# Poor peripheral binding depends in part on stimulus color

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## Abstract
We have compared two explanations for poor peripheral binding. Binding is the ability to assign the correct features (e.g., color, direction of motion, orientation) to objects. Wu, Kanai, and Shimojo (*Nature, 429*(6989), 262, 2004) showed that subjects performed poorly on binding dot color with direction of motion in the periphery. Suzuki, Wolfe, Horowitz, and Noguchi (*Vision Research, 82*, 58–65, 2013) similarly showed that subjects had trouble binding color with line orientation in the periphery. These authors concluded that performance in the periphery was poor because binding is poor in the periphery. However, both studies used red and green stimuli. We tested an alternative hypothesis, that poor peripheral binding is in part due to poor peripheral red/green color vision. Eccentricity-dependent changes in visual processing cause peripheral red/green vision to be worse than foveal vision. In contrast, blue/yellow vision remains centrifugally more stable. We tested 9 subjects in a replication and extension of Suzuki and colleagues' line orientation judgment, in red and green, and in blue and yellow. There were three central conditions: (1) red (or blue) all horizontal, green (or yellow) all vertical; (2) red (or blue) all vertical, green (or yellow) all horizontal; or (3) random pairing of color and orientation. In both the red/green and the blue/yellow color schemes, peripheral performance was influenced by central line orientation, replicating Suzuki and colleagues. However, the effect with blue/yellow lines was smaller, indicating that poor peripheral "binding," as hypothesized by both Wu and colleagues and Suzuki and colleagues, is due in part to their use of red and green stimuli.

People use their visual systems in order to view the world and navigate through the environment. However, visual acuity is far from being perfect, especially in the periphery. In order to limit neural resources, stimuli from the periphery of our field of view are processed at lower resolution than are stimuli from the center of our field of view, a phenomenon known as cortical magnification (e.g., Levi, Klein, & Aitsebaomo, 1985). Wu et al. (2004) examined the ability of subjects to bind the features of color and direction of motion correctly in the periphery. They found that subjects were greatly influenced by the alignment of features of stimuli presented centrally, perhaps because subjects were attempting to resolve the peripheral uncertainty by using information from the perceptually more robust central stimuli. Wu and colleagues found that red central dots moving up with green central dots moving

down induced a red-up/green-down binding percept in peripheral red-down/green-up dots. Similarly, Suzuki et al. (2013) found that their participants had a difficult time correctly binding the orientation and color of red and green horizontal and vertical lines in the periphery. Suzuki et al.'s subjects were also influenced by the alignment of features in central stimuli: red-horizontal/green-vertical central lines induced a red-horizontal/green-vertical percept in peripheral lines that were actually red-vertical/green-horizontal.

Two theories may help to describe this phenomenon. The first theory, known as the binding theory or feature-integration theory (Treisman & Gelade, 1980), explains that our brains pull multiple features of a stimulus together from separate processing areas in the cortex. Sometimes, errors are made in this process, which can lead to perceptual errors called *feature-binding errors* or *illusory conjunctions* (Treisman, 1996; Treisman & Gelade, 1980; Treisman & Schmidt, 1982). The second of these theories involves visual anatomy and physiology. Red/green visual accuracy has been shown to decrease in the periphery, more than does accuracy for other colors (Boynton, Schafer, & Neun, 1964; Dalhaus & Gunther, 2012; Hansen, Pracejus, & Gegenfurtner, 2009; Mullen &

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Kingdom, 2002; Murray, Parry, & McKeefry, 2006; Vakrou, Whitaker, McGraw, & McKeefry, 2005; Vanni, Henriksson, Viikari, & James, 2006; Vanston & Crognale, 2018), suggesting that the phenomena observed by Wu et al. (2004) and Suzuki et al. (2013) may have been caused by poor red/green peripheral vision. These two theories will be explored in greater depth before presenting our hypotheses.

Both Wu et al. (2004) and Suzuki et al. (2013) attributed the poor performance on peripheral red/green feature detection tasks to an error in the binding process. Binding theory (Treisman & Gelade, 1980) was proposed at a time when it was thought that different types of visual information were processed in different places within the brain (e.g., Livingstone & Hubel, 1988): color vision has been shown to be preferentially processed in visual cortical areas V4, especially within the "globs" (Conway, Moeller, & Tsao, 2007; McKeefry & Zeki, 1997; Seymour, Clifford, Logothetis, & Bartels, 2009; Zeki, 1978) and V8 (Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998); motion has been shown to be preferentially processed in V5 (Britten, Shadlen, Newsome, & Movshon, 1992; Newsome, Wurtz, Dürsteler, & Mikami, 1985; Seymour et al., 2009; Zeki, 1978); and neurons in V1, V2, and V3 have been shown to respond selectively to only one or two orientations (Gegenfurtner, Kiper, & Fenstemaker, 1996; Hubel & Wiesel, 1965, 1968; Zeki, 1978). Seymour et al. (2009) found that even within cortical regions, individual fMRI voxels selectively coded for color or motion, but not both. Shipp, Adams, Moutoussis, and Zeki (2009) similarly found that neurons in V2 cortical layers 3 and 4, which receive ascending signals, selectively respond to color or orientation or motion, but less frequently respond to two of these features.

More recent neurophysiological evidence refutes such strongly modular processing of visual information. Although Shipp et al. (2009) found that V2 neurons that receive ascending inputs are largely segregated in processing color, orientation and motion, the neurons in V2 cortical layers that receive feedback from higher cortical regions (layers 1, 5, and 6) show colocated processing of color and motion. In addition, some neurons in V1 have been shown to respond to both color and orientation (Garg, Li, Rashid, & Callaway, 2019; Shapley & Hawken, 2011; Shapley, Nunez, & Gordon, 2019). Our point is neither to argue the merits of binding theory, nor whether it is still relevant in light of the newer physiological evidence for more holistic processing of visual stimuli. Instead, we argue that low-level perceptual factors need to be kept in mind as well—factors such as the differential abilities of peripheral vision to process aspects of the stimuli, such as color.

Wu et al. (2004) and Suzuki et al. (2013) argued that misbinding was the reason that their subjects had trouble correctly determining the direction of motion or line orientation of red and green stimuli in peripheral vision. Binding theory posits that in order to make sense of a single stimulus with many different visual features, we must pull pieces of information from separate sections of the brain back together (Treisman, 1996). Otherwise, we would have all of this information, but would lack the ability to properly comprehend what the stimulus is doing in one instant. This process is known as *binding* or *feature integration*. According to binding theory, our brains sometimes make mistakes when attempting to pull all of the bits of information back together, causing binding errors in perception. For example, one object may be perceived as having the color of a second object, while the second object appears to be the color of the first (Treisman & Schmidt, 1982). This type of binding error is known as an *illusory conjunction*. Illusory conjunctions can occur with two objects that share a similar feature—the more similar, the higher the rate of illusory conjunctions (Ivry & Prinzmetal, 1991; Shevell & Wang, 2016). Further, binding errors have been shown to be more likely with peripheral stimuli (e.g., Neri & Levi, 2006). Wu et al. (2004) and Suzuki et al. (2013) argue that their subjects' decisions on whether peripheral red or green should be bound with dots moving up or down (or oriented horizontally or vertically) were influenced by the conjunctions of those features in the central stimuli.

However, visual anatomy and physiology provide an alternate explanation for the poor peripheral performance seen in Wu et al. (2004) and Suzuki et al. (2013). Both studies used red and green stimuli. Red/green color vision decreases in the periphery more so than does tritan (bluish/yellowish) vision (Boynton et al., 1964; Dalhaus & Gunther, 2012; Hansen et al., 2009; Mullen & Kingdom, 2002; Murray et al., 2006; Vakrou et al., 2005; Vanni et al., 2006; Vanston & Crognale, 2018). Red/green color vision is underlied by different retinal cells than is tritan vision. Red/green color vision begins with the long (L) and medium (M) wavelength-sensitive cones projecting to midget retinal ganglion cells (RGCs), whereas tritan color vision begins with the short-wavelength-sensitive (S) cones, contrasted with an L + M signal, projecting to small bistratified RGCs.

The receptive fields of the midget RGCs that underlie red/green vision have a center/surround organization. In the fovea, their receptive field centers receive input from a single L or M cone (Dacey, 1993b, 1999; Goodchild, Ghosh, & Martin, 1996; Kolb & Dekorver, 1991). With this single cone center (and thus pure L or M input), contrasted with a surround that most likely randomly receives input from neighboring L and M cones (Crook, Manookin, Packer, & Dacey, 2011; Diller et al., 2004; Lennie, Haake, & Williams, 1991; Mullen & Kingdom, 1996; but cf. Lee, Shapley, Hawken, & Sun, 2012), the receptive field gives good center versus surround chromatic opponency (Dacey, 1999; Lennie et al., 1991; Mullen & Kingdom, 1996, 2002). However, in the periphery midget RGC receptive field centers receive from multiple L and M cones (Crook et al., 2011; Dacey, 1993b; Goodchild et al., 1996; Lee, Martin, & Grünert, 2010)—although the

peripheral midget bipolar cells still largely receive from single cones in their receptive field centers, multiple bipolars feed into each midget RGC in the periphery (Lee & Silveira, 2016). This means that center versus surround chromatic opponency is worse in these receptive fields, and thus peripheral red/green vision is worse than in the fovea. However, psychophysical red/green performance does seem to decline closer to the fovea than the anatomy would predict—an issue that remains currently unresolved (Lee & Silveira, 2016).

Tritan vision does not use the same anatomical arrangement that red/green vision uses. The S cones project to small bistratified RGCs, which do not show a center surround organization like the midget RGCs do (Calkins, Tsukamoto, & Sterling, 1998; Chichilnisky & Baylor, 1999; Dacey, 1999; deMonasterio & Gouras, 1975; Lee et al., 2010; Lee & Silveira, 2016). Instead, the small bistratified RGCs select for S cones and contrast them with L and M cones (Chichilnisky & Baylor, 1999; Dacey, 1993a; Dacey & Lee, 1994). This selectivity for S cones remains across the retina, and thus tritan vision remains better into the periphery than does red/green vision (Boynton et al., 1964; Dalhaus & Gunther, 2012; Hansen et al., 2009; Mullen & Kingdom, 2002; Murray et al., 2006). This superior tritan peripheral performance carries through to cortical neurons (Vakrou et al., 2005; Vanni et al., 2006). In suprathreshold stimuli as well, red/green stimuli have been shown to decrease in perceived contrast as they move more eccentric, whereas tritan stimuli increase in perceived contrast from the fovea to 2.5°, but then maintain perceived contrast further into the periphery (Vanston & Crognale, 2018). By this logic, the inferior peripheral red/green color vision, and thus poorer distinction between red and green, may underlie the inability of the subjects in Wu et al. (2004) to accurately determine the direction of motion of red and green stimuli in peripheral vision, or the subjects in Suzuki et al. (2013) to accurately determine the orientation of the peripheral red and green lines. The more stable peripheral performance of the tritan system predicts that fewer peripheral conjunction errors should be seen with tritan stimuli.

The two theories lead to two hypotheses. If the poor peripheral performance seen by both Wu et al. (2004) and Suzuki et al. (2013) is due to binding errors that prevent accurate determination of the conjunction between color and direction of motion or orientation of red and green stimuli in the periphery, we hypothesize that tritan (bluish/yellowish) direction of motion or orientation detection in peripheral vision will also be biased by central stimuli. However, if the decreased peripheral accuracy seen by Wu et al. (2004) and Suzuki et al. (2013) was due at least in part to poor red/green peripheral vision, then we hypothesize that there will be less of a bias by central stimuli in tritan peripheral direction of motion or orientation detection.

## Methods

**Subjects** The data presented below are from nine subjects (one female, age 47 years; eight male, ages 19 to 22 years, $M = 20.9 \pm 1.1$; the unusual gender ratio is because Wabash College has an all-male student body). We were aiming for 10 subjects, the same number as Suzuki et al. (2013) had tested. However, the task turned out to be quite difficult, and we were unable to find a 10th subject who could do the task. An additional 15 subjects were tested, but they did not seem to understand the task or follow the directions. These subjects are discussed at the end of the Results section.

All of the subjects had normal color vision as determined by the Farnsworth-Munsell 100 Hue Test (error scores below 100 are considered to reflect normal color vision; we accepted error scores $\leq 50$). This experiment was approved by the Wabash College Institutional Review Board, and all subjects gave written informed consent. The protocol conforms to the Declaration of Helsinki.

**Apparatus** The stimuli were programmed in MATLAB (The MathWorks, Inc., Natick, MA), interfaced with Cambridge Research Systems' (CRS, Rochester, Kent, UK) ViSaGe visual stimulus generator. The stimuli were presented on a 20-in. NEC MultiSync FP2141[SB], with a 100-Hz refresh rate, 1,024 × 768 pixel resolution. The calibration of the monitor was verified with a PR-655 spectroradiometer (PhotoResearch, Syracuse, NY) or a ColorCAL (CRS) each day on which a participant was tested. Any day on which the luminances of the red and green (or violet and chartreuse) phases of the stimulus were off by more than ±2% Michelson contrast (e.g., $[LUM_{red} - LUM_{green}]/[LUM_{red} + LUM_{green}]$), the monitor was recalibrated by linearizing the voltage/luminance relationship independently for each of the three phosphors (red, green, and blue) in the display, using the Gamma Correction System (CRS) and a ColorCAL (CRS). CRS's MacLeod–Boynton color space was used. This color space uses the Smith and Pokorny (1975) cone fundamentals and transform matrices from Travis (1991). Responses were recorded with the use of a CB6 response box (CRS). Subjects placed their chins on a chin rest 57 cm from the monitor, in a dark, windowless room. All stimuli were viewed binocularly.

**Determining isoluminance** The stimuli used to study binding were presented at each subject's isoluminance to eliminate luminance artifacts. The L:M cone ratio, which largely underlies red/green isoluminance settings (Bieber, Kraft, & Werner, 1998; Kremers et al., 2000; Vimal, Pokorny, Smith, & Shevell, 1989), is known to vary across subjects, even those with normal color vision (Carroll, Neitz, & Neitz, 2002; Rushton & Baker, 1964), and across the retina (Bilodeau & Faubert, 1997; Hagstrom, Neitz, & Neitz, 1998). In addition, macular pigment concentration, which

selectively absorbs short wavelengths (Bone, Landrum, & Cains, 1992; Wooten & Hammond, 2005), thus making the bluish end of the tritan grating darker, also varies across the retina (Chen, Chang, & Wu, 2001; Wooten & Hammond, 2005).

**Isoluminance stimulus** The stimulus for determining isoluminance was a 6° diameter (Gabor filter standard deviation of 1), vertically oriented sinusoidal grating of 0.5 cycles per degree, counterphase flickering at 5 Hz. The overall stimulus size was chosen as it is similar to the width (6.75°) of the peripheral regions of the main task (see Horizontal/Vertical Line Stimuli section below). The temporal frequency was chosen to match the 200-ms (1/5 second) line stimulus presentation time in the main task. Isoluminance has been shown to vary with temporal frequency (Dobkins, Gunther, & Peterzell, 2000), thus it is important to match this to the stimulus presentation in the main task. The gratings were either red and green, or bluish and yellowish, presented on a mean gray background (color coordinates are presented in Table 1, in MacLeod–Boynton color space; MacLeod & Boynton, 1979). Isoluminance was determined at two eccentricities: 0° (fovea) and 10° (center of peripheral regions of oriented lines), right visual field only. A black fixation dot (0.2° diameter) remained in the center of the monitor for the duration of the block of 20 trials.

**Isoluminance procedure** The subjects set the red and green, or the bluish and yellowish, phases of the gratings to be isoluminant via heterochromatic flicker photometry (Dalhaus & Gunther, 2012; Ives, 1912). Subjects were informed of which color gratings (red/green or tritan) and eccentricity (0° or 10°) they would be working with—only one color and eccentricity were presented per block of trials. Subjects adjusted the relative luminances of the red and green (or bluish and yellowish) phases of the stimuli with coarse (adjust luminance 0.25 cd/m$^2$) and fine (adjust luminance 0.05 cd/m$^2$) buttons on the CB6 response box. If the standard deviation across the 20 trials was greater than 5% Michelson contrast [e.g., (Lum$_{red}$ −

Lum$_{green}$) / (Lum$_{red}$ + Lum$_{green}$) × 100%], the subjects completed additional trials until the most recent 20 met this criterion. We used these data as the isoluminance settings for the horizontal and vertical line stimuli, individualized for each subject at each eccentricity and color. The mean Michelson contrast for the isoluminance settings (± standard deviation) across the nine subjects and the range are presented in Table 2. Note that photometric isoluminance yields a Michelson contrast of zero.

**Horizontal/vertical line stimuli** As in Suzuki et al.'s (2013) Experiment 1b, subjects were presented with a 27° × 18° field of horizontal and vertical lines (each line was 3 × 1 pixels, or 0.405° × 0.135° in size), either red and green, or bluish and yellowish (see Table 1 for color coordinates, Fig. 1 for sample stimuli). The stimuli were divided up into three portions: a central block 13.5° × 18°, and left and right peripheral blocks each 6.75° × 18°. The peripheral blocks were nine stimuli wide, 24 stimuli tall in Suzuki et al. For ease of programming, ours were 10 stimuli wide, and 24 stimuli tall. Their central block was 18 stimuli wide (and 24 tall)—in order to maintain equal sizing between the central block and the two peripheral blocks, our central block was 20 stimuli wide (twice the width of a peripheral block, as in Suzuki et al.). The red and green stimuli, or the tritan stimuli, were isoluminant for each subject individually, at an average luminance of 15 cd/m$^2$ (Suzuki et al. used 14.8 cd/m$^2$). A white fixation point (2 × 2 pixels) was presented in the center of the field of stimuli. Small white tic marks indicated the boundaries between the central and peripheral fields, as in Suzuki et al. Stimuli were presented for 200 ms to minimize saccades and thus to keep the peripheral stimuli in the periphery.

In the central block of stimuli, we tested three of the conditions that Suzuki et al. (2013) did: random color/orientation pairing, red-horizontal (RH) and green-vertical (GV; their "Double 1" condition), and red-vertical (RV) and green-horizontal (GH; their "Double 2" condition; shown in Fig. 1, top). In all conditions there were equal numbers of red and green stimuli and horizontal and vertical stimuli. The differences were in how they were paired. We also tested bluish-horizontal (BH) and yellowish-vertical (YV), and bluish-vertical (BV) and yellowish-horizontal (YH) central conditions, in addition to the random color/orientation pairing (shown in Fig. 1, bottom).

The peripheral blocks of stimuli also contained 50% red (or bluish) and 50% green (or yellowish) stimuli. The green (or yellowish) stimuli were 50% horizontal, 50% vertical. The red (or bluish) stimuli were 0, 20, 40, 60, 80, or 100% horizontal, across different conditions.

Note in Table 1 that black presented as 0,0,0 in MacLeod–Boynton (1979) color space is read by the ViSaGe as being outside the monitor's gamut, and thus the software defaults to bright white. Thus, although black is in essence the lack of all

**Table 1** MacLeod–Boynton color space coordinates of stimuli

| Color | s | l–m | Luminance (cd/m$^2$) |
| --- | --- | --- | --- |
| Red | 0.016 | 0.280 | 15 |
| Green | 0.016 | 0.390 | 15 |
| Bluish | 0.028 | 0.335 | 15 |
| Yellowish | 0.004 | 0.335 | 15 |
| Black | 0.016 | 0.335 | 0 |
| White | 0.016 | 0.335 | 30 |
| Gray background | 0.016 | 0.335 | 15 |

**Table 2** Isoluminance settings

|  | RG fovea | RG periphery | Tritan fovea | Tritan periphery |
|---|---|---|---|---|
| $M \pm SD$ | $-0.0226 \pm 0.0279$ | $-0.0078 \pm 0.0233$ | $-0.0104 \pm 0.0069$ | $-0.0475 \pm 0.0102$ |
| Range | $-0.0470$ to $0.0427$ | $-0.0340$ to $0.0453$ | $-0.0213$ to $0.0013$ | $-0.0640$ to $-0.0280$ |

colors, it is entered as a gray (s = 0.016, l–m = 0.335), with zero luminance. Note also that the mean chromaticity of the red and green stimuli, and of the tritan stimuli, is the same as for the black background.

Further note that peripheral red/green vision can be enhanced by scaling the stimuli larger (e.g., Abramov, Gordon, & Chan, 1991; Tyler, 2015), but neither Wu and colleagues nor Suzuki and colleagues did so, and thus we do not scale the stimuli in our experiment here.

**Horizontal/vertical line procedure** The subjects' task was to determine whether the peripheral blocks contained more red (or bluish) horizontal lines than red (or bluish) vertical lines. They pressed the top left button on the CB6 response box if the peripheral blocks contained more horizontal lines, and the bottom left button if the peripheral blocks contained fewer horizontal lines (or more vertical lines). Subjects were instructed to ignore the horizontal and vertical lines in the



**Fig. 1** Horizontal/vertical line stimuli. The top figure shows a screenshot of the red/green stimuli with RVGH central condition. The bottom figure shows a screenshot of the tritan stimuli with random central condition. (Color figure online)

central field and instead attend to the peripheral blocks. Subjects were also told that the ratio of green (or yellowish) horizontal:vertical lines would always be 50:50. Subjects initiated each trial by pressing the top-right button on the CB6 response box.

There was a total of 36 conditions: three central block conditions, six different percentages red/bluish horizontal orientations in the peripheral blocks, and two color pairings (red/green and tritan). Each condition contained 20 trials, for a total of 720 trials. The order of presentation of the various conditions was randomized across trials. The 720 trials were split into four blocks of 180 trials each, so that subjects could take breaks between blocks.

**Fixation verification** In order to verify that subjects were fixating, and thus that the peripheral blocks were in the subjects' periphery, a letter/number task was implemented. Wu et al. (2004) and Suzuki et al. (2013) used eye trackers; we have successfully used the letter/number fixation task in our lab (Dalhaus & Gunther, 2012). Located directly above the fixation dot, a 20-pixel-tall white letter or number appeared for the same 200 ms as did the colored stimulus. Subjects responded whether the symbol was a letter or number, using the middle top and bottom buttons on the CB6 response box, respectively. If the subject answered the fixation task incorrectly or answered the line-orientation task prior to the fixation task, the trial was eliminated. There was no difference in the number of red/green versus tritan trials that were deleted because of missed letter/number tasks (red/green mean across subjects = 9.89 ± 9.253; tritan mean = 9.44 ± 8.413; paired $t$ test, $t(8) = 0.195$, $p = .850$). This fixation task may also serve to increase attentional demands foveally, which some have shown to enhance peripheral conjunction errors (Treisman & Schmidt, 1982), while others have not (Prinzmetal, Henderson, & Ivry, 1995).

## Results

First, in a two-way 3 (central conditions) × 6 (different percentage horizontal in the periphery) repeated-measures analysis of variance (ANOVA), we replicated Suzuki et al.'s (2013) findings of a main effect of central condition with the red/green stimuli, $F(2, 16) = 70.652$, $p < .001$, $\eta_p^2 = 0.898$ (see Fig. 2a). In a separate two-way repeated-measures ANOVA
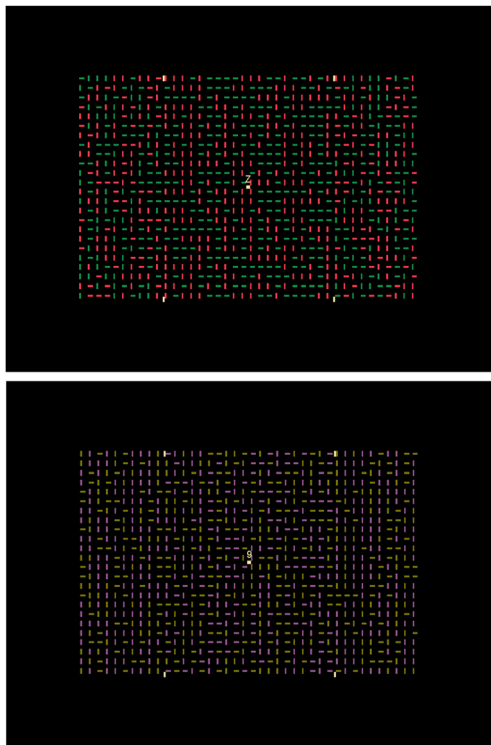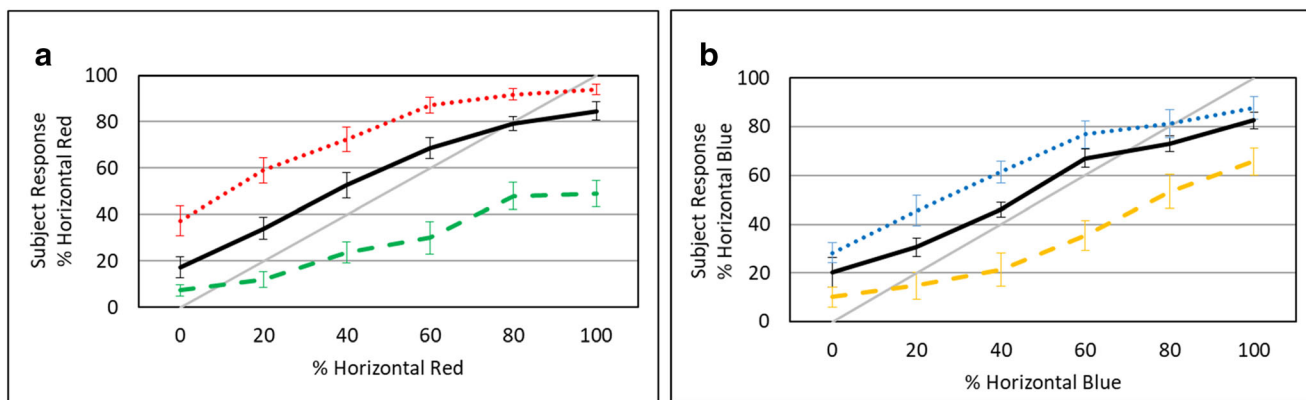
**Fig. 2** Shown are the data for the red/green (**a**) and the tritan (**b**) stimuli. Solid black lines represent the random central condition. Dotted red or blue lines show the RHGV or BHYV conditions, respectively. Dashed green or yellow lines show the RVGH or BVYH conditions, respectively. Solid gray lines show unity performance. Error bars represent ±*SEM*. (Color figure online)

on the tritan data, we again obtained a significant main effect of central condition, $F(2, 16) = 13.053$, $p < .001$, $\eta_p^2 = 0.620$ (see Fig. 2b). Individual subjects' data can be found in Appendices 1 (for the red/green condition) and 2 (for the blue/yellow condition). Line dot/dash and colors in the appendices are as in Fig. 2.

Our hypothesis was that the effect of the central condition on judgments of peripheral percentage horizontal that Suzuki et al. (2013) found with red and green stimuli is in part due to peripheral red/green color vision that decreases with eccentricity more than does peripheral vision for other colors (Boynton et al., 1964; Dalhaus & Gunther, 2012; Hansen et al., 2009; Mullen & Kingdom, 2002; Murray et al., 2006; Vanston & Crognale, 2018). Our data support this hypothesis in multiple ways. First, a three-way 2 (color conditions) × 3 (central conditions) × 6 (different percentage horizontal in the periphery) repeated-measures ANOVA showed a significant Color × Central Condition interaction, $F(2, 16) = 5.295$, $p = .017$, $\eta_p^2 = 0.398$. This is due to the effect size of the central condition being smaller with the tritan stimuli than with the red/green stimuli ($\eta_{p\ tritan}^2 = 0.620$ vs. $\eta_{p\ red/green}^2 = 0.898$). These effects can be seen in Fig. 2, in that the three central condition lines are closer together for the tritan stimuli (Fig. 2b) than for the red/green stimuli (Fig. 2a). We followed up this interaction with a post hoc repeated-measures ANOVA, on the difference in the percentage of times that each subject responded red (or blue) horizontal in the RHGV versus the RVGH (or BHYV vs. BVYH) conditions (R = red, G = green, B = blue, Y = yellow, H = horizontal, V = vertical), separately for each actual percentage horizontal red (or blue), as shown in Fig. 3. This yielded a significant main effect of color condition, $F(1, 8) = 6.335$, $p = .036$, $\eta_p^2 = 0.442$, showing that the size of the effect for the blue/yellow condition is smaller than the size of the effect for the red/green condition.

Suzuki et al. (2013) calculated the point of subjective equality (PSE)—the percentage actual red or blue horizontal when 50% of the red or blue lines were judged to be

horizontal—for each subject. Not all of our subjects reached the 50% mark (some RHGV or BHYV did not drop this low, and some RVGH or BVYH did not get this high; see Appendices 1 and 2 for individual subject data), thus we could not calculate this for each subject. Even with the data for all nine subjects averaged (see Fig. 2a), the RVGH line does not quite reach 50% (subjects averaged 49% perceived percentage horizontal when in fact 100% of the peripheral red lines were horizontal). However, estimating these values yields a difference of PSEs (ΔPSE) between RHGV (PSE ≈ 10%) and RVGH (PSE ≈ 100%) of approximately 90% actual peripheral red horizontal, versus approximately 55% actual peripheral blue horizontal for the BHYV (PSE ≈ 25%) versus BVYH (PSE ≈ 80%) comparison. Thus, we have shown nearly a two-fold smaller difference in PSEs for the tritan stimuli than for the red/green stimuli. Thus, by multiple different analyses, the data support our hypothesis that poor peripheral "binding" performance as seen by Suzuki et al. is at least in part due to their use of red/green stimuli.
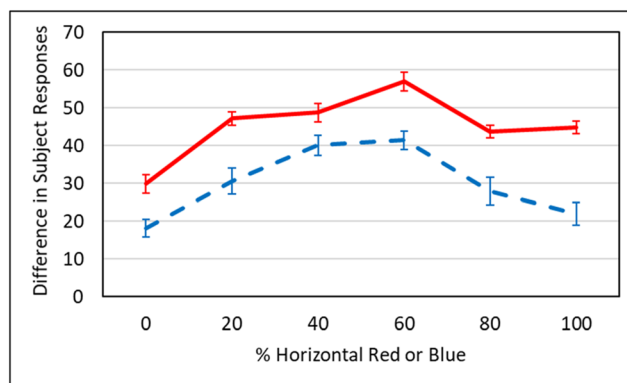


**Fig. 3** Shown are the differences between the RHGV and RVGH responses in Fig. 2a (red solid line) compared with the differences between the BHYV and the BVYH responses from Fig. 2b (blue dashed line). Error bars represent ±*SEM*. (Color figure online)

**Additional subjects tested** In the interest of transparency and fidelity of the data set, here we present an additional 15 subjects who did not seem to understand the task or follow the instructions. Five of these produced data that randomly bounced around 50% horizontal for all three central conditions (see Fig. 4a for a prototypical "random" responder). The other 10 subjects produced data logically separated by central condition, but nearly flat across peripheral percentage horizontal, appearing as though the subjects were responding to the central patches rather than to the peripheral ones (see Fig. 4b for a prototypical "central" responder). The slopes of the data from the central responders are statistically significantly flatter than the slopes from the peripheral responders: central responder mean slope = $0.0154 \pm 0.0062$, versus $0.1102 \pm 0.0086$ for the subjects who appear to be responding to the peripheral stimuli; $t(17) = 9.088$, $p < .001$. We have thus excluded the random and central responding subjects from the analyses that were presented above. However, we return to these subjects in the Discussion, in the framework of individual differences in crowding.

## Discussion

Through multiple analyses, our results show that poor peripheral binding is not the only explanation for the reliance by subjects on central information in making peripheral binding decisions as seen by both Wu et al. (2004) and Suzuki et al. (2013). Here, we show that poor peripheral red/green vision is also a factor, as supported by a significant Color × Central Condition interaction, a smaller effect size of central condition for tritan than for red/green stimuli, and by smaller ΔPSE for the tritan than for the red/green condition. However, even with tritan stimuli, perception of which is known to be more stable than red/green with changes in eccentricity (Boynton et al., 1964; Dalhaus & Gunther, 2012; Hansen et al., 2009; Mullen & Kingdom, 2002; Murray et al., 2006; Vanston & Crognale, 2018), we still see an influence of central line orientation/color binding on judgments of peripheral line orientation/color binding. Thus, the claim that binding is poor in peripheral vision remains. It just is not the entire explanation.

Suzuki et al. (2013) also pointed out that poor peripheral binding is not the whole story. They argued that the central region influences peripheral binding especially when there are both horizontal and vertical, and both red and green lines, and when the orientation-based grouping and segmentation, and the color-based grouping and segmentation, are correlated (the RHGV and RVGH conditions). In the random condition, where red and green were randomly paired with horizontal and vertical, veridical performance was seen on peripheral stimuli. Suzuki and colleagues tested an additional control, where all red and green lines were horizontal, or all were vertical. In this condition, they actually saw a contrast effect—red and green lines, all horizontal in the center, led to peripheral red lines being more likely to be perceived as vertical. Thus, the poor peripheral binding story is not a simple one. Our data add to this story, showing that the color of the lines also influences the extent of central influence on peripheral binding.

Some studies have shown that a foveal task can draw attention away from the periphery and thus diminish peripheral performance (Chan & Courtney, 1993; Schwartz et al., 2005; Treisman & Schmidt, 1982). Our fixation verification task may thus be having this effect. However, our hypothesis is that tritan peripheral performance should be less biased by the central condition than red/green peripheral performance is on the line orientation judgment task. There is no reason to suspect that the fixation task should affect peripheral red/green and tritan perception differently.

Two studies out of the Shevell lab initially might appear relevant to our hypothesis. Wang and Shevell (2014) looked at
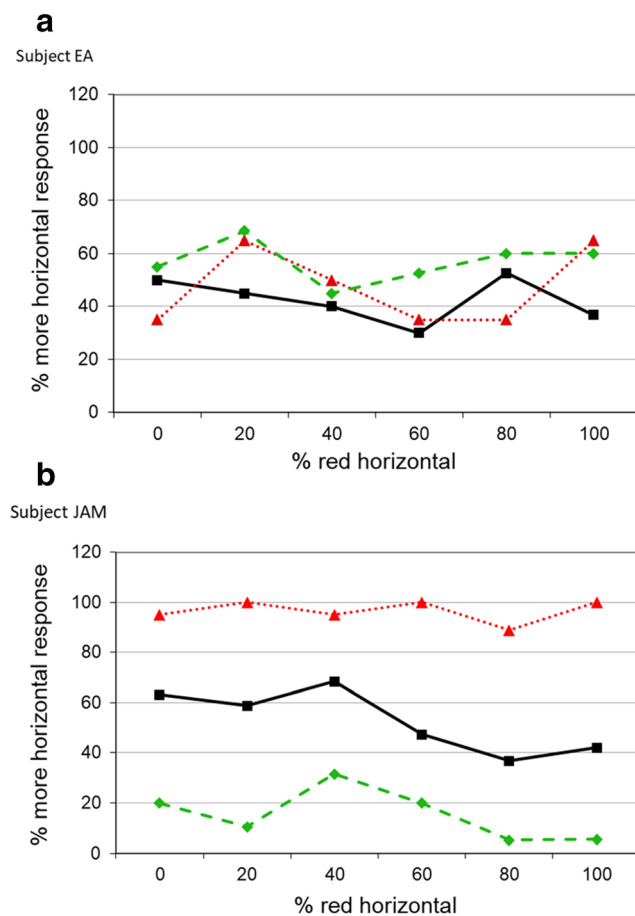


**Fig. 4** Shown are a prototypical "random" responder (**a**) and a prototypical "central" responder (**b**). The three lines represent the three central stimulus conditions: random color/orientation pairing (solid black line), red-horizontal/green-vertical (RHGV, red dotted line), and red-vertical/green-horizontal (RVGH, green dashed line). See text for further explanation. (Color figure online)

the involvement of S cones in binding errors. However, their question was different from ours; they tested how well red/green central stimuli could induce binding errors in peripheral red and green stimuli, as the red stimuli contained more and more S cone input (thus appearing purpler). They found that closer color matches between central and peripheral stimuli yielded stronger binding errors. They were not addressing our question of superior tritan peripheral vision as compared with red/green peripheral vision. Stepien and Shevell (2015) tested the experiments of Wu et al. (2004) and Suzuki et al. (2013), but with achromatic (white) stimuli instead of red and green. The focus of their hypothesis was also different from ours; they were interested in whether the influence of central objects on peripheral binding required chromatic colors. It is known that achromatic peripheral vision stays stronger in the periphery than does red/green (Hansen et al., 2009; Mullen & Kingdom, 2002; Mullen, Sakurai, & Chu, 2005), thus Stepien and Shevell's study could potentially be applied to our hypothesis that red/green peripheral binding errors are strong because of poor peripheral red/green vision causing subjects to rely more on information from central vision. However, they measured the misbinding of line orientation with direction of motion. Color was just an irrelevant source of noise in their red/green condition; it was not one of the features to be bound. Thus, their findings of a greater misbinding effect with the achromatic stimuli do not directly apply to our hypothesis.

**Individual differences in crowding** As discussed in the Results section, in addition to data from the nine primary subjects, we tested 15 subjects who were not able to perform the task as instructed, to respond to the orientation of the peripheral stimuli. Five of these subjects produced data that randomly bounced around 50% horizontal for all three central conditions ("random responders"; see Fig. 4a), while the other 10 subjects produced data logically separated by central condition, but nearly flat across peripheral percent horizontal ("central responders"; see Fig. 4b).

The lack of the ability of these subjects to perform the task correctly could be explained by individual differences in crowding. Crowding is when multiple stimuli (often letters; in the current study, horizontal and vertical lines), especially when presented in the visual periphery, prevent the normal resolution of the stimuli. For example, "B" by itself might be resolvable in the periphery, but not when presented surrounded by other letters such as "ABC." Our stimuli, with 10 lines within 6.75° (one line every 0.675°), is well within the stimulus density that typically induces crowding. Kooi, Toet, Tripathy, and Levi (1994) found, at 10° eccentricity (the center of our 6.75°–13.5° peripheral zone), that stimuli within 3°–6° of each other interfered with judgments of the target's orientation (horizontal vs. vertical) for black/white or red/green stimuli, and Yeshurun and Rashal (2010) found at 9°

eccentricity that stimuli needed to be spaced 4°–5° apart in order to be resolvable. At just under 6° eccentricity, in a densely cluttered display of horizontal and vertical lines, Van der Burg, Olivers, and Cass (2017) found that distractors 1° distant from the target produced crowding, while distractors farther away did not interfere with performance. Striking individual differences in crowding have been found at eccentricities ranging from 2.5° to 10° (Petrov & Meleshkevich, 2011; Toet & Levi, 1992), and Kooi et al. (1994) found substantial individual differences on their red/green color crowding task (in color normal subjects). Thus, our central responders may be subjects who experience heightened peripheral crowding, and were thus unable to respond based on peripheral line orientation or color. Instead, they appear to have responded based only on central condition, ignoring differences in the peripheral stimuli, leading to flat lines in Fig. 4b. It is also possible that our random responders also experienced heightened crowding, even for the central stimuli, and thus were not influenced by line orientation in either the central or peripheral portions of our stimuli.

Crowding has been shown to be affected by attention. When attention is drawn toward crowded peripheral stimuli, the effects of crowding are reduced (e.g., Yeshurun & Rashal, 2010). Our central fixation task could have had the opposite effect, drawing attention away from the periphery, thus enhancing crowding. If our central and random responders were attending more carefully to the fixation task, this might have heightened their peripheral crowding, thus impairing their performance on our task. However, a one-way ANOVA performed on fixation error rates showed no difference between the "good" subjects, the central responders, and the random responders: $F(2, 21) = 0.171$, $p = .844$, $\eta^2 = 0.016$.

Alternately, both the random and central responding groups of subjects may have been primarily interested in earning their research participation credits for their psychology courses, and did not really try to perceive the orientation of the lines (we did not record reaction times, so we cannot check if these subjects responded unusually rapidly to the stimuli). These two factors could even interact in subjects with heightened crowding and lower motivation to perform well.

## Conclusions

In summary, although we do find evidence for poor peripheral binding with tritan stimuli (colors shown to have superior peripheral performance compared to red/green), the influence of the central lines is weaker than for red/green stimuli. Thus, at least part of the poor peripheral performance seen by Wu et al. (2004) and Suzuki et al. (2013) is due to poor peripheral red/green vision.

Science, even vision science, has become increasingly siloed, with some researchers focusing on processes such as

binding and others focusing on color vision. The results of the current study highlight one hazard of this siloization, and a benefit of a broader understanding of visual perception (recognizing that even this is still siloed by sensory system, species, etc.).
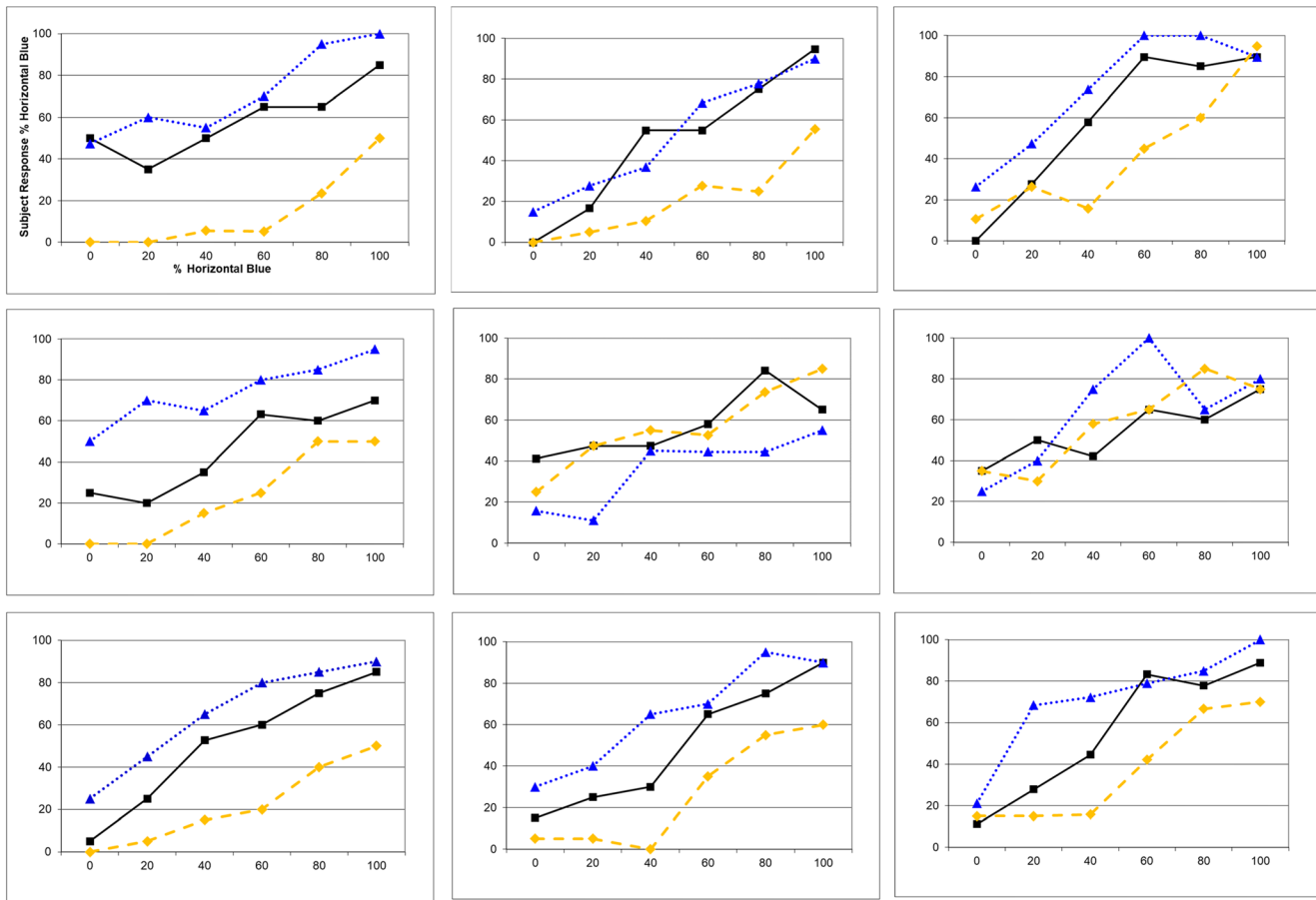
# Appendix 1. Individual subject data for the red/green condition
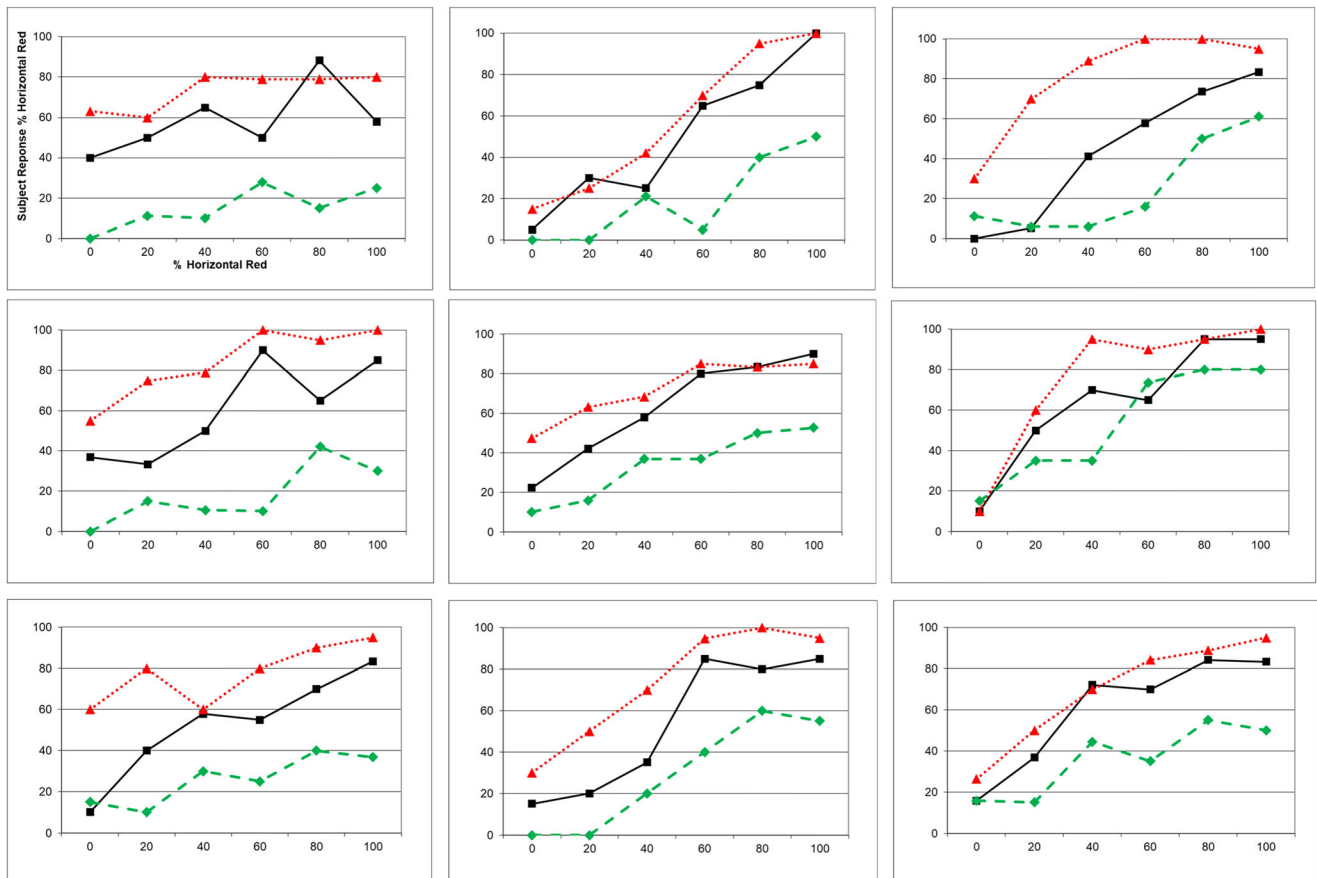
## Appendix 2. Individual subject data for the blue/yellow condition



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