The chromatic selectivity of visual crowding

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Precortical vision is mediated by three opponent mechanisms that combine receptoral outputs to form a luminance channel (L + M) and two chromatic channels, red–green (L/M) and blue–yellow (S/L + M). Here we ask the extent to which these basic color opponent mechanisms interact in the phenomenon of crowding, where nearby targets interfere with the processing of a central test target. The task was to identify the orientation of a Gabor patch while an annular plaid surrounded the patch. The radius of the annulus was varied in order to produce different separations of the test and flanker. The chromatic content of the Gabor and the annulus could be varied independently along the (L + M), (L/M), and (S/L + M) cardinal axes. For all targets, when the target and flanker shared the same chromaticity, performance decreased with decreasing separation of the target and annulus, i.e., a typical crowding effect was seen. When the test and flanker isolated different chromatic mechanisms, very little crowding was observed, even at the minimum separation of test target and annulus. In addition to this, intermediate chromaticities were found to produce intermediate levels of crowding. Finally, crowding effects using "half-wave rectified" stimuli suggest a locus for crowding effects beyond the level of color opponent mechanisms.

Keywords: crowding, color vision, spatial vision

Introduction

It is generally accepted that precortical vision is mediated by three opponent mechanisms that linearly combine the outputs of retinal photoreceptors to form a luminance channel (L + M) and two chromatic channels, red–green (L/M) and blue–yellow (S/L + M; Derrington, Krauskopf, & Lennie, 1984; De Valois, Abramov, & Jacobs, 1966). Subsequently, these basic color opponent mechanisms are thought to undergo considerable cortical reorganization in order to form multiple "higher order" mechanisms tuned to a variety of axes in color space (Lennie, Krauskopf, & Sclar, 1990).

It was originally believed that the achromatic luminance channel provides the basis for the perception of spatial form, while the chromatic mechanisms drive color perception (Livingstone & Hubel, 1988, 1987). More recently, this notion has been challenged and there is now a good deal of evidence that chromatic mechanisms are also able to support form vision. For example, studies using isoluminant chromatic stimuli have shown that the chromatic and achromatic mechanisms can perform similarly in tasks such as contour integration (McIlhagga & Mullen, 1996; Mullen, Beaudot, & McIlhagga, 2000), discrimination of radial frequency patterns (Mullen & Beaudot, 2002), and detection of spatial form in Glass patterns (Wilson & Switkes, 2005).

What is much less clear is the degree to which the achromatic and chromatic opponent mechanisms may interact in the processing of spatial information. For example, it has been shown that a luminance pedestal can enhance sensitivity to a chromatic test pattern, and vice versa (Cole, Stromeyer, & Kronauer, 1990; Gowdy, Stromeyer, & Kronauer, 1999). In contrast to this, Huang, Mullen, and Hess (2007) have reported that collinear facilitation, where detection of a central Gabor patch is facilitated by two aligned flanking Gabors, does not occur when the central target and flanks differ in their chromatic properties. Similar results have been found in studies of contour integration, where the ability to link together local elements is significantly impaired when alternate elements have different chromaticities (McIlhagga & Mullen, 1996; Mullen et al., 2000). In the present study, we ask the extent to which the basic color opponent mechanisms interact in the phenomenon of visual crowding.

Crowding refers to the detrimental effect that nearby or "flanking" objects have on the spatial processing of a test object (for a review, see Levi, 2008). Crowding appears to be a pervasive feature of vision, with crowding effects having been demonstrated for many tasks, including visual acuity (Bouma, 1970; Flom, Weymouth, & Kahneman, 1963), vernier acuity (Levi & Klein, 1985; Malania, Herzog, & Westheimer, 2007), orientation discrimination (Andriessen & Bouma, 1976; Westheimer, Shimamura, & McKee, 1976), hue discrimination (van den Berg,

Roerdink, & Cornelissen, 2007), and face recognition (Louie, Bressler, & Whitney, 2007). Both the strength and the extent of crowding are greater in the periphery compared to foveal vision (Toet & Levi, 1992), with the general "Bouma law" (Bouma, 1970; Pelli & Tillman, 2008) stating that the critical center-to-center spacing between target and flanker, beyond which there is no crowding, is approximately half the eccentricity.

The effect of stimulus color on crowding effects has been investigated to some extent previously. For example, it has been demonstrated that crowding can occur for chromatically defined targets, with crowding extents being similar to those for luminance stimuli (Tripathy & Cavanagh, 2002). Additionally, Põder (2007) found reduced crowding for a red target surrounded by black flankers compared to when both target and flankers were black. Gheri, Morgan, and Solomon (2007) also found that orientation acuity for elongated Gaussian blobs embedded in distractors was better when the surrounding blobs differed in color from the target. However, these kinds of "pop-out" effects are perhaps just one aspect of a general finding that crowding is diminished when the test and flanking objects are dissimilar in some respect (e.g., color, contrast polarity, shape, or depth; Kooi, Toet, Tripathy, & Levi, 1994). To date, there has been no systematic study of how crowding is affected when the chromatic content of the stimuli is controlled in order to isolate individual opponent mechanisms. Here we sought to investigate the degree of interaction between achromatic and chromatic mechanisms by measuring the strength of crowding that occurs when the chromatic content of the test and flanking stimuli are varied independently. To anticipate, we found that maximum crowding occurs when the target and flankers share a common chromatic axis and that very little crowding is observed when the test and flanking stimuli isolate different chromatic mechanisms.

Methods

Stimuli

In all experiments, the test stimulus was an achromatic or an isoluminant chromatic Gabor patch (Figure 1), tilted either clockwise or counterclockwise from vertical by 45°. The mathematical description of the clockwise Gabor element of such a stimulus is

$$\text{Luminance} = L + \exp\left(-\frac{x^2 + y^2}{2\sigma^2}\right)LC\sin\left(\sqrt{2}\pi f(x+y)\right) \tag{1}$$

while that of the counterclockwise element is

$$\text{Luminance} = L + \exp\left(-\frac{x^2 + y^2}{2\sigma^2}\right)LC\sin\left(\sqrt{2}\pi f(x-y)\right) \tag{2}$$

In Equations 1 and 2, x and y are, respectively, the horizontal and vertical distances from the center of the stimulus, L is the mean luminance (41 cd m^{-2}), C is the stimulus contrast (see below), f is the spatial frequency of the carrier grating (2 c deg^{-1}), and σ is the standard deviation of the Gaussian envelope (0.54°). The chromatic content of the test Gabors could be varied along the (L + M), (L/M), and (S/L + M) cardinal axes in MBDKL color space (Figure 1), in order to isolate one of the post-receptoral opponent mechanisms (Derrington et al., 1984; MacLeod & Boynton, 1979). The achromatic stimuli were defined in terms of their Michelson contrast. The contrast of the chromatic stimuli, which shared the same mean luminance and mean chromaticity as the achromatic stimuli, was defined as the proportion of maximum modulation available along the (L/M) and (S/L + M) color axes.

Before carrying out Experiment 1, test stimuli with differing chromaticities were equated for visibility for each observer in the following way. The contrast of the blue–yellow (S/L + M) stimulus was set to its maximum value and performance for identifying the orientation of this stimulus, when presented in isolation, was measured using exactly the same procedure outlined below for the "flanked" experiments. For all observers, performance was close to 95% correct (see dashed lines in Figure 4). Next, performance was measured for achromatic (L + M) and red–green (L/M) Gabor patches, over a range of contrasts (0.05–0.10 for L + M and 0.50–0.80 for L/M) and a plot was made of percent correct responses against stimulus contrast. These data were then fitted with a logistic function of the form

$$\% \text{ correct} = 50 + \frac{50}{1 + e^{-\frac{(C-\mu)}{\theta}}} \tag{3}$$

where μ is the contrast resulting in 75% correct on the two-alternative forced choice task and θ is a measure of the steepness of the psychometric function. The parameters of this curve fit were used to calculate the contrast of (L + M) and (L/M) stimuli that would yield the same performance level as that determined initially for the (S/L + M) Gabors (i.e., close to 95%). These values were then used to equate the contrast of the stimuli for use in Experiment 1.

In all experiments (except for one control experiment, see Figure 5), the test Gabor patches were surrounded by an annular plaid (Figure 2). The plaid represented the

Figure 1. Test stimuli were tilted Gabor patches, the chromatic content of which could vary along the (L + M), (L/M), or (S/L + M) chromatic axes.

mean of the clockwise and counterclockwise gratings defining the central Gabor patch, i.e.,

$$\text{Luminance} = L + \Big(LC \Big(\sin\big(\sqrt{2}\pi f(x + y) + \pi \big) \\ + \sin\big(\sqrt{2}\pi f(x - y) + \pi \big) \Big)/2 \Big) \quad (4)$$

The inclusion of the phase offset π reduces contour linking between the central carrier and the surround plaid. This plaid was windowed by a uniform annulus that had a width of 1.62°. The radius of this annulus could be varied (Figure 2), altering the proximity of the annulus to the test target. Proximity was defined as the center-to-center spacing between the test patch and the annulus, as indicated by r in Figure 2. Crucially, the chromatic content of the annular plaid could be varied independently of that of the test target. This means that the test and flanker could share the same chromaticity (Figure 3, left) or could have different chromaticities (Figure 3, center and right).

Procedure

All experiments were carried out using the method of single stimuli, with a binary classification design. On each trial, the task for observers was to identify the orientation of the central Gabor patch as being either clockwise or counterclockwise of vertical, in the presence of the flanking annulus. Various combinations of test patch/flanking annulus chromaticity were tested at various separations of test and flanker. Viewing was monocular with the right eye, and except in Experiment 2 where eccentricity was varied, all stimuli were presented at an eccentricity of 10° in the nasal visual field, in order to avoid the physiological blind spot. Eccentricity was defined relative to the center of the Gabor test patch. A small dark fixation mark was present on the screen throughout each block of trials and observers were encouraged to maintain fixation on this. At the end of each trial, observers indicated their response by pressing one of two keys on a keyboard, which, in turn, started the next trial. The time between making a response and the appearance of the subsequent stimulus was 250 ms, and

Figure 2. The Gabor test patches were surrounded by an annular plaid. Reducing the radius of this annulus (i.e., decreasing r) increases the proximity of the test stimulus to the annulus.

Figure 3. The chromatic content of the central Gabor patch and the annular plaid could be varied independently of one another. Thus, the two could share the same chromaticity (left) or could have different chromaticities (center and right). Various combinations of test patch/flanker chromaticity were tested.

stimuli were presented for 500 ms. Four blocks, each of 100 trials, were carried out at each separation of test patch/flanking annulus for each combination of test/flanker chromaticity. Results for each observer were expressed in terms of percentage of correct responses.

Apparatus

Stimuli were generated on an Apple PowerMac G4 computer using the macro capabilities of NIH Image (version 1.61) and were displayed on an Apple LCD Cinema Display. The display subtended $51° \times 35°$ at the viewing distance of 50 cm, which was maintained by a chin rest. At this distance, each pixel subtended 2′ arc. All stimuli were calibrated with a Photo Research PR650 spectral photometer.

Observers

The two authors, along with two observers who were naive as to the purpose of the study, participated in the experiments. All were experienced psychophysical observers and all had normal or corrected-to-normal vision and normal color vision.

Results

Experiment 1: Modification of chromaticity along cardinal axes

In Experiment 1, the chromaticity of the test Gabor and flanking annulus were varied, independently of one another, along one of three cardinal axes. All possible combinations of test/flanker chromaticity were tested.

Plots of percent correct responses against separation of test target and annulus are shown for each observer in Figure 4. Note that the abscissa is reversed, i.e., separation decreases from left to right. Performance for Gabor targets presented in isolation is indicated by the dashed lines marked "unflanked" and is close to 95% correct for all observers. In Figure 4a, data are shown for achromatic luminance targets. Here, when the flanking annulus is also achromatic (black squares and line), a typical crowding effect is seen, i.e., performance reduces significantly with decreasing separation of the test target and annulus (for observer JH, performance is reduced even at the largest separation). However, when the chromatic content of the annular plaid is modulated along either the L/M (red–green, indicated by red symbols) or S/L + M (blue–yellow, blue symbols) chromatic axes, much less crowding is seen, even at the smallest separation of test target and surrounding annulus.

A broadly similar pattern of results is seen for red–green (Figure 4b) and blue–yellow (Figure 4c) chromatic targets. In each case, the reduction in performance with decreasing separation of the test target and flanking annulus is significantly greater when they share a common chromatic axis, compared to when they differ in chromaticity. A 3-factor repeated measures ANOVA confirmed these basic observations. Crowding effects were consistent across the three test chromaticities as demonstrated by the non-significant contribution of test chromaticity as a factor ($F(2,4) = 1.452$, $p > 0.05$). In comparison, crowding was highly dependent upon whether the test and surround were the same or different chromaticity ($F(1,2) = 39.99$, $p = 0.024$). Surround proximity was highly significant ($F(2,4) = 111.8$, $p = 0.0003$), and importantly, there was a significant interaction between proximity and test/surround similarity ($F(2,4) = 21.4$, $p = 0.0073$). This latter interaction supports the observation that the magnitude of crowding is greatest at close surround proximities and when the test and surround share the same chromaticity. It is worth noting, however, that in the majority of cases
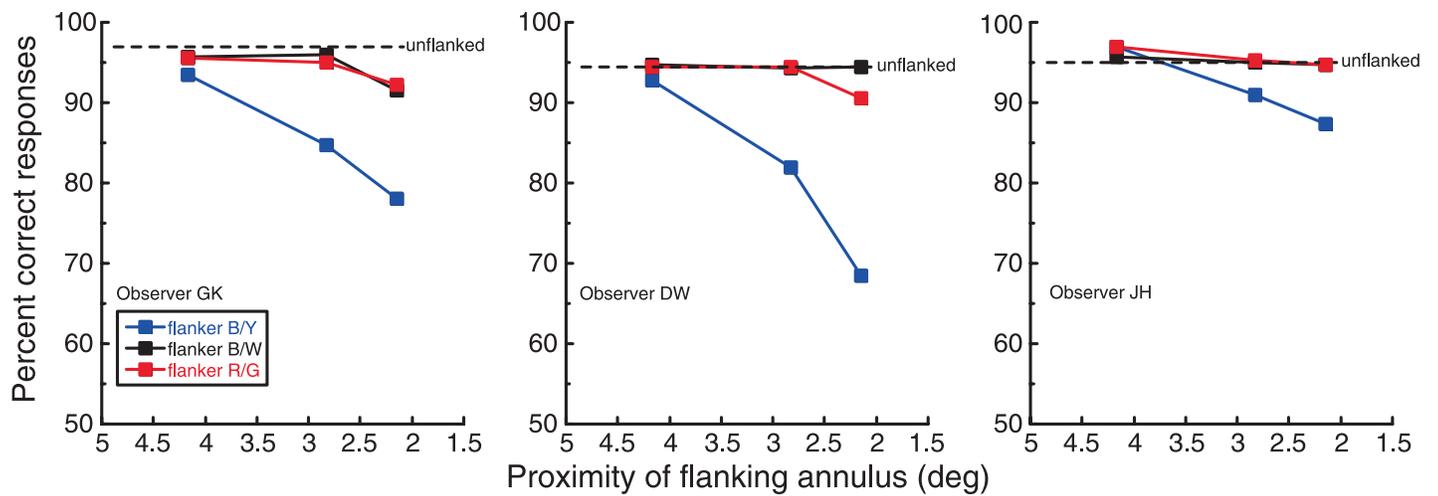
a) Black/White tartgets
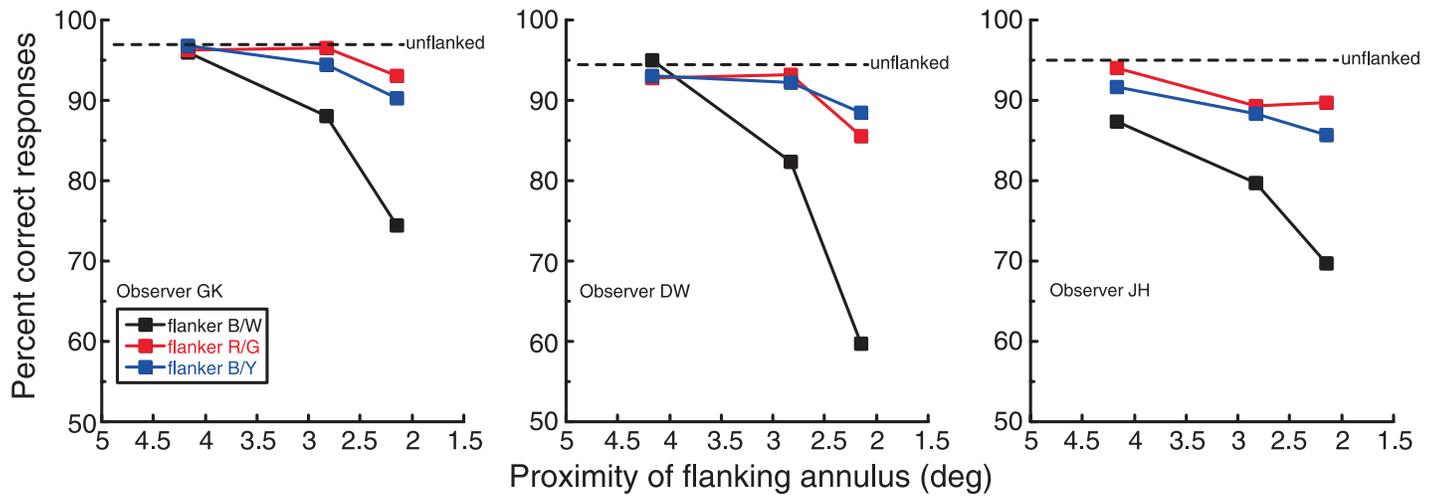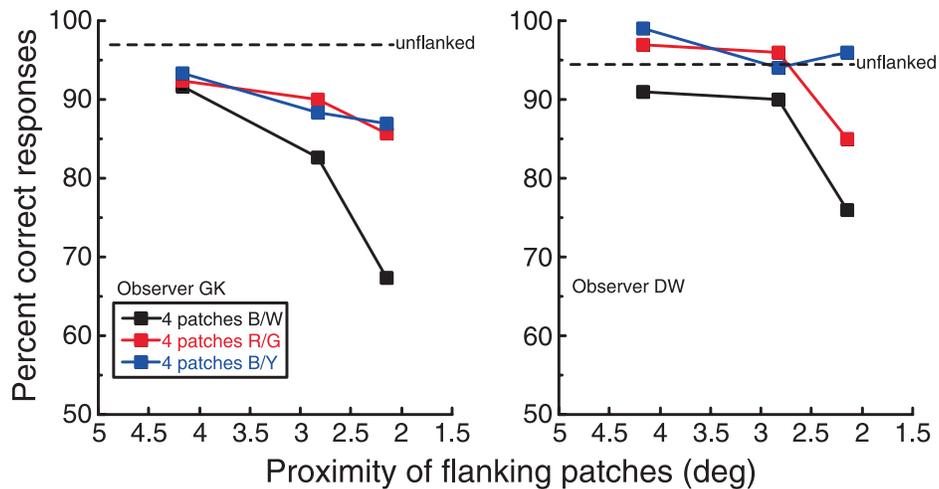

b) Red/Green targets
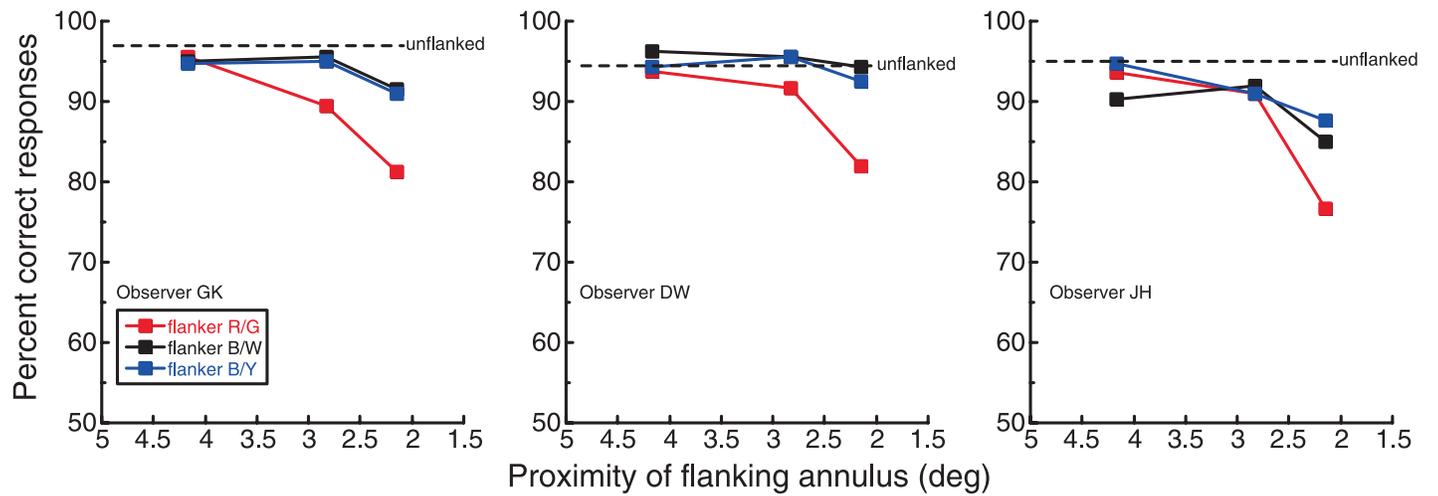
c) Blue/Yellow targets

Figure 5. Discrete flankers. Part of Experiment 1 was repeated (achromatic test patches, with achromatic, red–green and blue–yellow crowders), replacing the flanking annulus with 4 discrete patches. When compared to Figure 4a, the data for the two observers tested show a similar pattern, both qualitatively and quantitatively.

where the test and flanking stimuli had differing chromatic content, the presence of the annulus still caused some reduction in performance, at least at the smallest separation.

There is evidence in the literature that somewhat different crowding effects may be expected when using an annulus when compared to using discrete flankers, with an annulus having been shown to be less potent as a crowding stimulus (Levi & Carney, 2009; Mareschal, Morgan, & Solomon, 2008). In order to ensure that the small amount of cross-chromaticity crowding shown in Figure 4 is not simply an effect of using an annulus, we repeated part of Experiment 1 for two observers, replacing the surrounding annulus with 4 discrete flanking "patches" (plaids), positioned above, below, left, and right of the test patch. The diameter of each flanking patch was chosen to be the same as the width of the annulus (see Stimuli section) and proximity was again defined as the center-to-center spacing between the test and flankers. Achromatic test Gabors were surrounded by achromatic, red–green and blue–yellow flankers. Plots of the data are shown in

Figure 4. Plots of percent correct responses against separation of test target and flanking annulus are shown for various combinations of target/flanker chromaticity for each observer. Performance for unflanked Gabor targets presented in isolation is indicated by the dashed lines. The data in (a) are for achromatic test targets. When the flanking stimulus is also achromatic (black squares and line), performance reduces significantly with decreasing separation of test and flanker, i.e., a typical crowding effect is seen. When the annulus has a different chromaticity (red and blue symbols), little crowding is seen, even at the smallest separation. A similar pattern of results is seen when the test targets are (b) red–green and (c) blue–yellow: significant crowding is seen when the test and flanking stimuli have the same chromatic content, but little is seen when they have different chromaticities.

Figure 5 and highlight a pattern of results that is similar, both qualitatively and quantitatively, to that shown in Figure 4a, for both observers tested. This confirms that the results of Experiment 1 are not an artifact of the stimuli used.

Experiment 2: Are we really measuring crowding?

It has become apparent that a number of other visual phenomena exist, which, like crowding, are characterized by degradation of a target in the presence of other features, but which, most likely, represent different neural processes. These phenomena include masking (Pelli, Palomares, & Majaj, 2004) and surround suppression (Petrov, Carandini, & McKee, 2005; Petrov, Popple, & McKee, 2007). When seeking to study crowding, it is therefore important to establish that crowding is, in fact, the phenomenon under investigation. Pelli et al. (2004) suggest that one "diagnostic test" for crowding is that the effect should scale with eccentricity and be independent of signal size.

In order to confirm that the data presented in Figure 4 do reflect genuine crowding, we looked for evidence that the observed effect scales with eccentricity. We measured percent correct responses for an achromatic test patch surrounded by an achromatic annulus, at various target eccentricities (5°, 10°, 15°, and 20°) and various separations of target and annulus. The target size and the width of the annulus were the same for each eccentricity. Results for 2 observers are shown in Figure 6a. The main finding is that, as eccentricity increases, larger separations of target and annulus are required to maintain similar levels of performance. This is highlighted in Figure 6b, which shows that data can be made to collapse across eccentricity
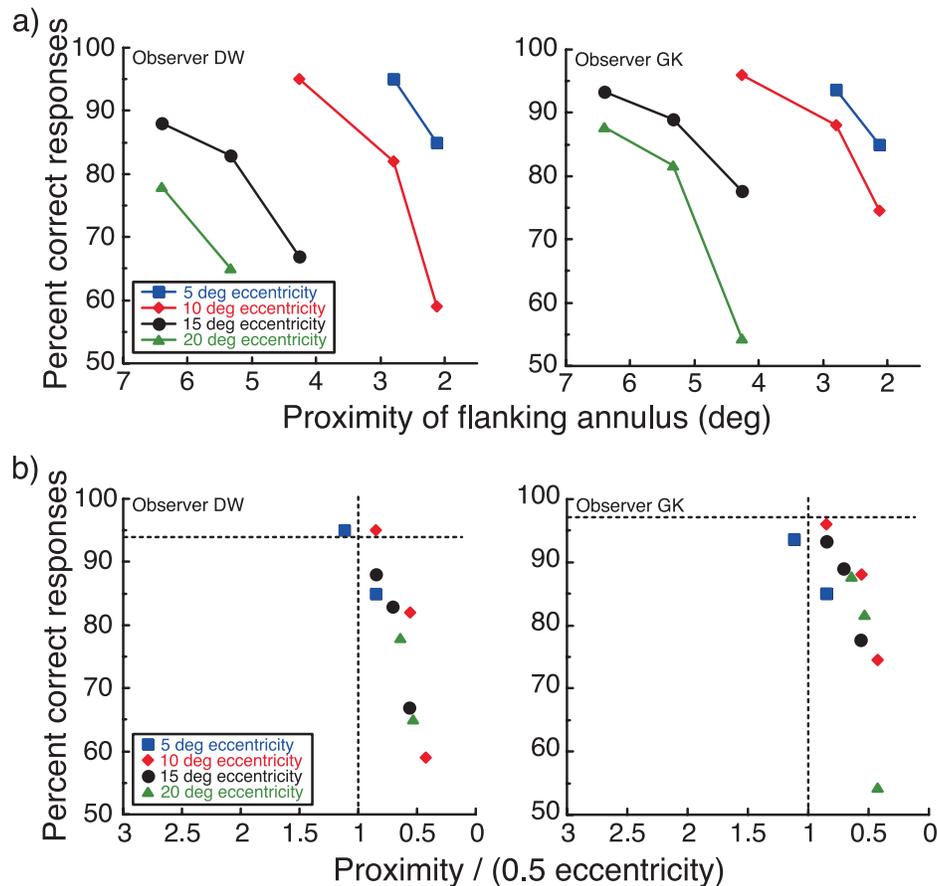
Figure 6. Scaling of performance with eccentricity. (a) Plots of percent correct responses against separation of target and flanker are shown for achromatic stimuli presented at various eccentricities. As eccentricity is increased, increasing separations of test/flanker are required to maintain similar levels of performance. (b) The abscissa represents proximity as a proportion of 0.5E, with the result that data from all eccentricities collapse to a single function.

simply by expressing surround proximity in multiples of 0.5E. Performance falls sharply at all eccentricities once surround proximity falls below 0.5E. We are confident, therefore, that the results of Experiment 1 reflect a crowding effect.

Experiment 3: Modification of chromaticity along non-cardinal axes

Confident that our task measures crowding, we next addressed the question of whether *any* difference in chromaticity between test stimulus and surround is sufficient to abolish crowding, or whether the decisive factor is the extent to which the physical chromaticity of the stimuli leads to the involvement of common post-receptoral mechanisms. We investigated this by measuring crowding effects along various oblique (non-cardinal) chromatic axes. Red–green test stimuli were surrounded by an annulus, the chromaticity of which was defined relative to the red–green cardinal axis and could differ from that of the test target by 0 (red–green), 30, 60, 90

(orthogonal: blue–yellow), 120, and 150 degrees in color space. As in Experiment 1, stimuli with different chromaticities were equated for visibility, using the same method as described previously (see Stimuli section).

Results are shown in Figure 7 for two observers. The data support the findings of Experiment 1 that maximal crowding occurs for a surround that shares a common chromaticity to the test (0 degrees) and that relatively little crowding is found for an orthogonal surround (90 degrees). Critically, intermediate surround chromaticities produce intermediate levels of crowding, despite having a different chromatic appearance to the test stimulus. What appears to be important, therefore, is not the chromatic similarity between test and surround *per se* but the extent to which the physical chromaticity of test and surround results in the involvement of common post-receptoral mechanisms.

Experiment 4: Half-wave rectification

One topic of debate in the color vision literature concerns whether the post-receptoral chromatic mechanisms are
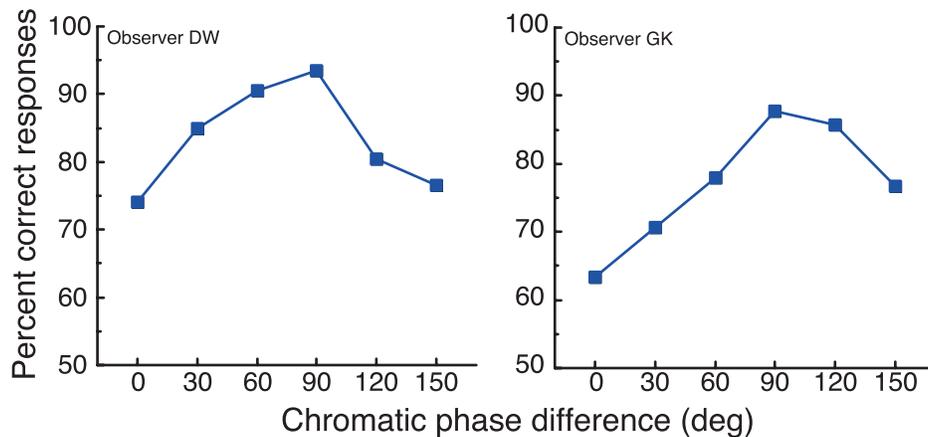
Figure 7. Modification of chromaticity along non-cardinal axes. Percent correct responses were measured for a red–green test stimulus flanked by an annulus, the chromaticity of which could differ from that of the test by 0, 30, 60, 90, 120, and 150 degrees in color space. In agreement with the results of Experiment 1, maximum crowding is observed when the test and surround are both red–green (i.e., 0 deg phase difference), but little is seen when the surround is blue–yellow (90 deg phase difference). Importantly, intermediate levels of crowding are seen for intermediate flanker chromaticities.

either "bipolar" or "rectified" in nature. Our stimulus arrangement is ideally suited to investigate this issue further. We amended our "bipolar" red–green and blue–yellow chromatic stimuli of the main experiment by "half-wave rectifying" them such that they could appear as gratings of red, green, blue, or yellow stripes against the equiluminant gray background (Figure 8).

Stimuli of different colors were once more equated for visibility using the same method as described previously (see Stimuli section). This time, the yellow target was set to the maximum contrast available and the contrast of each of the other target colors (blue, red, and green) was equated relative to this. Targets of each color were then surrounded by a half-wave rectified annulus that was

either of the same (e.g., red target with red flanker) or of the complementary color to the target (e.g., blue target with yellow flanker). Performance was again measured for various separations of test and flanking stimuli.

Results for two of the observers from Experiment 1, along with those for one additional naive observer, are shown in Figure 9. Data for red and green targets are shown in Figure 9a, and those for blue and yellow targets are shown in Figure 9b. The main finding from this experiment is that when the test target and flanking annulus are of the same color, performance reduces with decreasing separation of test and flanker, i.e., again a typical crowding effect is observed. However, when the target and flanker are of complementary colors, a
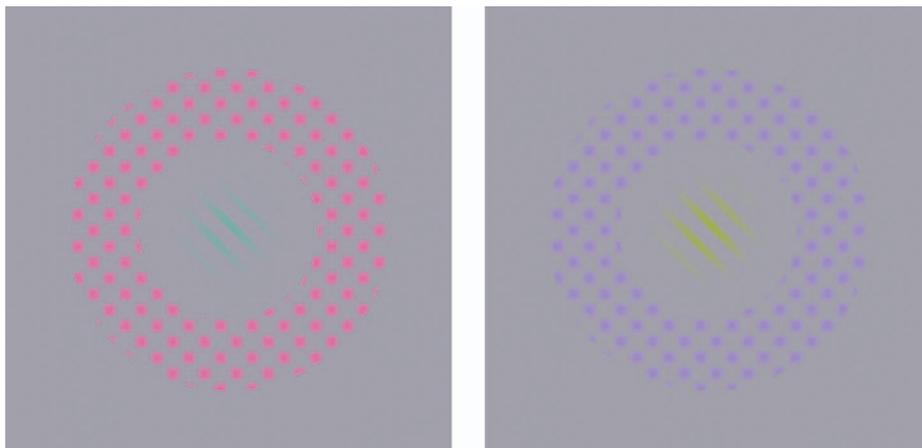

Figure 8. Half-wave rectified stimuli. In a further experiment, the "bipolar" stimuli from the main experiment were subjected to "half-wave rectification", such that they could appear as red, green, blue, or yellow patterns against an equiluminant gray background. Gabor test targets of each of these colors were flanked by an annulus of either the same or of the complementary color, and performance was measured for various separations of target and flanker.

a) Red and green targets
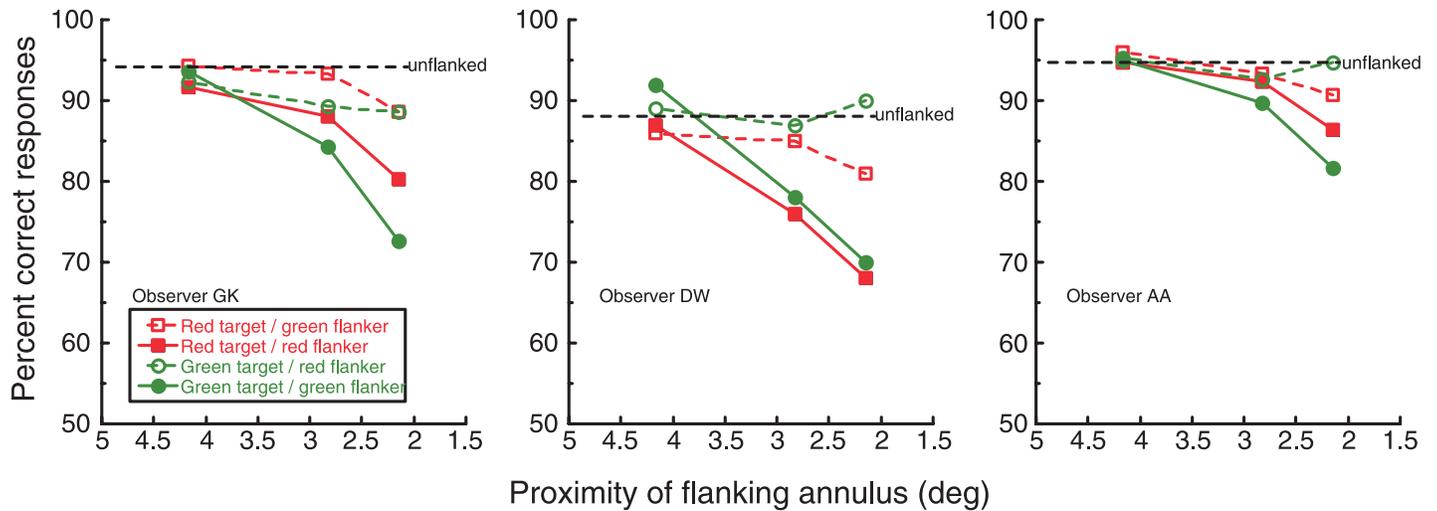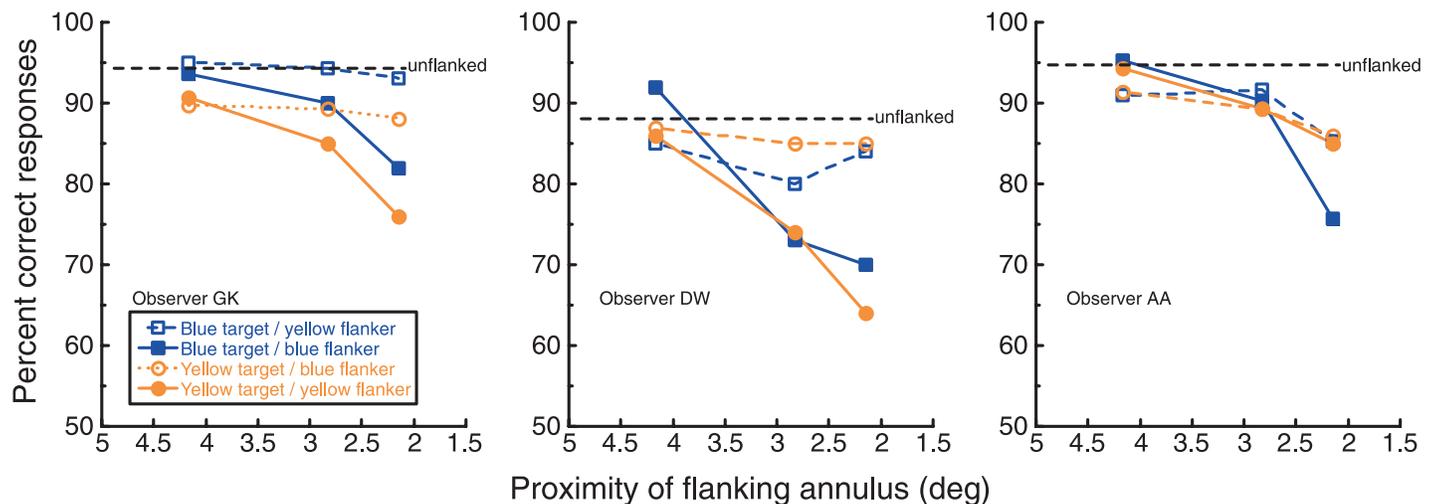

b) Blue and yellow targets

Figure 9. Plots of percent correct responses against separation of target and flanker for half-wave rectified chromatic stimuli. Performance for unflanked targets presented in isolation is indicated by the black dashed lines. The data in (a) are for test targets that were either red or green and in (b) are for blue and yellow targets. The basic finding is that when the test and flanking stimuli are of the same color, performance reduces with decreasing separation of test and flanker. However, when the target and flanker are of complementary colors, significantly less reduction in performance is seen.

significantly smaller reduction in performance is seen. This was confirmed by a 3-factor repeated measures ANOVA. Test color was not significant ($F(3,6) = 0.256$, $p \gg 0.05$), but there was a significant difference between performance when the flanking stimulus contained the same chromaticity compared to when it had the opposite chromatic polarity ($F(1,2) = 33.07$, $p = 0.0289$). The basic crowding effect was indicated by a significant effect of proximity ($F(2,4) = 68.03$, $p < 0.001$) and there was a significant interaction between proximity and chromatic similarity between test and surround ($F(2,4) = 16.08$, $p = 0.0122$). As for Experiment 1 (Figure 4), this interaction

indicates that the crowding effect is maximal at close proximities when the test and surround share the same chromaticity.

Discussion

Our main finding is that, for all test targets (both chromatic and achromatic), when the target and flanking annulus are identical in their chromatic content, crowding

increases with decreasing separation of the target and annulus. When the test and flanking stimuli have different chromatic properties, reduced crowding is observed, even at the minimum separation of test target and annulus, with the exact magnitude of the crowding effect being dependent on the extent to which the test and surround stimulate the same post-receptoral mechanism.

It has been reported previously that crowding effects occur within red and green isoluminant chromatic stimuli as well as for those defined by variations in luminance (Kooi et al., 1994; Tripathy & Cavanagh, 2002). Our results confirm and add to these previous findings by showing that, provided the test target and flanker have the same chromatic content, significant crowding effects occur when the stimulus chromaticity is modulated along each of the three cardinal chromatic axes. Tripathy and Cavanagh (2002) also reported that the extent of crowding is similar for chromatic and achromatic targets. While it was not our intention to map out the extent of crowding zones precisely (we only used three levels of crowding proximity), qualitative evaluation of our data support Tripathy and Cavanagh's (2002) assertion. Figure 4 shows that, when the target and surround share the same chromaticity, crowding is negligible at our largest separation of 4.17° (0.417E, slightly smaller than Bouma's "critical spacing"; Bouma, 1970; Pelli & Tillman, 2008), but for all chromaticities, crowding becomes significant at our intermediate proximity (2.83°).

Crowding effects between achromatic and chromatic opponent mechanisms are difficult to identify from previous literature. Põder (2007) reported a modest reduction in crowding when a target letter differed in color from the crowding flanks. However, the purpose of this study was to examine the so-called color "pop-out", and no attempt was made to isolate the individual post-receptoral opponent mechanisms. The central colored target and the surrounding achromatic flankers were neither equiluminant with each other nor with their surround. This may account for the relatively small magnitude of Põder's (2007) effects; since the chromatic target also contained luminance contrast, a persistence of crowding might well have been expected. When chromatic content is carefully controlled (Figure 4), the difference in extent of crowding within and between chromatic channels becomes highly significant.

That is not to say, however, that our stimuli were perfect. While we attempted to equate visibility between stimuli with different chromaticities, such attempts are always susceptible to slight departures from a perfect match and hence minor differences in stimulus salience (Felisberti, Solomon, & Morgan, 2005). In addition, we defined our chromatic stimuli according to photometric rather than perceptual equiluminance. In addition, variations in LCD displays with viewing angle mean that, even at the modest eccentricity of 10°, slight variations in photometric output in comparison to the "straight ahead" calibration measurements may have occurred. Neither did we take account of variations in the off-axis performance

of the eye itself. The significance of these considerations, however, is that the small cross-condition crowding effects that were present in Figure 4 are likely to be even smaller if it were possible to present "perfect" isoluminant chromatic stimuli.

Of particular interest in the processing of spatial form is the degree of interaction that takes place between the basic achromatic and chromatic cone opponent mechanisms. The results of the current study indicate that the processing of achromatic and chromatic information is segregated, at least at the level of the visual system where crowding occurs. However, although it is accepted that crowding occurs somewhere in visual cortex (Levi, 2008), its exact locus is, in itself, an issue for debate.

A further contention in the color vision literature concerns the nature of the post-receptoral mechanisms as being "bipolar" or "rectified". The traditional view is that each cone opponent mechanism responds in a bipolar way to signal opponent colors. However, an alternative viewpoint, proposed by Sankeralli and Mullen (2001), is that the poles of each opponent mechanism are separable, with each pole being subserved by a distinct mechanism. This is equivalent to the "fourth stage" of the multi-stage color model proposed by De Valois and De Valois (1993). Their suggestion is that later stage color cells (post-V1) are not spectrally opponent but simply respond to some regions of color space while giving no response to others. They go on to state that chromatic opponency at this later stage is between, rather than within, color mechanisms. This clearly has implications for crowding, since mechanisms that are separate would not be expected to influence one another.

We addressed this issue in Experiment 4, using stimuli that were subject to "half-wave rectification", and showed that when the test target and flanking annulus had the same color (or chromatic "polarity"), performance reduced with decreasing separation of test and flanker, but when the target and annulus were of complementary colors (different "polarities"), a significantly smaller reduction in performance was seen. These crowding effects for half-wave rectified chromatic stimuli are indicative of a late-stage locus for visual crowding. The red and green (or blue and yellow) stripes of our half-wave rectified stimuli share a common neural target in the color opponent processing mechanisms of the early stages of color vision, yet result in relatively low levels of interaction in the form of crowding. It suggests that crowding effects occur at a stage where unipolar chromatic mechanisms have been made explicit by a process such as rectification of color information from earlier opponent signals. Other psychophysical data, such as masking and pattern detection, support the explicit nature of late-stage rectified color mechanisms (Sankeralli & Mullen, 2001; Wilson & Switkes, 2005). Presumably, similar unipolar "black or white" mechanisms underlie the established lack of cross-polarity crowding effects in the achromatic domain (Kooi et al., 1994).

Nevertheless, theories of crowding based upon segregation of early channels are complicated by the presence of crowding despite significant differences in orientation of test and surround (Solomon, Felisberti, & Morgan, 2004). Such differences would be expected to involve distinct orientationally selective mechanisms in V1 and are certainly sufficient to produce a strong impression of "pop-out" between target and surround (Felisberti et al., 2005). A potential explanation for such cross-orientation crowding effects lies in the observation that first-order orientation is pooled beyond V1 to create orientationally isotropic second-order filters (McGraw, Levi, & Whitaker, 1999). Thus, while color crowding appears to be explained by the segregation of post-receptoral channels into rectified color mechanisms, channel combination or pooling may underlie the persistence of crowding effects across other dimensions such as orientation. The common link is a transformation of early responses to produce later stage crowding effects.

Our results suggest a method by which performance in crowding-limited tasks might be enhanced through appropriate selection of the chromatic content of the stimulus. One important task, which has significant implications for quality of life, is that of reading. The rapid increase in the number of patients with age-related macular degeneration (ARMD) highlights the importance of crowding, since these patients are forced to use their peripheral retina to read, with the ensuing limitations of the well-established increase in crowding effects with eccentricity (Bouma, 1970; Toet & Levi, 1992). It is well established that such patients suffer from poor reading ability despite increases in text size and training (Legge, Rubin, Pelli, & Schleske, 1985) and that this inferiority of peripheral reading is maintained even when the complication of eye movements is taken into account (Latham & Whitaker, 1996).

Several attempts have been made previously to reduce crowding effects in peripheral reading, using various manipulations including changing the spacing between letters in words (Chung, 2002) and training observers to be able to "uncrowd" letters in the periphery (Chung, 2007). The results of the current study suggest that manipulating the chromatic content of letters in words, in such a way that adjacent characters do not share the same chromaticity, may reduce crowding and thereby increase reading speed. It should be noted, however, that Chung and Mansfield (2009) have recently shown that, while crowding between adjacent letters in words is reduced when the letters have alternating contrast polarity, this does not lead to an improvement in peripheral reading speed. Additionally, it is possible that grouping effects between letters sharing the same chromaticity might actually disrupt reading, in much the same way as alternation between upper and lower case letters does (Coltheart & Freeman, 1974). Even if this proves to be the case, it is conceivable that varying text color between alternate words or lines might result in a reduction in crowding and an ensuing improvement in reading ability.

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