

Visual crowding effect in the parvocellular and magnocellular visual pathways

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The crowding effect, defined as the detrimental effects of nearby items on visual object recognition, has been extensively investigated. Previous studies have primarily focused on finding the stage(s) in the visual hierarchy where crowding starts to limit target processing, while little attention has been focused on potential differences between the parvocellular (P) and magnocellular (M) pathways in crowding mechanisms. Here, we investigated the crowding effect in these parallel visual pathways. In **Experiment 1**, stimuli were designed to separately engage the P or M pathway, by tuning stimulus and background features (e.g., temporal frequency and color) to activate the targeted pathway and saturate the other pathway, respectively. Results showed that at the same eccentricity and with the same tasks, targets processed in the M pathway appeared to be more vulnerable to crowding effect. In **Experiment 2**, crowding effects were studied using three different types of stimuli and visual tasks (form, color, and motion), presumably with different degrees of dependence on the P and M pathways. Results revealed that color, motion, and form discrimination were increasingly more affected by crowding. We conclude that processing in the M and P pathways are differentially impacted by crowding; and importantly, crowding seems to affect processing of spatial forms more than other stimulus properties.

Introduction

A central function of the visual system is identifying objects in our environment. Often the objects are in the visual periphery and surrounded by other items. While recognizing and discriminating objects in isolation are easy daily tasks, they become substantially harder when objects are cluttered. Crowding is described as the detrimental effects of nearby items on visual

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recognition of objects (Whitney & Levi, 2011). Especially in peripheral vision, people's ability in recognizing even simple objects is remarkably impaired by the neighboring objects regardless of the category of those objects. Given that objects are often in our visual periphery and rarely in isolation, crowding is considered as a bottleneck of object recognition (Levi, 2008). Although crowding can be observed with numerous different visual stimuli including letters, faces, moving versus static objects, with low or high spatial frequencies, in low or high contrasts, a prominent example of crowding's influence in daily life is in the domain of reading. Many studies investigated the impact of crowding on reading (Pelli, Tillman, Freeman, Su, Berger, & Majaj, 2007; Levi, Song, & Pelli, 2007; Chung, 2007; Martelli, Di Filippo, Spinelli, & Zoccolotti, 2009). Taken together, understanding the mechanisms of crowding effect is crucial to have a comprehensive understanding of processes in reading and object recognition.

The crowding phenomenon has been studied since the 1930s (Ehlers, 1936). A landmark research from Bouma (1970) showed that for visual recognition of a target at θ° eccentricity, the nearby objects (flankers), need to be at least $\theta/2^\circ$ away from the target in order to prevent the crowding effect. A number of studies also revealed key properties of crowding based on the location of the target and flankers in the peripheral visual field. Flankers placed along the fovea-target radial direction impair the recognition performance more than on the tangential direction (radial/tangential anisotropy; Toet & Levi, 1992), and the far flanker (flanker more eccentric than the target) is more detrimental than the near flanker (flanker closer to the fovea than the target) (inward-outward anisotropy; Bouma, 1970). It was also shown that crowding is stronger in the upper than lower visual field (He, Cavanagh, & Intriligator, 1996) despite the fact that the area of cortical representation



of upper and lower visual fields is roughly the same in the primary visual cortex. Furthermore, the number of flankers (Pelli, Palomares, & Majaj, 2004) and whether they could be grouped (Manassi, Sayim, & Herzog, 2012) affect crowding. In addition, stronger crowding is observed with higher target-flanker similarity (Kooi, Toet, Tripathy, & Levi, 1994).

In contrast to the extensive characterization of the spatial properties of crowding, there is a lack of understanding of the neural mechanisms of crowding. Previous studies have often focused on investigating the stage(s) in the visual hierarchy where crowding starts to limit target processing (Pelli, 2008; Anderson, Dakin, Schwarzkopf, Rees, & Greenwood, 2012; Millin, Arman, Chung, & Tjan, 2014; Chicherov, Plomp, & Herzog, 2014). While there is no consensus on a specific locus of crowding in the visual system, it has been proposed that crowding may occur at multiple stages of visual processing (Louie, Bressler, & Whitney, 2007; Fischer & Whitney 2011; Anderson et al., 2012; Manassi & Whitney, 2018). Fischer and Whitney (2011) argued that crowding does not stop object processing at a particular point in the visual system or that objects are not broken down to their low-level features. Theories for neural mechanisms of crowding range from proposals emphasizing the role of receptive fields and hypercolumns to proposals addressing more high-level processes including feature integration and attentional processes (Levi, Klein, & Aitsebaomo, 1985; He et al., 1996; Pelli et al., 2004; for a review, see Levi, 2008). Importantly, there is little consideration on the role of parallel visual pathways and the potential difference of crowding among them.

From the retina to the primary visual cortex, visual information is processed along two major channels, the magnocellular (M) and the parvocellular (P) pathways. Information processed in the primary visual cortex is further processed along the ventral “perception” and the dorsal “action” pathways, with the dorsal stream receiving more input from the M pathway and the ventral stream receiving more input from the P pathway (Nassi & Callaway, 2009). Neurons in these two channels differ from each other in terms of both their anatomy and corresponding functions. Many studies have shown that the two visual pathways are tuned to a number of distinct visual features. For example, the P pathway is very sensitive to color whereas the M pathway is blind to color (Livingstone & Hubel, 1987). The P pathway favors spatial details while the M pathway cannot resolve high spatial frequencies (Derrington & Lennie, 1984). On the other hand, the M pathway is very fast at processing visual information, while the P pathway is relatively slow. In relation to these distinctive features of the two pathways, different visual phenomena have been investigated to uncover whether one pathway is more involved compared to the other in daily visual functions. To

name a few, researchers have looked at binocular rivalry (Carlson & He, 2000), dyslexia (Stein, 2001) and consciousness (Tapia & Breitmeyer, 2011). However, no published research has reported the relationship between crowding and parallel visual pathways.

There are a large number of studies investigating the effects of stimulus properties in crowding (Tydgat & Grainger, 2009; Grainger, Tydgat, & Issele, 2010; Pelli, 2008). Surprisingly, given that visual parallel pathways represent biases towards different stimulus properties and thus these neural pathways are differentially involved in processing different types of stimuli, little consideration was explicitly given to the possibility that the nature of the crowding effect could be different across these visual pathways. For example, a recent study showed that crowding effect is dissociable in color and motion processing, which allowed the authors to make the point that crowding is not a singular process (Greenwood & Parsons, 2020). However, color and motion are stimulus properties that are biased to be processed in the parvocellular and magnocellular pathways. To further our understanding, we ask the question of how these biases in the feature dimensions influence crowding. Uncovering these possible pathway differences will help us to better understand the neural correlates of crowding.

To our knowledge, this study is the first in the field that explicitly investigated the potential differences of the crowding effect in different visual pathways. We studied the vulnerability to crowding in the two parallel pathways with stimuli designed to selectively engage the P pathway or the M pathway. In **Experiment 1**, we aimed to isolate the two pathways by using biased stimulus for the targeted pathway and backgrounds to saturate the other pathway. In **Experiment 2**, we used different stimuli and tasks to investigate crowding properties for form, color, and motion discrimination. In both experiments, we measured the critical spacing of crowding, the minimal distance between target and flanking objects that allows identification of the target object. A smaller critical spacing would indicate weaker crowding effect.

Experiment 1

Experiment 1 investigated the spatial properties of crowding with stimuli designed to separately engage the parvocellular or magnocellular pathway, by tuning stimulus features to activate the targeted pathway and manipulating background to saturate the other pathway. The same target discrimination task was used for all stimuli.

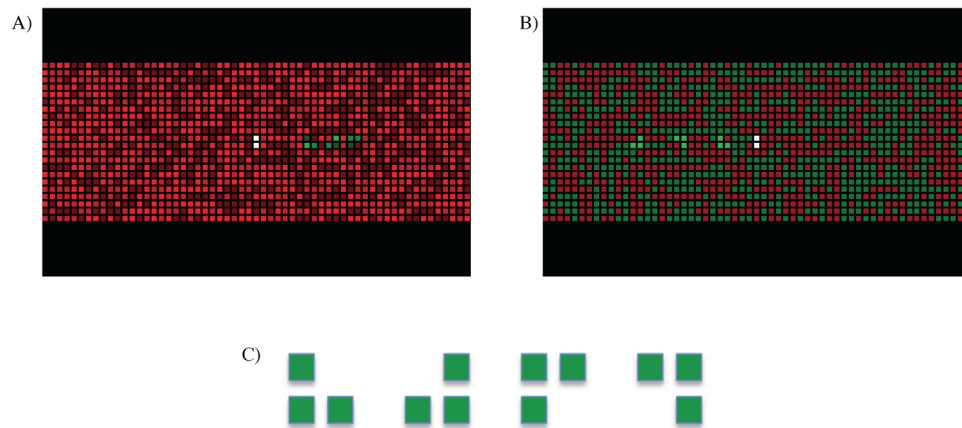


Figure 1. Stimuli for Experiment 1. (A) P pathway biased condition. Stimuli defined by green color and background defined by red color. Both the stimuli and background constantly flickering at a fast rate, by changing in luminance. (B) M pathway biased condition. Stimuli defined by luminance flicker while the background is isoluminant, stable, green-red colored. (C) Possible orientations for the target and flankers in Exp1.

Methods

Participants

Thirteen undergraduate students from the University of Minnesota, aged between 18-30 years, with normal or corrected vision participated in the study. All participants were recruited from the University of Minnesota Psychology Department's Research Experience Program participant pool, and gave written informed consent to participate in accordance with the policies approved by the human subjects review committee of the University of Minnesota.

Apparatus and stimuli

The stimuli were generated using MATLAB with the Psychtoolbox extensions (Brainard, 1997; Pelli, 1997) and displayed on a 24-inch TOBII T60XL screen (refresh rate: 60 Hz, resolution: 1920 × 1200). The monitor was calibrated using a Photo Research PR-655 spectrophotometer, luminance gamma curves were measured and inverted with a look-up table.

Achromatic contrast discrimination and pulsing stimuli have been used to assess the M and P pathways' functions in psychophysical experiments (Pokorny & Smith, 1997; Leonova, Pokorny, & Smith, 2003; McAnany & Levine, 2007). A similar paradigm was developed in the current experiment to test crowding effect in parallel pathways. In the P pathway biased condition, the background was filled with fast flickering (30 Hz) small red squares, constantly changing in their luminance. The target and flankers were defined as three squares forming an L shape, displayed in green and flickering at a fast rate, so that the luminance modulation was similar to the background (Figure 1A).

The mean luminance of each square was equal to the mean luminance of the background. In the M pathway biased condition, the background was filled with isoluminant green and red squares, and each square was $0.5^\circ \times 0.5^\circ$ in size. The target and flankers were defined as three squares in the periphery, forming an "L" shape. They differed in their luminance modulation (Figure 1B) from the background and these L-shaped three-squares flickered at a fast rate (30 Hz) to be distinguished from the stable background. In both conditions, in each trial, the target and flankers were randomly assigned to one of the four possible orientations (Figure 1C), with the possibility of the target and flankers having the same orientation. Two flankers were aligned horizontally to the target, with one flanker on each side (of the target). The stimuli were presented for 200 ms and the eccentricity of the target was 9° in the radial direction with respect to the fixation point.

Procedure

The viewing distance was 60 cm and participants' heads were stabilized with a chinrest. The middle two squares in the background were presented in white color to serve as a fixation point. Participants were instructed to look at these two white squares throughout the whole experiment.

Before the main crowding experiment, participants were asked to complete a minimal flicker procedure. This procedure was designed to find the subjective isoluminance values for red-green stimuli for each participant. Participants were asked to fixate their eyes on the black dot in the middle of the screen and adjust the luminance of a square located in their peripheral vision that was presented in the right or left of the

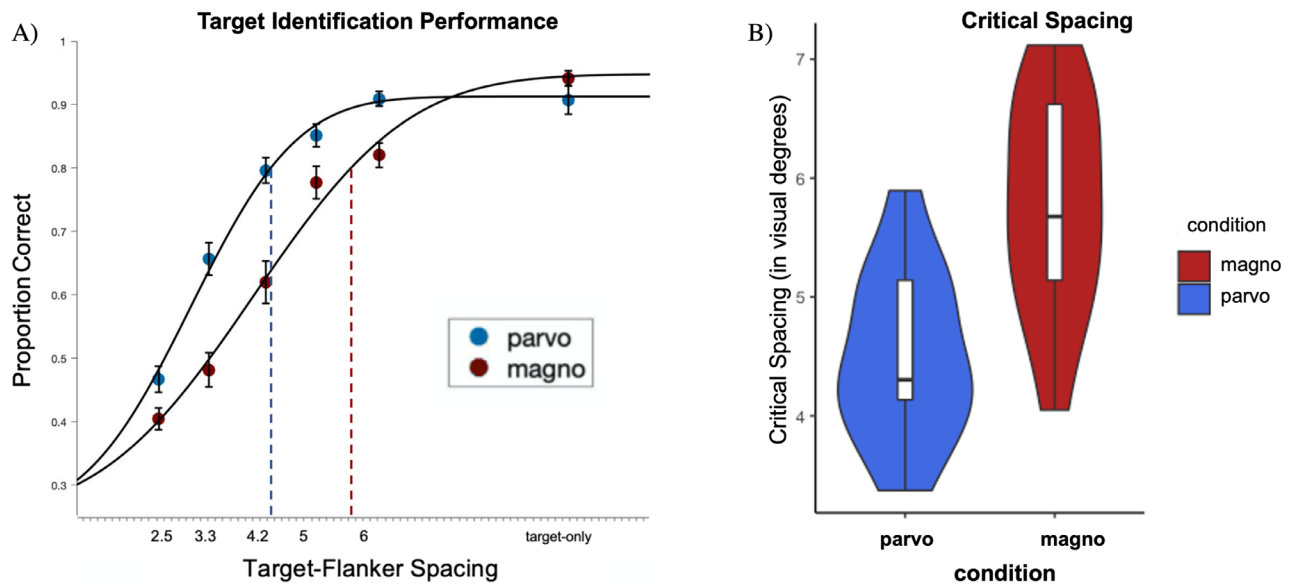


Figure 2. Results of Experiment 1. (A) Target identification accuracy as a factor of target-flanker spacing. Two curves for M pathway biased (magno) and P pathway biased (parvo) conditions, fitted with psychometric function. The dashed lines indicate the value of critical spacing for the two conditions, corresponding to 80% accuracy. (B) Violin plot of critical spacing data for both Magnocellular pathway (magno) and Parvocellular pathway (parvo) conditions. The width of the bar represents the density of distribution of the individual data. The white bar indicates the interquartile range with the median line, and 95% interval is shown with the black vertical line.

black dot at 9° eccentricity. Participants used the arrow keys on the keyboard until the flickering was minimal. This procedure was repeated eight times, four times on each side of the screen. Four different green values were obtained from this procedure for each participant as isoluminants of given red values. The luminance of red squares were one of the four values; 11.46, 15.94, 20.43, and 24.91 cd/m^2 . Only these sets of four red and green values were used to render the background and the stimuli in the experiment.

Eye-tracking was performed both during the minimal flicker procedure and main experiment to make sure participants maintained fixation. The screen-based eye-tracker TOBII T60XL was used and data were recorded binocularly. Participants were calibrated using a standard nine-point grid.

In the main experiment, participants were instructed to perform a peripheral orientation discrimination task. While participants fixate at the fixation point in the middle of the screen, target and flankers briefly appeared either right or left side of the fixation. After the presentation of the stimuli, the word “response” was presented, prompting the participant to report the orientation of the target “L” shape. Participants responded by pressing the corresponding key for the particular orientation. They were instructed to respond in two seconds after the target/stimuli presentation, and the next trial was presented immediately following the response. All participants completed two conditions, each aiming to target either M or P visual pathways.

The order of the conditions was counterbalanced. Each condition consisted of six blocks, varying in their interstimulus spacing, in other words, the distance between the flankers and the target. The spacing in the blocks were 2.5°, 3.3°, 4.2°, 5°, 6°, and one baseline block (0°) presenting no flankers. Each block consisted of 96 trials, as a total of 576 trials for each pathway condition. Critical spacing for each condition was defined as the distance where participants were able to reach 80% identification accuracy.

The accuracy performance was fitted as a function of target-flanker spacing with a cumulative Gaussian sigmoid curve using the Psignifit toolbox software for MATLAB (Wichmann & Hill, 2001).

Results and discussion

Consistent with prior research (Bouma, 1970; Greenwood, Bex, & Dakin, 2010; Toet & Levi, 1992; Pelli et al., 2004), target identification performance improved as target-flanker spacing increased in both M pathway and P pathway conditions. Figure 2A shows the proportion of correct responses to different target-flanker spacings for both conditions. Average performance in the P pathway biased condition was better throughout the whole interstimulus spacing range. The critical spacing for each condition was defined at 80% correct identification.

Figure 2B shows the critical spacing for each individual participant along with the averages for each condition. We found that the critical spacing in the M-biased condition ($M = 5.76^\circ$) was significantly larger compared to that of the P-biased condition ($M = 4.49^\circ$) (paired- t (12) = 4.3, $p < 0.001$), and that this difference was consistent across all subjects, despite the individual differences in critical spacing values. In both experiments, participants' performance was around 90% in non-crowded (baseline) condition, and around 40% to 45% in the most difficult crowding condition (2.5° interstimulus spacing), suggesting that the difference in critical spacing between the two conditions was not due to possible differences in task difficulty.

Results of Experiment 1 indicate that the P pathway compared to the M pathway can better resist crowding in form perception, or that the crowding effect in this experiment is more severe in the M pathway than in the P pathway. Our results do not suggest specific differences in the underlying crowding mechanisms in different visual pathways, and instead may reflect that at the same eccentricity, neurons in the P pathway tend to have smaller receptive fields than that in the M pathway (Dacey & Petersen, 1992; Nassi & Callaway, 2009).

The goal of the first experiment was to isolate the two pathways and study their spatial properties in crowding, however, in real life, visual objects rarely, almost never, completely fit the description of P pathway or M pathway stimulus. Therefore, in Experiment 2, we investigated crowding using stimuli that are in different functional categories and are more relatable to real life, yet with clear link to the idea of two parallel pathways.

Experiment 2

This experiment examines the question of whether recognition performance in crowding yields different patterns depending on the parallel visual pathways, by applying different stimuli categories and their corresponding visual tasks. Three different stimuli and their corresponding tasks were used to investigate function-specific crowding properties. Specifically, color (primarily P pathway), motion (more M pathway than P pathway) and form (more P pathway than M pathway) discrimination tasks are implemented.

Methods

Participants

Twenty-five undergraduate students from the University of Minnesota, aged between 18-30 years, with normal or corrected vision participated in the

study. None of the participants from the first study were included in this experiment. All participants were recruited from the University of Minnesota Psychology Department's Research Experience Program participant pool. They gave written informed consent to participate in accordance with the policies approved by the human subjects review committee of the University of Minnesota.

Apparatus and stimuli

As in Experiment 1, the stimuli were generated using MATLAB with the Psychtoolbox extensions (Brainard, 1997; Pelli, 1997) and displayed on a 24-inch TOBII T60XL screen (refresh rate: 60Hz, resolution: 1920 × 1200).

In the motion condition (targeting the M pathway), the target and flankers were 2.5° squares, filled with isoluminant red/green vertical bars with the spatial frequency of 1.6 cyc/deg and luminance of 18.9 cd/m². (Figure 3A). The chromatic gratings had the spatial frequency of 0.5 cyc/deg, was modulated sinusoidally, and moved to the right or left direction, alternating randomly. The final stimulus was essentially an achromatic sine wave grating moving from the right or left, overlaid above the chromatic gratings, simulating movement across the red/green gratings (Figure 3D). This motion-on-color paradigm was adapted from Wen et al. (2015). The temporal frequency of the luminance grating was 15 Hz. Based on previous evidence that the P pathway is consumed by the high-contrast color modulation and that the detection of motion of the low-contrast luminance grating is controlled by the M pathway, this task aimed to target the M pathway (Merigan, Byrne, & Maunsell, 1991).

The novel experimental paradigm in the color condition was developed based on previous studies that tested chromatic information in the periphery in relation to the parvocellular pathway (Lee, Pokorny, Smith, Martin, & Valberg, 1990; Cooper, Sun, & Lee, 2012). In this condition (targeting the P pathway), the background was gray with a black fixation dot (1°) in the middle of the screen. The target and flankers were defined as squares in the periphery, 2.6° in size. Target squares were presented as a single shade of yellow, whereas the flankers were divided into four quadrants, each with a different shade of yellow (Figure 3B). The luminance of target and flankers were 18.9 cd/m² and their hue values were individually determined for each participant. Given the fact that the P pathway is highly responsive to color information while the M pathway is insensitive to it (Schiller, Logothetis, & Charles, 1990), this task almost exclusively engaged in P pathway.

Lastly, in the form condition, the target and flankers consisted of a green vertical bar and a red horizontal bar, forming a 2.5° cross shape (Figure 3C). In all trials, the red horizontal bar was overlaid on top of

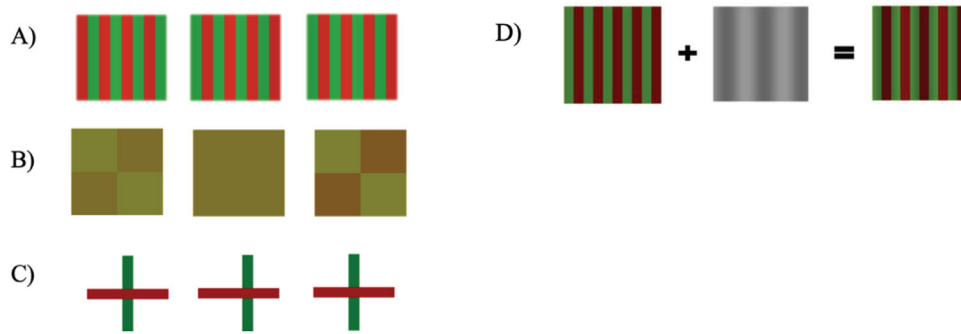


Figure 3. Three stimuli sets for [Experiment 2](#). (A) Motion crowding condition. Motion that is obtained by the luminance change of the bars is not shown in the figure. (B) Color crowding condition. (C) Form crowding condition. In all conditions, middle object is the target with two flankers in each side. (D) The motion-on-color paradigm, figure adapted from [Wen et al., 2015](#).

the green vertical bar at the intersection, and the two bars were isoluminant (luminance: 18.9 cd/m^2). This line displacement task was chosen among possible form discrimination tasks in order to equate the task difficulty with the motion and color discrimination tasks. This task allows 2AFC response structure with task difficulty flexibly adjusted for the participants. The aim of this task was to target both parallel visual pathways. Based on the evidence that form discrimination is primarily performed in the P pathway along with some information carried by the M pathway ([Livingstone & Hubel, 1987](#)), this task was expected to engage both visual pathways with an emphasis on the P pathway.

In all three conditions, two flankers were always aligned horizontally to the central target. The stimuli were presented for 250 milliseconds and the eccentricity of the target was 11° in the radial direction with respect to the fixation point.

Procedure

The procedure was very similar to [Experiment 1](#). In this experiment the fixation point was a black dot (visual angle of 1°).

Before the main crowding experiment, as in [Experiment 1](#), participants were asked to complete the minimal flicker procedure. In addition, participants also completed a color threshold test. This test allowed researchers to obtain subjective color thresholds for each participant. In this procedure, similar to the minimal flicker procedure, participants fixated on the white dot in the middle of the screen and adjusted the hue of a square that was presented in the periphery at 11° . Participants were instructed to adjust the hue until they find the “perfect” yellow. As they changed the hue of the square using the arrow keys on the keyboard, the luminance of the square stayed constant. This trial was repeated six times, three times on each side

of the screen. The starting hue value in each trial was randomized to avoid biases. The average of the six trials was calculated to determine the subjective “yellow” value and was implemented in the color condition of the main experiment. Given the success of the participants in the first experiment in keeping their gaze at the fixation point, eye-tracking was not used in this experiment.

In the main experiment, each condition had a specific task based on the stimuli used. In the color condition, participants were asked to decide if the hue of the target square was closer to green or red color, compared to their internal “perfect” yellow representation. As noted above, the target stimulus was manipulated based on each participant’s subjective result in the color threshold procedure. Target stimuli were created by adding/subtracting 3, 5, 7, 9 steps to/from the “perfect” value (i.e., if a participant’s average value from color threshold test is $[128 \ 120 \ 0]$, the manipulated colors for step 3 would be $[128 \ 123 \ 0]$ or $[128 \ 117 \ 0]$). The order of the different steps of hue manipulation was counterbalanced in each block. Flankers were divided into quadrants and each quadrant had a different hue value. These values were, again, based on each participant’s subjective results, by subtracting/adding 0, 10, 20, 30 steps. The representation of different hues in different corners of the main square was randomized. The response procedure was the same as [Experiment 1](#) except that participants were instructed to press the “up” arrow key, if they think the target stimulus’ hue is closer to green, and the “down” arrow key if it is closer to red.

In the motion condition, the task was deciding the direction of the “moving” wave, which was created by applying a luminance sine-wave grating, perceived over the chromatic gratings. The direction was defined either to the left or to the right both in the target and flankers. The direction of the moving wave was chosen randomly, with the possibility that one or both of the flankers

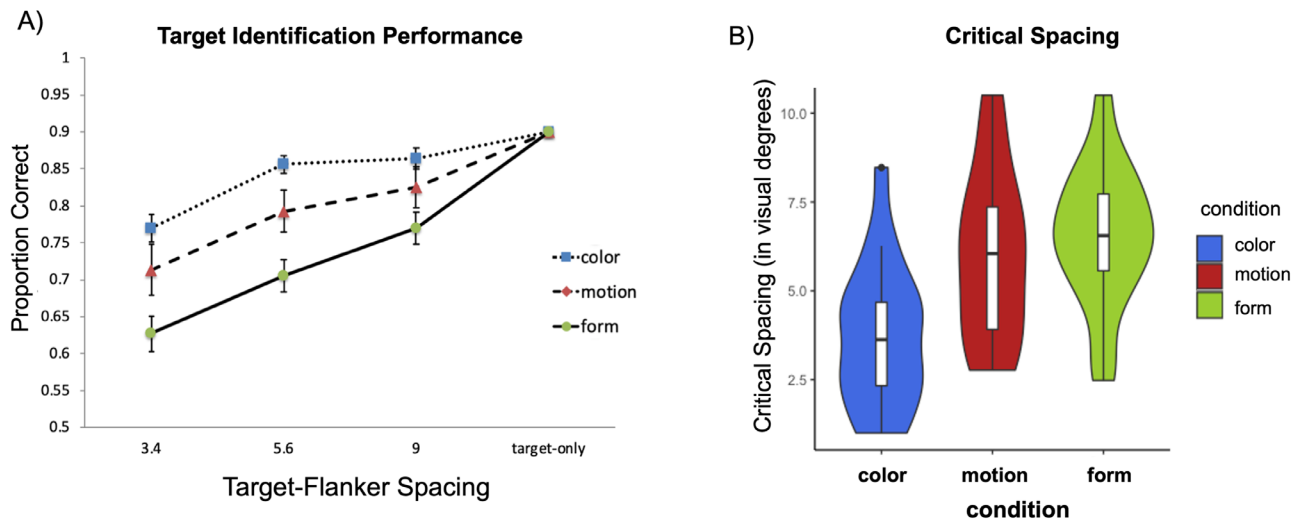


Figure 4. Results for [Experiment 2](#). (A) Target identification performance as a factor of target-flanker spacing for all three conditions. Data is normalized to fix the target-alone condition at 0.9. (B) Violin plot of critical spacing data for color, motion and form conditions, respectively. The width of the bar represents the density of the distribution of the individual data. The white bar indicates the interquartile range with the median line, and 95% interval is shown with the black vertical line.

and the target could move in the same direction. Participants were instructed to press the “right” or “left” arrow key in the response period immediately following the presentation of the gratings, based on their perception of the moving sinusoidal grating.

In the form condition, participants were asked to decide whether the red horizontal bar was longer in the right or left side of the green vertical bar in the global cross sign shape. The horizontal bar was manipulated to be shifted to right or left 0.25° for target and 0.25° or 0.35° for flankers. The side (right or left) and the degree (for flankers) to which the horizontal bar was shifted were randomized in each trial for both the target and the flankers, allowing for the possibility of the target and one or more flankers to have the same direction and/or degree of shifting. Participants responded by pressing the “right” or “left” arrow key, indicating the longer side of the horizontal bar in the target.

All participants completed all three conditions, and the order of the conditions was counterbalanced. Each condition consisted of 4 blocks, varying in their inter-stimulus spacing. As in [Experiment 1](#), one of the blocks was defined as the baseline, as there was no flanker presented. In addition to the baseline block (0°), the spacing in the other 3 blocks were 3.4° , 5.6° , and 7.7° . Each block consisted of 56 trials, with a total of 224 trials for each condition.

Seven participants were later excluded from the analyses as they did not reach 80% accuracy in the target-only (noncrowded) block in at least one of the three conditions. High level performance in the target-only condition indicates that participants can

perform object recognition tasks in their periphery in the absence of distractors.

Results and discussion

Like in [Experiment 1](#), recognition performance improved as the target-flanker spacing increased. [Figure 4A](#) demonstrates the target identification performance as a function of target-flanker spacing in the normalized data. Data was normalized to fix the target identification performance at 90% accuracy at the target-only block for all three conditions.

The rate of improved target identification with increasing target-flanker spacing differed across conditions. For example, form discrimination, which is the most commonly used task in crowding studies (presumably engaging both P and M pathways), showed the most severe crowding effect and considerable benefits of large target-flanker spacing. On the other hand, in the color discrimination task (presumably biased towards the P pathway), minimal crowding effect and little benefit from larger target-flanker spacing were observed. We quantified the crowding effects using critical spacing, as described in [Experiment 1](#). The average critical spacing value was 3.72° for the color condition, 5.98° for the motion condition and 6.56° for the form condition. [Figure 4B](#) shows the critical spacing for each individual participant along with the averages for each condition. A repeated measures analysis of variance (ANOVA) showed a significant difference in critical spacing among conditions ($p < 0.05$). Post hoc pairwise comparisons revealed that the difference

between color-form conditions was significant ($p < 0.01$).

These results can be interpreted such that form discrimination, which requires spatial integration of multiple features of an object, is more vulnerable to crowding than motion and color discrimination, which are based on a single property of the target object and do not involve spatial integration. Thus current results support the idea that feature integration plays an important role in crowding effect (Pelli, Palomares, & Majaj, 2004). Additionally, our results showed that color discrimination of a flanked target is much less affected by the typical crowding effect.

In everyday life, the visual system detects and discriminates objects in the periphery that are moving, have certain colors, and possess forms composed of multiple features. The results of the current experiment further our understanding of how motion, color, and form differentially relate to crowding, and provides quantitative measures of crowding effects for these functionally important and ecologically valid properties.

General discussion

Understanding the neural correlates of crowding is important, given that crowding is considered to be a primary limiting factor for object recognition in the periphery (Levi, 2008). Crowding is proposed to occur at multiple stages of the visual system (Louie et al. 2007; Anderson et al., 2012; Manassi & Whitney, 2018), with neural correlates identified from retinal ganglion cells (RGCs) to higher-level object recognition mechanisms (Levi, Klein, & Aitsebaomo, 1985; Herzog & Manassi, 2015; Kwon & Liu, 2019). The current study investigated whether spatial properties of crowding vary in two major visual pathways where the information is processed in parallel in the visual system. **Experiment 1** demonstrated that, at a particular eccentricity, the P pathway is spatially more resistant to the crowding effect compared to the M pathway. One explanation for this difference is that the parasol ganglion cells, which project to the magnocellular layers of the lateral geniculate nucleus (LGN), have larger receptive fields than the midget ganglion cells which project to the parvocellular layers of LGN (Rodieck, Binmoeller, & Dineen, 1985; Dacey & Petersen, 1992; Dacey, 2000). For stimuli that are processed mainly in the M pathway, the spatial extent of the information integration is larger, which may lead to stronger crowding effect compared to the stimuli mainly processed in the P pathway. Additionally, in a recent study, Kwon and Liu (2019) showed that the spatial asymmetries in crowding (e.g. radial/tangential anisotropy, inner vs. outer flanker effect) could be explained by the sampling density of RGCs across the visual field. Although Kwon and Liu

(2019) did not differentiate between parasol and midget cells, their study, together with known properties of these cells (Dacey, 1994), provide support for our hypothesis that the characteristics of crowding effect may vary across the parallel visual pathways starting from an early stage.

We also investigated the relationship between the spatial properties of crowding effect and the two visual pathways in the context of higher-level visual processing by using three different tasks. Our findings illustrate that the crowding effect is not uniform across different visual tasks that differentially engage the two major visual pathways. In the form discrimination task, the crowding effect was more sensitive to target-flanker spacing; whereas the color discrimination task was relatively insensitive to target-flanker spacing with an overall weaker crowding effect. Interestingly, the motion discrimination task showed intermediate level of sensitivity to target-flanker spacing. We note that in both experiments, color defined stimuli were less affected by crowding compared to targets defined by luminance flicker or motion. Form discrimination apparently was most vulnerable to crowding, possibly because it requires integration of multiple features and involves both the M and P pathways.

Our findings provide additional evidence for non-uniformity of the crowding effect as suggested by a number of previous studies (Bex & Dakin, 2005; Kennedy & Whitaker, 2010; Greenwood & Parsons, 2020). Although most previous studies focused on form crowding (Pelli, Palomares, & Majaj, 2004; Lev, Yehezkel, & Polat, 2014; Tripathy, Cavanagh, & Bedell, 2014; Agaoglu & Chung, 2016), it has been demonstrated that we need to consider the differences in the nature of stimuli and tasks to fully understand crowding. In a study of motion crowding using non-static Gabor patches, it was shown that theories such as compulsory averaging, developed to account mostly for form discrimination, must be modified to capture the characteristics of motion crowding (Bex & Dakin, 2005). Another study that examined the relationship of the crowding effect with chromaticity found that when target and flankers had different chromatic properties, crowding effect is reduced (Kennedy & Whitaker, 2010). The authors indicated that this difference in the crowding is more than a color “pop-out” effect, as most of the other previous studies found (Kooi et al., 1994; Pöder, 2007; Sayim, Westheimer, & Herzog, 2008), rather, it suggests that processing of achromatic and chromatic information is segregated in the context of crowding. These studies shed light on the idea of multiplicity of crowding, as was explicitly demonstrated in a recent study by Greenwood and Parsons (2020) that crowding effect is not a singular process. Although Greenwood and Parsons (2020) did not address the relative sensitivity to crowding between color or motion, it seems to be the

case in their results that the overall magnitude of color crowding was lower than motion crowding, consistent with the results of [Experiment 2](#) in the current study.

In comparing the crowding effect across stimuli and tasks, it is important to match the performance levels across them. We note that the task difficulties were not perfectly matched across stimuli and tasks in our study despite our best attempt. We tried to mitigate this problem by including a practice session in the beginning of all tasks to ensure that all participants were able to perform above 80% accuracy for non-crowded conditions. In addition, we tried to reduce the effect of task difficulty by normalizing data across conditions. However, we acknowledge that the possibility that the pattern of results in our study was affected by differences in the task difficulty across the three conditions. Future studies with different stimuli and tasks than the ones used in the current study will help to address the generalizability of our conclusions.

In summary, results from [Experiment 1](#) suggest that the processing in the M pathway may be more susceptible to spatial crowding effect compared to processing in the P pathway. This observation could be partially explained by the differential receptive field sizes between these two pathways at the same eccentricities. Using stimuli with different functional properties in [Experiment 2](#), our results show that crowding was more severe in discriminating forms which requires integrating simple components into distinct items, compared to extracting motion direction and color information.

Keywords: crowding, parallel visual pathways, temporal frequency, color, motion

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