010) considered the possibility that AIB was due to gain reduction in early visual areas but rejected this as a complete explanation of AIB since they found that an AIB-suppressed target was able to induce a measurable amount of tilt induction and surround suppression. In contrast, Wallis and Bex (2011) showed that AIB-

suppressed flankers did not cause crowding. By using a more sensitive statistical model, the current study has refined the results of Wallis and Bex. We replicated their primary finding that under AIB, crowding is related to the number of perceived flankers. However, we also found that the number of physically presented flankers, after having discounted any effect due to the number of perceived flankers, also has an effect on crowding. In other words, relative to the neural locus of AIB, the neural locus of crowding is more similar to those of tilt induction and surround suppression than the results of Wallis and Bex implied. We speculate that AIB-related crowding would be upstream from the locus of IOS. This idea is broadly consistent with recent studies that adaptation is purely monocular (Cass, Johnson, Bex, & Alais, 2012). Taken together, a low-level locus of crowding is most consistent with the totality of these results. However, inferring the locus of crowding from psychophysical data always involves a lot of assumptions, and can never be very precise. Still, this should not distract us from the real question addressed in this paper—whether visual awareness is a necessity for crowding. Our results clearly showed that the answer is no.

## Conclusion

Visual awareness is not a necessary condition for crowding. Using two classes of stimuli and two paradigms, we showed that crowding of a target may or may not depend on visual awareness of its flanking stimuli, depending on how visual awareness is manipulated. Our results imply that the primary neural locus of crowding is at an earlier stage of visual processing than that of interocular suppression but at a similar or later stage than that of adaptation-induced blindness. These findings are incompatible with theories implicating a high-level origin of crowding.

*Keywords:* visual crowding, object recognition, interocular suppression, adaptation induced blindness, spatial vision

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## Footnote

<sup>1</sup>In Experiment 1, all observers indicated that they could always detect something at the target location, although they might not be able to tell the orientation of that “something.” In Experiment 2, we did not specifically ask observers if they could not detect the target. In Experiment 3, none of the observers reported that they did not see at least one letter on the screen.

## References

- Aghdaee, S. M. (2005). Adaptation to spiral motion in crowding condition. *Perception*, *34*(2), 155–162, doi.org/10.1068/p5298.
- Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language*, *59*(4), 390–412, doi.org/10.1016/j.jml.2007.12.005.
- Balas, B., Nakano, L., & Rosenholtz, R. (2009). A summary-statistic representation in peripheral vision explains visual crowding. *Journal of Vision*, *9*(12):13, 1–18, doi:10.1167/9.12.13. [PubMed] [Article]
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48, doi:10.18637/jss.v067.i01.
- Blake, R. (2001). A primer on binocular rivalry, including current controversies. *Brain and Mind*, *2*(1), 5–38, doi.org/10.1023/A:1017925416289.
- Blake, R., & Fox, R. (1974). Adaptation to invisible gratings and the site of binocular rivalry suppression. *Nature*, *249*(5456), 488–490, doi.org/10.1038/249488a0.
- Blake, R., Tadin, D., Sobel, K. V., Raissian, T. A., & Chong, S. C. (2006). Strength of early visual adaptation depends on visual awareness. *Proceedings of the National Academy of Sciences, USA*,

- 103(12), 4783–4788, doi.org/10.1073/pnas.0509634103.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10(4), 433–436, doi.org/10.1163/156856897X00357.
- Cass, J., Johnson, A., Bex, P. J., & Alais, D. (2012). Orientation-specificity of adaptation: Isotropic adaptation is purely monocular. *PLOS ONE*, 7(11), e47425, doi.org/10.1371/journal.pone.0047425.
- Chakravarthi, R., & Cavanagh, P. (2009). Recovery of a crowded object by masking the flankers: Determining the locus of feature integration. *Journal of Vision*, 9(10):4, 1–9, doi:10.1167/9.10.4. [PubMed] [Article]
- Cham, J., & Cheung, S.-H. (2010). Crowding without visual awareness. *Journal of Vision*, 9(8): 991, doi: 10.1167/9.8.991. [Abstract]
- Chen, J., He, Y., Zhu, Z., Zhou, T., Peng, Y., Zhang, X., & Fang, F. (2014). Attention-dependent early cortical suppression contributes to crowding. *The Journal of Neuroscience*, 34(32), 10465–10474, doi.org/10.1523/JNEUROSCI.1140-14.2014.
- Chung, S. T. L., Levi, D. M., & Legge, G. E. (2001). Spatial-frequency and contrast properties of crowding. *Vision Research*, 41(14), 1833–1850, doi.org/10.1016/S0042-6989(01)00071-2.
- Fang, F., & He, S. (2005). Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nature Neuroscience*, 8(10), 1380–1385, doi.org/10.1038/nn1537.
- Freeman, J., & Simoncelli, E. P. (2011). Metamers of the ventral stream. *Nature Neuroscience*, 14(9), 1195–1201, doi.org/10.1038/nn.2889.
- Haynes, J.-D., Deichmann, R., & Rees, G. (2005). Eye-specific effects of binocular rivalry in the human lateral geniculate nucleus. *Nature*, 438(7067), 496–499, doi.org/10.1038/nature04169.
- He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature*, 383(6598), 334–337, doi.org/10.1038/383334a0.
- Hesslmann, G., & Malach, R. (2011). The link between fMRI-BOLD activation and perceptual awareness is “stream-invariant” in the human visual system. *Cerebral Cortex*, bhr085, doi.org/10.1093/cercor/bhr085.
- Ho, C., & Cheung, S.-H. (2011). Crowding by invisible flankers. *PLOS ONE*, 6(12), e28814, doi.org/10.1371/journal.pone.0028814.
- Kwon, M., Bao, P., Millin, R., & Tjan, B. S. (2014). Radial-tangential anisotropy of crowding in the early visual areas. *Journal of Neurophysiology*, 112(10), 2413–2422, doi.org/10.1152/jn.00476.2014.
- Leopold, D. A., & Logothetis, N. K. (1996). Activity changes in early visual cortex reflect monkeys’ percepts during binocular rivalry. *Nature*, 379(6565), 549–553.
- Levi, D. M. (2008). Crowding—an essential bottleneck for object recognition: A mini-review. *Vision Research*, 48(5), 635–654, doi.org/10.1016/j.visres.2007.12.009.
- Levi, D. M., Hariharan, S., & Klein, S. A. (2002). Suppressive and facilitatory spatial interactions in peripheral vision: Peripheral crowding is neither size invariant nor simple contrast masking. *Journal of Vision*, 2(2):3, 167–177, doi:10.1167/2.2.3. [PubMed] [Article]
- Logothetis, N. K., & Schall, J. D. (1989, Aug). Neuronal correlates of subjective visual perception. *Science*, 245(4919), 761–763.
- Maier, A., Wilke, M., Aura, C., Zhu, C., Ye, F. Q., & Leopold, D. A. (2008). Divergence of fMRI and neural signals in V1 during perceptual suppression in the awake monkey. *Nature Neuroscience*, 11(10), 1193–1200, doi.org/10.1038/nn.2173.
- Millin, R., Arman, A. C., Chung, S. T. L., & Tjan, B. S. (2014). Visual crowding in V1. *Cerebral Cortex*, 24, 3107–3115, doi.org/10.1093/cercor/bht159.
- Motoyoshi, I., & Hayakawa, S. (2010). Adaptation-induced blindness to sluggish stimuli. *Journal of Vision*, 10(2):16, 1–8, doi:10.1167/10.2.16. [PubMed] [Article]
- Moutoussis, K., & Zeki, S. (2006). Seeing invisible motion: A human fMRI study. *Current Biology*, 16(6), 574–579, doi.org/10.1016/j.cub.2006.01.062.
- Nandy, A. S., & Tjan, B. S. (2007). The nature of letter crowding as revealed by first- and second-order classification images. *Journal of Vision*, 7(2):5, 1–26, doi:10.1167/7.2.5. [PubMed] [Article]
- Nandy, A. S., & Tjan, B. S. (2012). Saccade-confounded image statistics explain visual crowding. *Nature Neuroscience*, 15(3), 463–469, doi.org/10.1038/nn.3021.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442, doi.org/10.1163/156856897X00366.
- Pelli, D. G., Palomares, M., & Majaj, N. J. (2004). Crowding is unlike ordinary masking: Distinguishing feature integration from detection. *Journal of Vision*, 4(12):12, 1136–1169, doi:10.1167/4.12.12. [PubMed] [Article]
- Pelli, D. G., & Tillman, K. A. (2008). The uncrowded

- window of object recognition. *Nature Neuroscience*, *11*(10), 1129–1135, doi.org/10.1038/nn.2187.
- Pelli, D. G., & Zhang, L. (1991). Accurate control of contrast on microcomputer displays. *Vision Research*, *31*(7–8), 1337–1350, doi.org/10.1016/0042-6989(91)90055-A.
- Pöder, E. (2008). Crowding with detection and coarse discrimination of simple visual features. *Journal of Vision*, *8*(4):24, 1–6, doi:10.1167/8.4.24. [PubMed] [Article]
- Polonsky, A., Blake, R., Braun, J., & Heeger, D. J. (2000). Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nature Neuroscience*, *3*(11), 1153–1159, doi.org/10.1038/80676.
- R Development Core Team. (2013). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available at <http://www.R-project.org>
- Rajimehr, R., Vaziri-Pashkam, M., Afraz, S.-R., & Esteky, H. (2004). Adaptation to apparent motion in crowding condition. *Vision Research*, *44*(9), 925–931, doi.org/10.1016/j.visres.2003.11.020.
- Roth, H. L., Lora, A. N., & Heilman, K. M. (2002). Effects of monocular viewing and eye dominance on spatial attention. *Brain*, *125*(9), 2023–2035, doi.org/10.1093/brain/awf210.
- Sengpiel, F., Baddeley, R. J., Freeman, T. C. B., Harrad, R., & Blakemore, C. (1998). Different mechanisms underlie three inhibitory phenomena in cat area 17. *Vision Research*, *38*(14), 2067–2080, doi.org/10.1016/S0042-6989(97)00413-6.
- Sengpiel, F., & Blakemore, C. (1994). Interocular control of neuronal responsiveness in cat visual cortex. *Nature*, *368*(6474), 847–850, doi.org/10.1038/368847a0.
- Sengpiel, F., Blakemore, C., & Harrad, R. (1995). Interocular suppression in the primary visual cortex: A possible neural basis of binocular rivalry. *Vision Research*, *35*(2), 179–195, doi.org/10.1016/0042-6989(94)00125-6.
- Sheinberg, D. L., & Logothetis, N. K. (1997). The role of temporal cortical areas in perceptual organization. *Proceedings of the National Academy of Sciences, USA*, *94*(7), 3408–3413.
- Tong, F., & Engel, S. A. (2001). Interocular rivalry revealed in the human cortical blind-spot representation. *Nature*, *411*(6834), 195–199, doi.org/10.1038/35075583.
- Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, *8*(8), 1096–1101, doi.org/10.1038/nn1500.
- Veenemans, A., Cavanagh, P., & Chakravarthi, R. (2009). Crowding by invisible flankers. *Journal of Vision*, *9*(8): 996, doi:10.1167/9.8.996. [Abstract]
- Wade, N. J., & Wenderoth, P. (1978). The influence of colour and contour rivalry on the magnitude of the tilt after-effect. *Vision Research*, *18*(7), 827–835, doi.org/10.1016/0042-6989(78)90123-2.
- Wallis, T. S. A., & Bex, P. J. (2011). Visual Crowding Is Correlated with Awareness. *Current Biology*, *21*(3), 254–258, doi.org/10.1016/j.cub.2011.01.011.
- White, K. D., Petry, H. M., Riggs, L. A. L., & Miller, J. (1978). Binocular interactions during establishment of McCollough effects. *Vision Research*, *18*(9), 1201–1215, doi.org/10.1016/0042-6989(78)90105-0.
- Whitney, D., & Levi, D. M. (2011). Visual crowding: A fundamental limit on conscious perception and object recognition. *Trends in Cognitive Sciences*, *15*(4), 160–168, doi.org/10.1016/j.tics.2011.02.005
- Wilke, M., Logothetis, N. K., & Leopold, D. A. (2006). Local field potential reflects perceptual suppression in monkey visual cortex. *Proceedings of the National Academy of Sciences, USA*, *103*(46), 17507–17512, doi.org/10.1073/pnas.0604673103.
- Wolfe, J. M. (1984). Reversing ocular dominance and suppression in a single flash. *Vision Research*, *24*(5), 471–478, doi.org/10.1016/0042-6989(84)90044-0.
- Wunderlich, K., Schneider, K. A., & Kastner, S. (2005). Neural correlates of binocular rivalry in the human lateral geniculate nucleus. *Nature Neuroscience*, *8*(11), 1595–1602, doi.org/10.1038/nn1554.

## Appendix

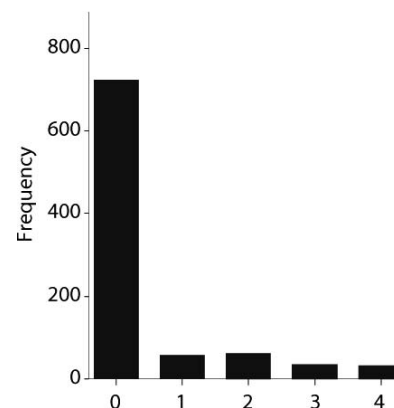


Figure A1. Frequency of the number of perceived flankers in Experiment 1. Observer perceived no flankers in a majority of the trials, despite the fact that one or more flankers were always present in a trial.

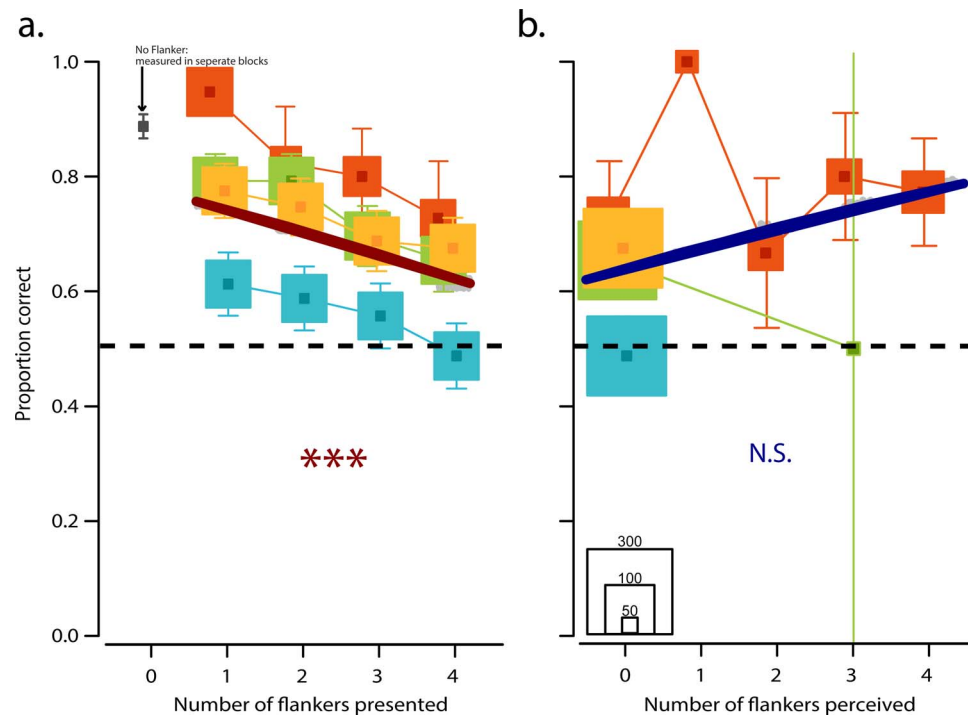


Figure A2. Reanalysis of Experiment 1 using partial data sets as in Wallis and Bex (2011). (a) Accuracy of orientation discrimination as a function of the number of presented flankers, for trials when observers did not report seeing any flankers. Accuracy decreases with increasing number of presented flankers (thick maroon line, slope:  $\beta = -0.22$ ,  $SE = 0.06$ ,  $z = -4.024$ ,  $p = 5.71e-05$ ). (b) Accuracy of orientation discrimination as a function of the number of perceived flankers, for trials when the number of presented flankers was four. Accuracy does not change significantly with the number of perceived flankers (thick blue line,  $\beta = 0.21$ ,  $SE = 0.11$ ,  $z = 1.92$ ,  $p = 0.055$ ). The dotted lines indicate chance performance. Error bars represent standard error. Size of the square symbols shows the number of trials of a given condition for a given observer. Different observers' data are represented with different colors. Fitted lines were generated from the logistic models:

(a) `Physical_model = glm(correct ~ presented, data = trials_with_0_perceived_flankers, family = binomial(link = "logit"))`

(b) `Perceptual_model = glm(correct ~ perceived, data = trials_with_4_flankers, family = binomial(link = "logit"))`

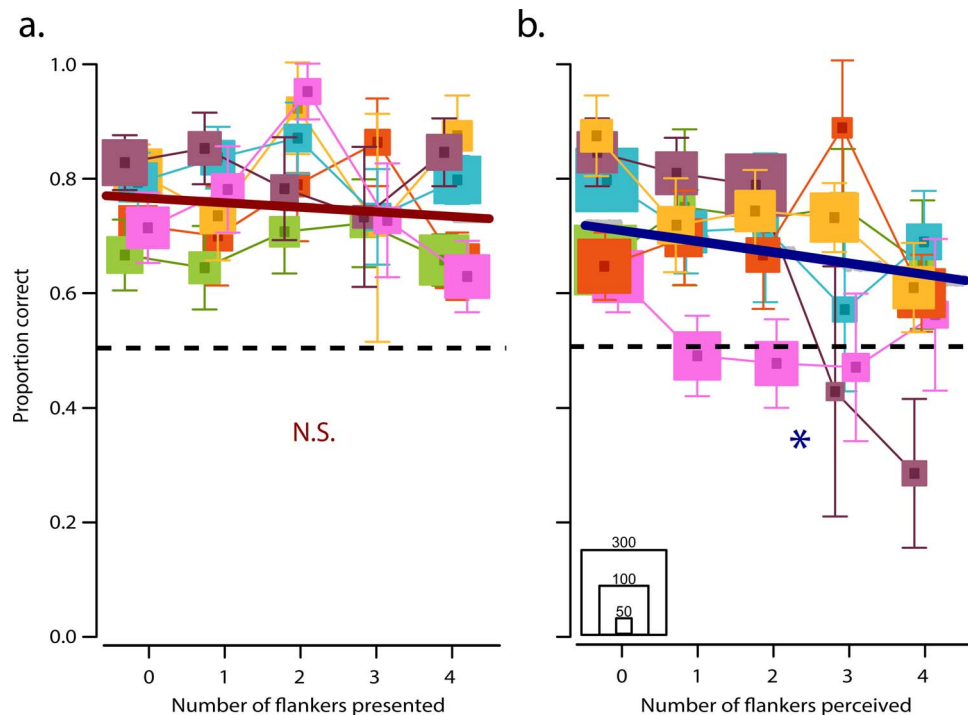


Figure A3. Reanalysis of Experiment 2 using partial data sets as in Wallis and Bex (2011). (a) Accuracy of orientation discrimination as a function of the number of presented flankers using only trials when an observer did not report seeing any flankers. Accuracy does not change significantly with the number of presented flankers (thick maroon line, slope:  $\beta = -0.05$ ,  $SE = 0.04$ ,  $z = -1.358$ ,  $p = 0.174$ ). (b) Accuracy of orientation discrimination as a function of the number of perceived flankers using only trials where the number of presented flankers was four. Accuracy decreases with increasing number of the perceived flankers (thick blue line,  $\beta = -0.11$ ,  $SE = 0.04$ ,  $z = -2.51$ ,  $p = 0.012$ ). The dotted lines indicate chance performance. Error bars represent standard error. Size of the square symbols shows the number of trials of a given condition for a given observer. Different observers' data are represented with different colors. Fitted lines were generated from the logistic models:

(a) `Physical_model = glm(correct ~ presented, data = trials_with_0_perceived_flankers, family = binomial(link = "logit"))`

(b) `Perceptual_model = glm(correct ~ perceived, data = trials_with_4_flankers, family = binomial(link = "logit"))`



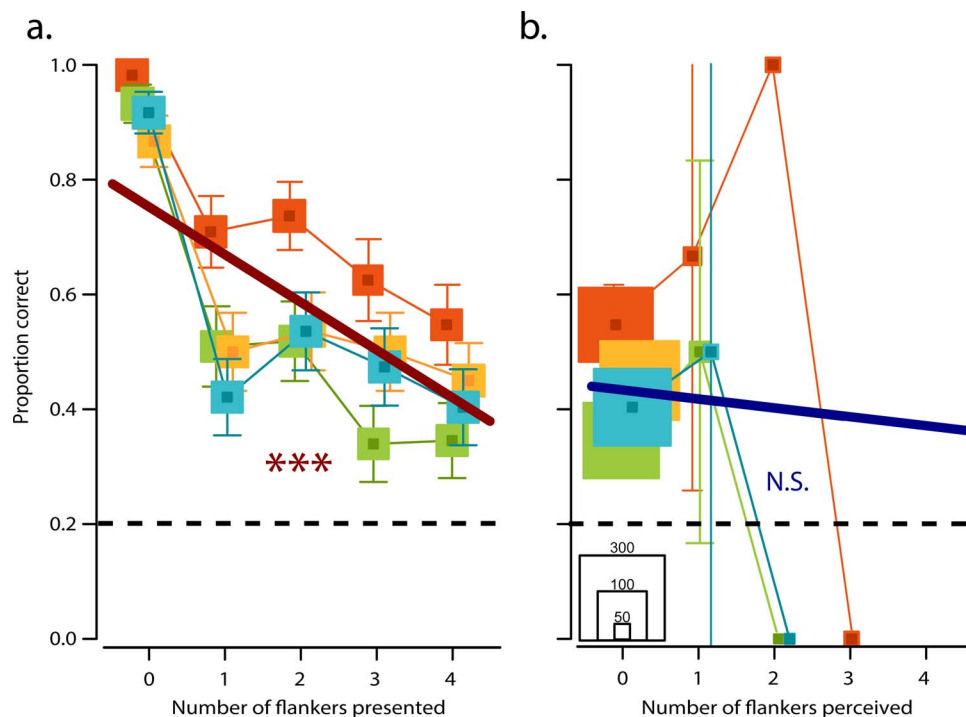


Figure A4. Reanalysis of Experiment 3 using partial data sets as in Wallis and Bex (2011). (a) Accuracy of orientation discrimination as a function of the number of presented flankers, using data from trials when an observer reported seeing no flankers. Accuracy decreases with increasing number of the presented flankers (thick maroon line, slope:  $\beta = -0.43$ ,  $SE = 0.04$ ,  $z = -9.671$ ,  $p < 2e-16$ ). (b) Accuracy of orientation discrimination as a function of the number of perceived flankers, using data from trials when the presented number of flankers was four. Accuracy does not change significantly with the number of perceived flankers (thick blue line,  $\beta = -0.11$ ,  $SE = 0.32$ ,  $z = -0.34$ ,  $p = 0.738$ ). The dotted lines indicate chance performance. Error bars represent standard error. Size of the square symbols shows the number of trials of a given condition for a given observer. Different observers' data are represented with different colors. Fitted lines were generated from the logistic models:

(a) `Physical_model = glm(correct ~ presented, data = trials_with_0_perceived_flankers, family = binomial(link = "logit"))`

(b) `Perceptual_model = glm(correct ~ perceived, data = trials_with_4_flankers, family = binomial(link = "logit"))`

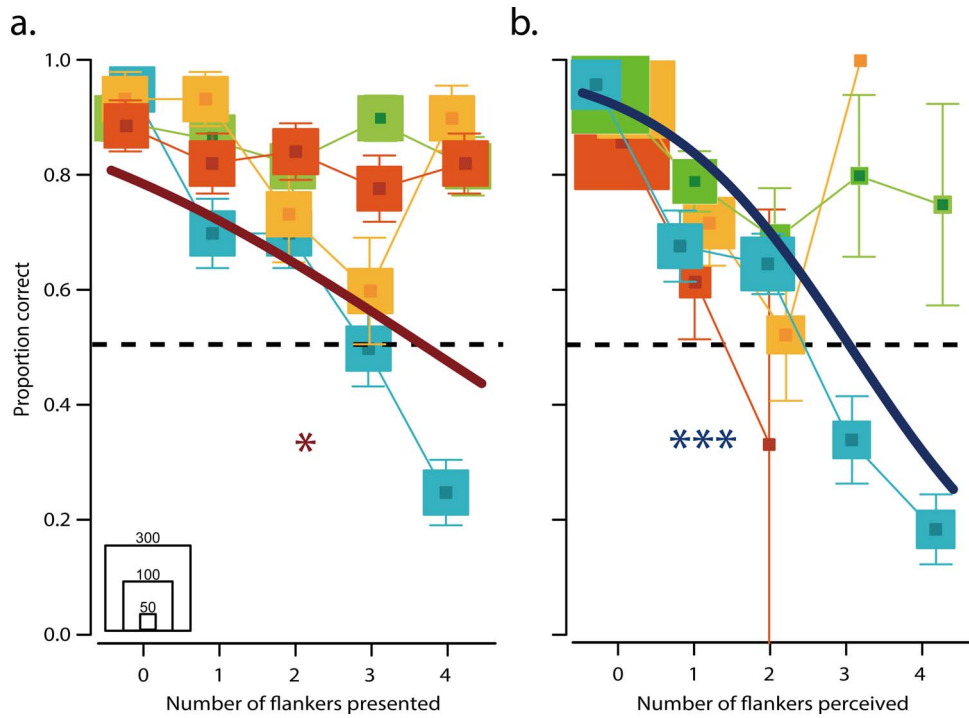


Figure A5. Reanalysis of data in Wallis and Bex (2011) using our statistical model. In their paper, using a different analysis, Wallis and Bex reported performance (or crowding) depended only on the number of perceived flankers, but not on the number of presented flankers. Applying our analysis on their data, we found that both the number of presented flankers ( $p = 0.0162$ ) and the number of perceived flankers ( $p < 2e-16$ ) had significant effects on performance.