

The role of color in motion feature-binding errors

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Color-motion feature-binding errors occur in the periphery when half of the objects are red and move downward, and the other half are green and move upward. When red and green objects in the central visual field are similar but move in the opposite directions (red upward, green downward), peripheral objects often take on the perceived motion direction of the like-colored central objects (Wu, Kanai, & Shimojo, 2004). The present study determined whether color is essential to elicit these motion-binding errors, and tested two hypotheses that attempt to explain them. One hypothesis holds that binding errors occur because peripheral and central objects become linked if they have combinations of features in common. A peripheral object's link to central objects overwhelms its posited weak peripheral representation for motion feature binding, so the peripheral object appears to move in the direction of the linked central objects. Eliminating color by making all stimuli achromatic, therefore, should not increase peripheral binding errors. An alternative hypothesis is that binding errors depend on the overall feature correspondence among central and peripheral features represented at a preconjunctive level. In this case, binding errors may increase when all objects are changed to achromatic because chromatic central/peripheral correspondence is maximal (100%). Experiments showed more motion-binding errors with all-achromatic objects than with half red and half green objects. This and additional findings imply that peripheral motion-binding errors (a) can be elicited without color and (b) depend at least in part on the similarity of central and peripheral features represented preconjunctively.

Introduction

We constantly perceive cohesive objects in the external world, but the neural processes that create such organized perceptual experiences are not well understood. Visual features of an object, such as shape, color, and motion direction, are processed in separate neural pathways and must be integrated for the percept of a cohesive whole (Livingstone & Hubel, 1988). The complexity of the integration process is revealed by some failures to combine features correctly. These feature-binding errors provide insight into the normal integration process.

Feature-binding errors occur when one perceives a combination of visual features that is not physically present in the external world. According to feature-integration theory (FIT), the detection of individual visual features occurs automatically at early, parallel stages of visual processing, whereas accurate feature binding requires focused attention and occurs at a later stage of processing (Treisman, 1996; Treisman & Gelade, 1980). At the feature detection stage, the theory assumes that the feature information is “free floating spatially” (Treisman & Gelade, 1980, p. 100). Without focused attention, therefore, the free-floating nature of the feature information can result in an erroneous combination of an object's perceived visual features (i.e., a feature-binding error).

On the other hand, observers readily experience feature-binding errors even while continuously attending to a stimulus (Wu, Kanai, & Shimojo, 2004). Binding errors occur for peripherally presented stimuli for the features of color and motion direction when the

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same colors and directions of motion are present in the central visual field. For example, observers perceive peripheral moving objects to move in the same direction as central objects that share the same color and shape, even though each peripheral object physically moves in the opposite direction. Specifically, consider a central visual field with red objects moving vertically upward and green objects moving vertically downward; and peripheral regions with red objects moving downward and green objects moving upward. When fixating at the center, observers often perceive the color-motion combination presented in the central visual field as also occurring in the periphery. In other words, the whole percept appears to be a single “sheet” of red objects all moving vertically upward and a separate sheet of green objects all moving vertically downward (Kanai, Wu, Verstraten, & Shimojo, 2006; Sun, 2011; Suzuki et al., 2013; W. Wang & Shevell, 2014; Wu et al., 2004).

A possible account of binding errors in the periphery is based on Barlow’s (1981) “linking feature” hypothesis. The theory proposes that peripheral objects become linked to central objects that have common visual features in an attempt to disambiguate the visual scene (Barlow, 1981). The ambiguity results from limited retinal neural bandwidth in the periphery compared to the central visual field. Visual features that may link peripheral to central objects include orientation, shape, object size, direction of motion, speed, and color. In the case of the red and green objects mentioned above, the peripheral moving objects could be linked to central moving objects if they have the same color, shape, and speed, but not direction of motion. On this account, color serves an important role by strengthening the link between central and peripheral moving objects, thereby increasing the frequency of color-motion feature-binding errors.

The idea that color plays an important role in creating binding errors is strengthened by the observation that red and green moving objects in the center very rarely cause feature-binding errors with red and equal-energy spectrum (EES) “white” objects in the periphery (Sun, 2011; W. Wang & Shevell, 2014). Although the red color is shared among some central and peripheral objects, there is no color link between the green objects in the center and the “white” objects in the periphery. Without a common color in center and periphery, these objects may be too weakly linked to cause a binding error.

Color’s status as a “linking feature” that could increase the frequency of illusory motion in the periphery does not require exact chromatic correspondence between center and periphery. Instead, peripheral feature-binding errors still occur when the chromaticities of central and peripheral objects are somewhat different. A larger chromatic difference

between central and peripheral objects reduces binding errors in a graded fashion; that is, binding-error frequency decreases monotonically as the chromatic difference between central and peripheral regions increases (W. Wang & Shevell, 2014). This suggests that the more similar central and peripheral objects are in color, the stronger the link is between them, which results in more color-motion binding errors.

Whereas color-motion binding errors still occur when the chromaticity of central and peripheral objects is not identical, it remains unclear if color is necessary at all to link central and peripheral objects for motion-binding errors. Investigating how color contributes to misbinding will clarify its role in the visual process of feature binding. The present study, therefore, addresses the following question about color. Is color required to elicit peripheral motion-binding errors? The “linking feature” hypothesis proposed by Barlow (1981) suggests that eliminating color should reduce peripheral feature-binding errors, because color would not serve as a cue to link central and peripheral objects. Other common features, however, still could provide feature links resulting in some binding errors. If so, this would imply that feature-binding errors do not require a chromatic link, though color may strengthen the link. Alternatively, color links may be essential for motion-binding errors, so colorless achromatic stimuli may not result in feature-binding errors. Experiments here determined whether binding errors were reduced with all-achromatic stimuli.

Another possible outcome, of course, is that binding errors may increase without color. In this case, the presence of color would *increase* veridical perception. This result would be inconsistent with the “linking feature” hypothesis and instead would support the view that binding errors depend on an ambiguity-resolving process driven by the *overall* feature correspondence among all central and peripheral objects (Shevell, 2012). This result has been found for object shape. When all of the objects in the center and periphery are the same shape (e.g., all squares, so 100% shape correspondence), then observers perceive peripheral illusory motion frequently (80% or more of the time; Sun, 2011). If shape correspondence among central and peripheral objects is reduced to 50%, 25%, or 0%, however, then the likelihood of perceiving illusory motion in the periphery decreases monotonically (Shevell, 2012; Sun, 2011). In the studies here, an increase in feature-binding errors with all-achromatic colorless objects, compared to half red and half green objects as used by Wu et al. (2004), would support the hypothesis of overall similarity of *single* features in the central and peripheral areas because the overall chromatic correspondence among colorless objects (100%) is greater than the 50% correspondence with half red and half green objects.

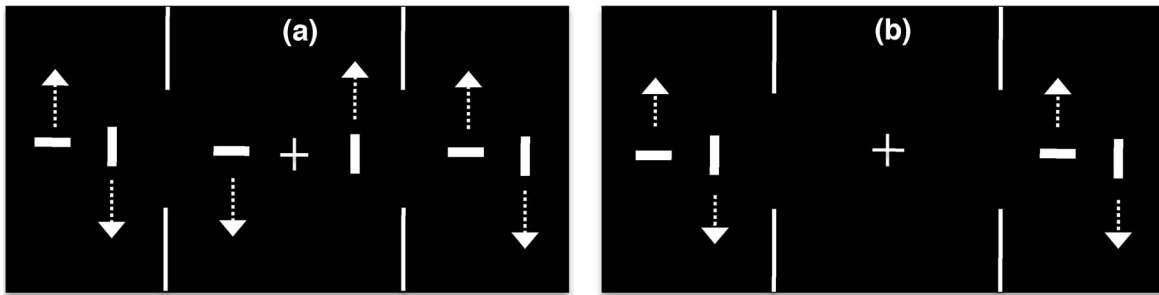


Figure 1. Schematic examples from the achromatic condition for (a) with-center stimuli and (b) no-center stimuli.

Methods

Apparatus

Stimuli were generated using an Apple Macintosh iMac computer and presented on an NEC Accu-Sync 120 cathode ray tube (CRT) color display. The CRT display was set to 1280×1024 pixel resolution at a refresh rate of 75 Hz noninterlaced. A spectroradiometer (PhotoResearch 650) was used to measure the spectral power distribution of the R (red), G (green), and B (blue) guns. Using a photometer (International Light 1700), the light level of each phosphor was measured throughout its range to find 990 equal steps (0.1% increments) between 1% and 100% of the phosphor's maximum.

Stimuli

Examples of the experimental stimuli are shown in Figures 1 and 2. The visual field was 28° wide \times 22° high and was separated into a central and two peripheral regions. The central region was 14° wide, and the left and right peripheral regions were each 7° wide. Four white vertical bars marked the beginning of the peripheral regions, and a white cross was presented in the center of the display as a fixation point. There were 320 moving objects, each one a horizontal or vertical line, in the central visual field, and 160 moving horizontal or vertical lines in each of the left and right peripheral fields. Each line was 0.33° long by 0.16° wide. Overall, the object density was about one object per square degree.

The speed of the moving lines was $14.1^\circ/\text{s}$, which ensured the perception of vertical motion in both the central and peripheral regions (Baker & Braddick, 1985). The luminance of all of the lines in both experiments was fixed at 12.5 cd/m^2 , and the background of the stimulus was dark ($< 0.01 \text{ cd/m}^2$).

All stimuli were specified in an l, s cone-based chromaticity space (MacLeod & Boynton, 1979) modified so the unit of $s = S/(L+M)$ was 1.0 for EES

“white.” In this space, the horizontal and vertical axes correspond to relative L versus M-cone [$l = L/(L+M)$] and relative S-cone [$s = S/(L+M)$] stimulation, respectively. For each observer, heterochromatic flicker photometry was used to equate phosphor radiances for equiluminant stimuli.

Each of the experiments had various *chromaticity* conditions. Experiment 1 included an all-achromatic condition and a red/green (r/g) chromatic condition. In the all-achromatic condition, all of the lines were metameric to EES “white” ($l = 0.665, s = 1.00$). In the central region, half of the lines were oriented vertically and moved in one vertical direction, while the other half were oriented horizontally and moved in the opposite vertical direction (e.g., vertical lines moved upward, horizontal lines moved downward). In the peripheral regions, horizontal and vertical lines moved in the opposite directions (e.g., vertical lines moved downward, horizontal lines moved upward; see Figure 1a for a schematic example). This opposite pairing of orientation and motion direction was always present between periphery and center. In the r/g chromatic condition, all of the vertical lines were one color (red or green), and all of the horizontal lines were the other color (see Figure 2a for a schematic example). The chromaticity of the red lines was $l = 0.800, s = 0.20$, and the chromaticity of the green lines was $l = 0.641, s = 0.20$. All combinations of color, orientation, and direction of motion were counterbalanced. Experiment 3 also included these all-achromatic and r/g chromatic conditions. Experiments 2 and 3 had additional chromaticity conditions, which will be discussed with their corresponding results.

There were also two different *center* conditions in all three experiments: a with-center condition and a no-center condition. The with-center condition served as the main experimental condition and had objects presented in the central and peripheral visual areas (as in Figures 1a and 2a). The no-center condition had no objects presented in the central area (see Figures 1b and 2b). The no-center condition served as a control: Observers should report the veridical motion direction in the periphery because they cannot use information from the center to disambiguate peripheral motion

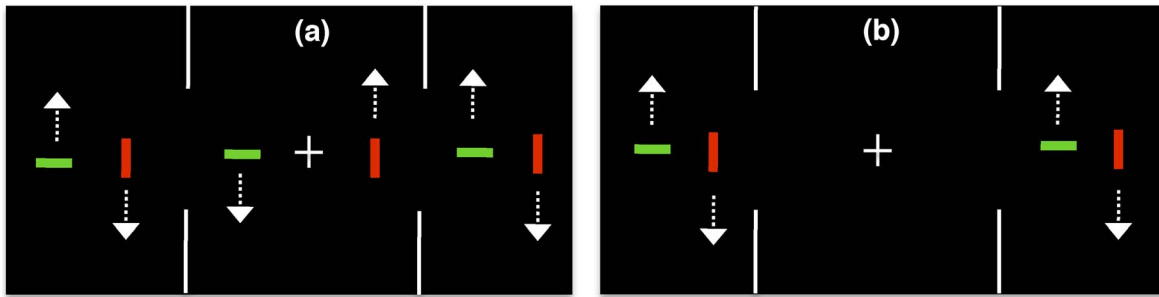


Figure 2. Schematic examples from the r/g chromatic condition for (a) with-center stimuli and (b) no-center stimuli.

(Suzuki, Wolfe, Horowitz, & Noguchi, 2013; Wu et al., 2004). The with-center and no-center conditions were run in each chromaticity condition, and they were presented in random order. The two combinations of orientation and direction of motion were counterbalanced (i.e., peripheral vertical lines moved upward or downward on half of the trials).

Procedure

In Experiment 1, each observer completed four separate sessions of each chromaticity condition (four all-achromatic sessions and four r/g chromatic sessions). Each session was completed on a separate day, for a total of eight days of participation. The first session of each chromaticity condition was considered practice and served to familiarize observers with the task and the stimulus. Observers were randomly assigned to the experimental chromaticity condition completed first (all-achromatic or r/g chromatic). Each observer completed one entire chromaticity condition (all-achromatic or r/g chromatic, four sessions over four days) before moving on to the other condition. Each session had 40 trials (20 with-center and 20 no-center) and each trial lasted for 20 s. The trials were separated by a 5-s visual masking period composed of “white” (EES) filled-in circles moving in random directions within the entire $28^\circ \times 22^\circ$ visual field. Each session lasted for 17 min. This procedure was slightly modified in Experiments 2 and 3, as described at the beginning of each experiment in the Results section.

In all experiments, observers were instructed to report the direction of motion of the vertical lines in the peripheral areas while maintaining their fixation on the cross in the center of the field. Observers used a chin rest that was mounted in front of the CRT display, which minimized head movements and centered their gaze on the fixation point.

In order to record responses, observers used a video game controller and were instructed to press and hold down one preassigned button when perceiving the peripheral vertical lines to be moving upward and a different preassigned button when perceiving the

peripheral vertical lines to be moving downward. The response buttons made alert sounds to confirm that the computer registered the responses.

The observers also had the option to press nothing, which would indicate that the peripheral vertical lines were not perceived to be moving cohesively in either direction (upward or downward) at that moment. Observers were informed that they could change their response as often as necessary within a trial and to report accurately what they perceived. Responses were measured approximately every 107 ms.

Observers

A total of five observers participated in the experiments. Experiments 1 and 2 had the same three observers (1, 2, and 3), who were undergraduate students at the University of Chicago (mean age = 19.7 years). Observer 3 did not participate in Experiment 3, so two new observers participated (4 and 5; mean age = 32.4 years). All observers had normal color vision, as tested with a Neitz anomaloscope and Standard Pseudoisochromatic Plates (Ichikawa, Hukami, Tanabe, & Kawakami, 1978). Observers 1, 3, 4, and 5 were naïve as to the design and purpose of the experiments. Observer 2 is an author and had prior experience in feature-binding experiments. Each observer completed a consent form in accordance with the policy of the University of Chicago’s Institutional Review Board.

Results

Experiment 1

A motion-binding error was defined as a response that was inconsistent with the physical motion direction of the peripheral vertical lines. For instance, when the vertical lines in the peripheral regions moved physically upward, but the reported direction was downward, then this response was considered a binding error. The

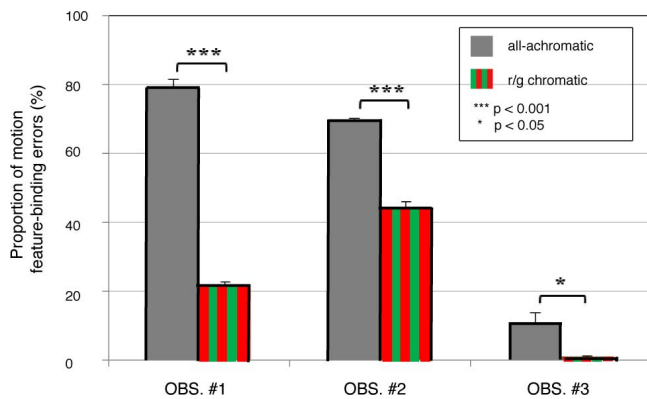


Figure 3. Results for the effect of chromaticity for individual observers. The vertical axis is the proportion of time each observer perceived the peripheral vertical lines as moving in the direction opposite to their physical direction of motion during with-center trials, for all-achromatic or r/g chromatic stimuli. Error bars are standard errors across three sessions for each experimental condition. (Calculation of standard errors was done in the inverse-sine transformed metric but converted here to a proportion for clarity of presentation).

proportion of time with a feature-binding error was determined for each 20-s trial period. Each proportion was subjected to a standard inverse-sine transformation to stabilize the variance from an underlying binomial distribution (Kirk, 2013) before completing two-way analyses of variance (ANOVA). For an extreme proportion near zero (due to at most a single binding-error response of 107 ms during the 20-s trial), the transformed value was set to $1/2n$, where n was the number of trials for one condition in a single session ($n = 20$). The two factors analyzed were Chromaticity (r/g chromatic and all-achromatic) and Center (with-center and no-center). The results for each observer were analyzed separately.

The proportion of response time with motion feature-binding errors in the with-center condition is shown in Figure 3 on the vertical axis, separately for each observer (horizontal axis). The proportion was calculated by averaging the fraction of time each observer reported a motion-binding error during with-center trials across the three sessions of each chromaticity condition (all-achromatic or r/g chromatic). The gray bars show the measurements for the all-achromatic condition and the red/green-striped bars for the r/g chromatic condition.

Surprisingly, every observer reported significantly more motion feature-binding errors in the all-achromatic compared to the r/g chromatic condition, $F(1, 8) = 209.6$ ($p < 0.001$), 111.8 ($p < 0.001$), and 8.67 ($p < 0.05$) for observers 1, 2, and 3, respectively. A simple-main-effects analysis for only with-center cases showed that each of the three observers experienced peripheral binding errors more frequently with all-achromatic

compared to r/g chromatic stimuli, $F(1, 8) = 407.7$ ($p < 0.001$), 221.1 ($p < 0.001$), 10.03 ($p < 0.05$), respectively; see Figure 3. This finding indicates peripheral motion-binding errors not only occur with stimuli without color, but in fact are more likely to occur with all-achromatic than with red and green chromatic stimuli.

In order to verify that the percept of motion feature-binding errors is not a motion aftereffect, the proportion of time with misbinding during with-center trials was compared to the proportion with no-center trials, for the all-achromatic and r/g chromatic conditions. If peripheral feature misbinding is *not* a motion aftereffect, then observers should almost never report feature-binding errors on all-achromatic and r/g chromatic no-center trials because there is no motion information in the center that could influence the perceived peripheral motion. Furthermore, if orientation-motion combinations in the center affect the perceived motion direction in the periphery, then observers should experience more peripheral feature misbinding in the with-center compared to no-center condition.

For two of the observers (1 and 2), the stimuli in the central region had a clear effect on feature-binding errors in both the all-achromatic and r/g chromatic conditions (Figure 4). These two observers experienced significantly more illusory motion in the periphery when the center was present relative to when it was not, $F(1, 8) = 897.3$ ($p < 0.001$), 3259.2 ($p < 0.001$) for Observers 1 and 2, respectively. Results for Observer 3 trended in the same direction, but were only marginally significant, $F(1, 8) = 3.8$, $p = 0.087$ (Figure 4), primarily because this observer very rarely experienced peripheral binding errors in the r/g chromatic with-center condition. Overall, these findings replicate the results of previous studies in that there were more motion-binding errors in the with-center compared to no-center condition (Suzuki et al., 2013; Wu et al., 2004).

Experiment 2

Experiment 1 revealed more peripheral feature-binding errors when all objects were achromatic compared to when they had two colors (red and green). Experiment 2 determined whether this increase in binding errors was caused by eliminating chromatic content entirely (as in Experiment 1) or, instead, was due to a single chromaticity for all objects in view (achromatic, red or green).

This was tested in conditions analogous to the all-achromatic condition of Experiment 1, except that now all of the objects were either all-red ($l = 0.800$, $s = 0.20$) or, in separate sessions, all-green ($l = 0.641$, $s = 0.20$). Each observer completed three sessions with each color of stimuli. The color of objects was alternated across

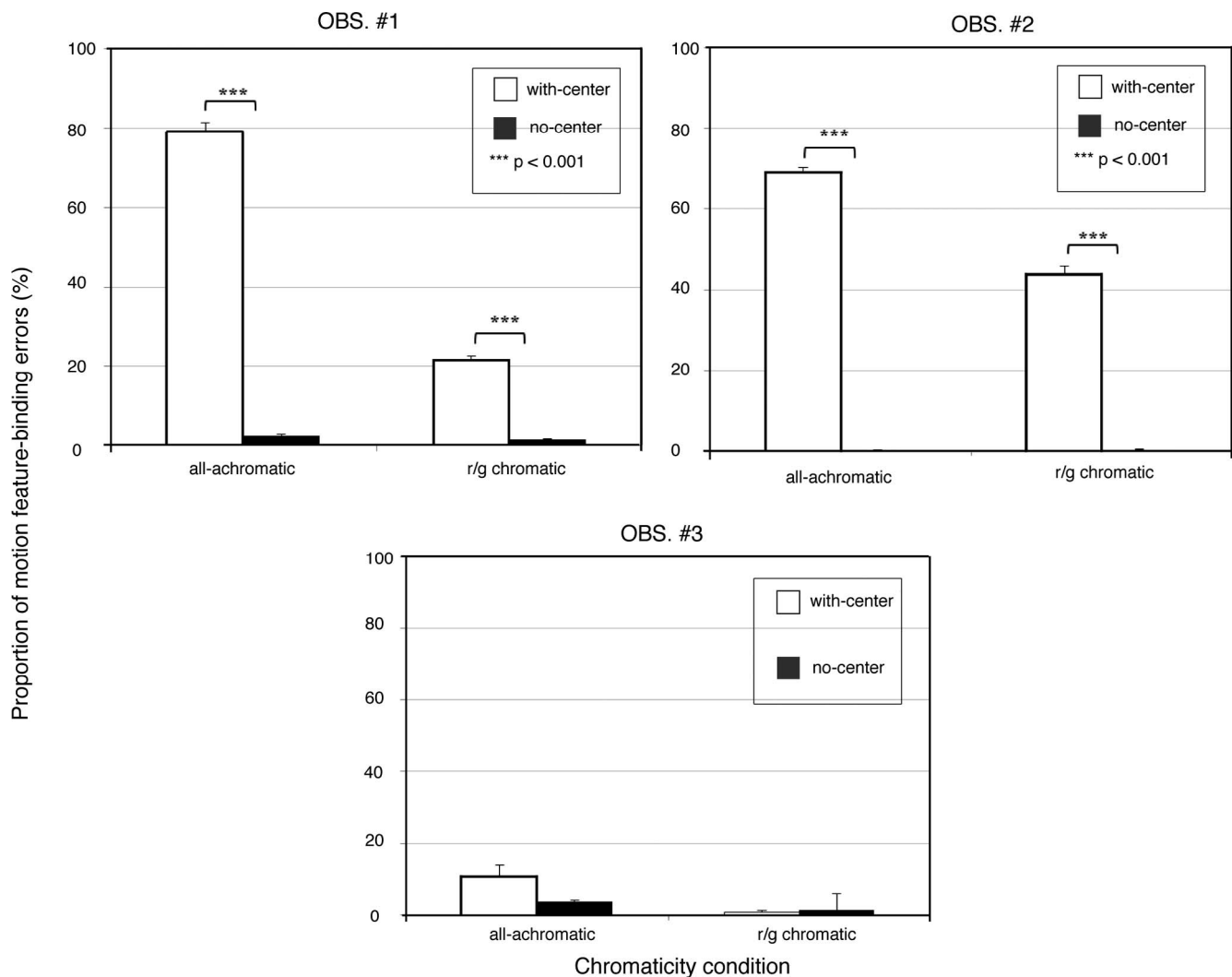


Figure 4. Results for effect of central stimuli for individual observers. The proportion of time each observer perceived the peripheral vertical lines as moving in the direction opposite to their physical direction of motion is shown in the with-center and the no-center conditions for all-achromatic or r/g chromatic stimuli.

days (e.g., if the observer completed an all-red session the first day, the next day was all-green). The observers were randomly assigned to the color condition they completed first. Otherwise, the experimental procedure and the observers were the same as in Experiment 1.

The proportion of motion-binding errors (vertical axis) as a function of observer (horizontal axis) is shown in Figure 5. The red/green-striped (gray) bars show results from the r/g chromatic (all-achromatic) condition from Experiment 1. The solid red bars and solid green bars represent the all-red or all-green conditions, respectively, in Experiment 2.

For each of the three observers, a two-way ANOVA revealed a significant main effect of Chromaticity (now r/g chromatic, all-achromatic, all-red, or all-green): $F(3, 16) = 51.85$ ($p < 0.001$), 38.003 ($p < 0.001$), and 7.83 ($p < 0.01$) for Observers 1, 2, and 3, respectively; a main effect of Center, $F(1, 16) = 1284.3$ ($p < 0.001$),

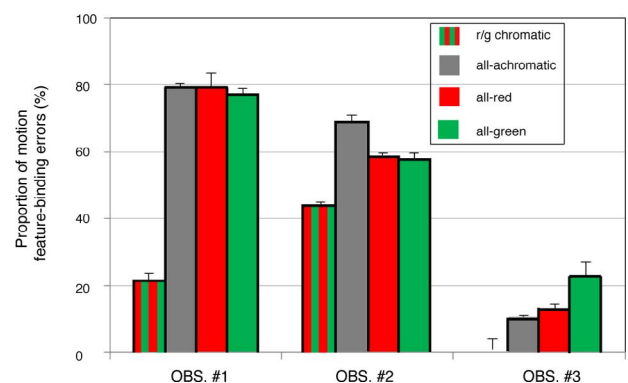


Figure 5. Results for the r/g chromatic, all-achromatic, all-red, and all-green conditions for each individual observer for with-center trials.

6742.1 ($p < 0.001$), 42.2 ($p < 0.001$), respectively; and an interaction between Chromaticity and Center, $F(3, 16) = 45.7$ ($p < 0.001$), 38.0 ($p < 0.001$), 6.1 ($p < 0.01$), respectively. A simple-main-effects analysis showed a significant difference in the proportion of time with motion-binding errors between the different chromaticity conditions considering only the with-center cases, $F(3, 16) = 291.7$ ($p < 0.001$), 222.7 ($p < 0.001$), 40.8 ($p < 0.001$), respectively; see Figure 5. Finally, as expected, there was no significant effect of Chromaticity for the no-center trials, $F(3, 16) = 0.9$, near 0, 1.15, all $p > 0.35$. (The near zero F value for Observer 2 reflects all proportions extremely close to zero, that is 107 ms or less of binding errors during 20 s of observation.)

Additionally, for the all-red and all-green chromatic conditions, a simple-main-effects analysis revealed significantly more feature-binding errors during with-center compared to no-center trials for each of the all-red stimuli and all-green cases, all-red: $F(1, 16) = 472.3$ ($p < 0.001$), 1694.6 ($p < 0.001$), 16.7 ($p < 0.001$), respectively; all-green: $F(1, 16) = 415.8$ ($p < 0.001$), 1669.0 ($p < 0.001$), 37.8 ($p < 0.001$), respectively. This finding implies that the proportion of time with feature-binding errors during with-center trials could not be explained by a motion aftereffect.

In order to assess the differences in motion-binding errors between particular chromaticity conditions, planned nonorthogonal comparisons were performed (all following p values are Bonferroni corrected). First, the proportion of feature-binding errors in the with-center r/g chromatic condition was compared to the average proportion across the all-achromatic, all-red, and all-green single-chromaticity conditions. This comparison revealed that all three observers experienced significantly more peripheral motion-binding errors in the single-chromaticity conditions compared to the r/g chromatic condition. Observer 1: $t(16) = -17.08$, $p < 0.001$; Observer 2: $t(16) = -12.41$, $p < 0.001$; Observer 3: $t(16) = -6.17$, $p < 0.001$. Next, the proportion of feature-binding errors in the with-center all-achromatic condition was compared to the average proportion across the all-red and all-green conditions. The results showed no significant difference for Observer 1, $t(16) = 0.28$, $p > 0.5$, and significant though opposite directions of difference for Observer 2, $t(16) = -2.7$, $p < 0.05$, and Observer 3, $t(16) = 7.59$, $p < 0.001$. Finally, the frequency of peripheral feature misbinding in with-center all-red trials was compared to the frequency in with-center all-green trials. There was no significant difference for any observer, $t(16) = 0.75$, 0.31, and -2.34 , respectively for the three observers, $p > 0.09$. Overall, there exist some small and inconsistent differences in the frequency of motion-binding errors among the all-achromatic, all-red, and all-green conditions, but, most importantly, every observer experi-

enced significantly fewer peripheral motion-binding errors in the r/g chromatic condition compared to the all-achromatic, all-red, and all-green conditions.

Experiment 3

The findings from Experiments 1 and 2 generally show fewer peripheral feature-binding errors in the r/g chromatic condition compared to any single-chromaticity condition. It remains unclear, however, why observers were more likely to perceive the veridical direction of motion in the periphery in the r/g chromatic condition compared to the single-chromaticity conditions. A possible explanation is that presenting objects of two different colors (as in the r/g chromatic condition) is more likely to capture observers' attention, thereby increasing their probability of perceiving the veridical motion direction in the periphery. Experiment 3 tested this attentional capture hypothesis as a way to explain the findings from Experiments 1 and 2.

The attentional capture hypothesis was tested with a new condition similar in many ways to the r/g chromatic condition. In the new condition, half of the vertical and half of the horizontal lines in the center and periphery were red, and the other half of the vertical and horizontal lines in center and periphery were green. Thus each line, regardless of orientation or location, had a 50% probability of being red or green, so there was no correlation between orientation and color. This condition, termed the r/g random condition, was similar to the earlier r/g chromatic condition in that half of the objects were red and half of the objects were green, but now line orientation (vertical or horizontal) was independent of color.

Two observers (1 and 2) had participated in Experiments 1 and 2, and two other observers (4 and 5) were new. The order of the r/g chromatic, all-achromatic, and new r/g random conditions was randomized. Two sessions were completed in a single day with a 15-min break between them. Only with-center trials were run (no no-center trials).

There are two possible outcomes for Experiment 3. First, observers may be as likely (or less likely) to perceive illusory motion in the r/g random condition as in the r/g chromatic condition. This result would indicate less frequent binding errors in these two conditions compared to the all-achromatic, all-red, and all-green conditions, so would be consistent with two stimulus colors in the periphery capturing greater attention than when all stimuli have the same color, thus giving a more veridical perceived direction of peripheral motion. Alternatively, the proportion of time with peripheral feature-binding errors could be greater in the r/g random condition compared to the r/g chromatic condition. This result would not support the attentional capture hypothesis as a way to explain less

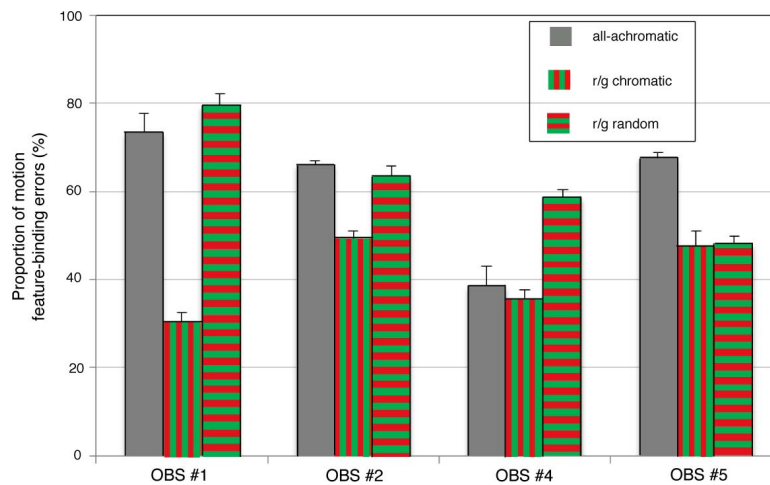


Figure 6. Results for the r/g chromatic, all-achromatic and r/g random conditions for each individual observer for with-center trials.

frequent feature-binding errors in the r/g chromatic condition compared to the single-chromaticity conditions. Instead, it would imply that the simple presence of two colors and the attention they may capture is not the critical factor that reduces feature-binding errors, compared to the single-chromaticity conditions.

The proportion of peripheral feature-binding errors (vertical axis) as a function of observer (horizontal axis) is shown in Figure 6 for the three chromaticity conditions of Experiment 3. The red/green vertically-striped (gray) bars show results from the r/g chromatic (all-achromatic) condition (as in earlier experiments but repeated here in a randomized set). The red/green horizontally-striped bars represent the r/g random condition in Experiment 3.

A one-way ANOVA revealed a main effect of Chromaticity for all observers, $F(2, 6) = 41.4$ ($p < 0.001$), 16.0 ($p < 0.01$), 11.7 ($p < 0.01$), and 17.8 ($p < 0.01$) for Observers 1, 2, 4, and 5, respectively. In order to assess the differences in feature-binding errors among conditions, planned nonorthogonal comparisons were performed (again, all of the following p values are Bonferroni corrected). First, the average proportion of feature-binding errors in the r/g chromatic condition was compared to the average proportion in the all-achromatic condition. As expected, this revealed that the likelihood of a binding error in the all-achromatic condition was greater than in the r/g chromatic condition for Observers 1, 2, and 5, $t(6) = -7.28$, -5.29 , and -5.22 , respectively, all $p < 0.01$. Observer 4 did not show this effect, $t(6) = -0.54$, $p > 0.5$. Overall, however, this generally replicates the results from Experiment 1.

Next, to investigate whether the mere presence of two different colors reduces feature-binding errors via attentional capture, the average proportion of feature-binding errors in the r/g chromatic condition was compared to the average proportion in the r/g random

condition. The results for Observers 1, 2, and 4 were significantly higher in the r/g random condition, $t(6) = -8.37$, ($p < 0.001$), -4.39 ($p < 0.01$), and -4.44 ($p < 0.01$), respectively, though not for Observer 5, $t(6) = 1.18$, $p > 0.5$. The results for Observers 1, 2, and 4 clearly reject the attentional capture hypothesis as a way to explain the less frequent binding errors in the r/g chromatic condition compared to the single-chromaticity conditions, because the color difference in the r/g random condition did not lead to the lower frequency of binding errors found in the r/g chromatic condition.

Discussion

The contribution from color to peripheral feature-binding errors

The original report of sustained motion-binding errors in the periphery had moving-dot stimuli of two colors (Wu et al., 2004). For example, in the central visual field, half of the dots were red and moved upward while the other half were green and moved downward. Dots in the periphery were similar except red and green dots moved in the opposite directions (red downward, green upward). The remarkable feature-binding failure was that all red dots (central and peripheral) often appeared to move in the same upward direction, which was opposite to the physical direction in the periphery. Dots of two colors were essential for this experimental design, which required observers to decide whether most red peripheral dots moved upward or downward. Even putting aside the task requirement to report on red dots, without two colors the central and peripheral stimuli would be identical (both would be dots of a single color, with half

of them moving upward and half downward) so no feature-binding errors could be detected.

The present study aimed to unravel the specific role of color in peripheral feature-binding errors. To that end, red and green dots were replaced by short horizontal and vertical line segments (Figure 1). In some conditions, all lines had the same chromaticity (achromatic, red, or green); in another condition, all vertical lines were red and all horizontal lines green (or vertical green and horizontal red, counterbalanced).

One clear finding is that color is *not* required to elicit peripheral motion-binding errors. When all the objects were achromatic lines (half vertical, half horizontal), peripheral feature-binding errors often were perceived, sometimes for more than 50% of the viewing time. Thus, object orientation (horizontal or vertical) can substitute for object color and still result in frequent feature-binding errors in the periphery. Objects of different colors are not necessary.

A second result reveals the specific influence of introducing colors to objects that move in different directions and that already are differentiated by their orientations. An all-achromatic condition composed of vertically oriented lines moving in one direction and horizontally oriented lines in the other was compared to a condition with added redundant color (for example, all vertical lines were red and all horizontal lines green). Surprisingly, adding the redundant color reduced the frequency of binding errors. Although different colors for dots moving in opposite directions within each visual area were essential for eliciting the original binding errors demonstrated by Wu et al. (2004), in general introducing color differences among objects can reduce, rather than enhance, binding errors when another feature (here orientation) already serves to differentiate those objects moving in one direction or the other.

A possible explanation for the drop in binding errors caused by adding redundant colors is the potential difference in attention allocated with two colors compared to one. Attention is well known to alter the accuracy of feature binding (Treisman & Gelade, 1980), so if the presence of two peripheral colors captures more attention than one color, then binding errors should decline. This hypothesis was tested in Experiment 3 with half of the objects in each area red and the other half green, as before, but now without the systematic (and redundant) correspondence with orientation. Instead, in each visual area, a random half of the horizontal lines was red and the other half green, and similarly for the vertical lines. If two colors in the periphery instead of one serve only to attract additional attention, then the frequency of binding errors should be the same as with redundant colors (the r/g chromatic condition). Instead, in comparison to redundant colors, random assignment of colors to horizontal and vertical objects increased the frequency of binding errors for

every observer (significantly so for three of four of them). This is contrary to the prediction that two peripheral colors reduce binding errors by only capturing more attention than a single color.

Individual differences in feature-binding errors

Individual differences were apparent in the proportion of total time with motion feature-binding errors in Experiments 1 and 2. Among the three observers, Observer 3 experienced a smaller overall proportion of motion feature-binding errors in every experimental condition, compared to the other two observers. This was especially clear in the r/g chromatic condition in which all observers had the fewest binding errors. Despite these individual differences, however, the same overall pattern of results was found for all three observers (see Figures 3 and 5).

Theoretical implications

As discussed earlier, Barlow's "linking feature" hypothesis predicts peripheral feature-binding errors cannot be less frequent in the r/g chromatic condition compared to the single-chromaticity conditions. According to this hypothesis, color serves as an additional visual feature that links central and peripheral moving objects, thereby increasing peripheral binding errors by strengthening the link between central and peripheral objects that share the same *combination* of features (say, green *and* horizontal).

The results here show that feature-binding errors in the periphery are more common in the single-chromaticity conditions (all-achromatic, all-red, and all-green conditions) than in the r/g chromatic condition, contrary to the "linking feature" prediction. These results instead are consistent with feature-binding errors that depend, at least in part, on the overall feature correspondence among *individual* features in the central and peripheral areas (Shevell, 2012; Sun, 2011). Consider each single-chromaticity condition. Every central object has the same chromaticity as *all* of the peripheral objects; also every central object matches half of the peripheral objects in orientation (i.e., horizontal or vertical). In the r/g chromatic condition, on the other hand, every central object matches only half of the peripheral objects in chromaticity (and also half in orientation), so the overall single-feature commonality among central and peripheral objects is weaker than in the single-chromaticity cases. Importantly, note that the classic color-motion misbinding stimulus with red and green dots (Wu et al., 2004), discussed in the Introduction, has single-feature correspondence among central and peripheral areas similar

to the single-chromaticity conditions here. In their stimuli, every central object matched all the peripheral objects in shape (shape is a stand-in for orientation) and half of the peripheral objects in chromaticity. Thus, considering the feature dimensions of (a) shape/orientation and (b) color, both their study and the single-chromaticity conditions here link central and peripheral areas 100% for one feature and 50% for the other.

More than just preconjunctive feature correspondence

Prior to combining visual features into an integrated object (e.g., a green horizontal line), consider a “preconjunctive” stage where visual features are represented separately. This is similar to the free-floating concept of FIT (Treisman & Gelade, 1980) insofar as an object’s orientation and color are represented separately before being integrated. The results above show that correspondence between central and peripheral areas at the level of *single* features (say, green), not joint features (green *and* horizontal), contributes to motion feature-binding errors. Assuming that objects in the center are represented more reliably than objects in the periphery, greater correspondence increases binding errors in peripheral areas by extending central feature binding to perceived feature combinations in the more sparsely represented periphery. Using single features to link areas of the visual field in the service of determining feature binding is appealing because the linkage precedes the conjunctive binding that the linkage ultimately may transform.

Experiment 3 raises the question of *which* single features affect motion binding. It reveals that simple correspondence of the single features of color and of orientation is not the answer because the r/g chromatic and r/g random conditions have identical preconjunctive correspondence for each feature (50% for color and 50% for orientation) yet give different frequencies of feature-binding errors (a difference that reached statistical significance for three of four observers).

The difference between these two conditions is that color is related systematically to direction of motion in the r/g chromatic condition; that is, every red object in the center moves in only one direction, and the same is true for every green object in the center, every red object in the periphery, and every green object in the periphery (Figure 2a). Thus, given an object’s location in center or periphery, its color (and also its orientation) consistently is related to only one direction of motion. Therefore, both color and orientation are features that link to a single direction of motion in the center, and also to a single direction in the periphery. On the other hand, color in the r/g random condition is not consistently assigned to one direction of motion

anywhere so color is not informative about motion. In terms of extrapolating central feature binding to the periphery, color is not a useful link between central and peripheral motion because every object in the periphery has a color that matches like-colored central objects that may move upward or downward (half in each direction). In comparison to the all-achromatic condition, there was no consistent reduction in binding errors caused by introducing random color (Experiment 3), unlike what was found for the r/g chromatic condition. This suggests that color is ignored at the preconjunctive stage in the r/g random condition because it fails to provide consistent information about motion direction.

An important question is how an irrelevant feature like color in the r/g random condition is disregarded when extrapolating feature binding from center to surround. Prior studies of binding provide a basis for speculation. First, the color of moving objects in one region is known to influence the perceived motion of like-colored objects in another region when motion in the first region is coherent (all objects of a given color move in the same direction) and in the other region is incoherent (like-colored objects move in various directions; Noguchi et al., 2011). Stimuli of a given color in the r/g random condition, in either the center or surround, always were incoherent, so the lack of influence from color is not unexpected.

Second, the effect of coherence is posited to depend on an early representation of feature combinations that contributes to scene analysis (Noguchi, Shimojo, Kakigi, & Hoshiyama, 2011). Feature binding may occur at more than one level of the visual system (Holcombe & Cavanagh, 2001; Treisman, 1999; Wolfe & Cave, 1999). Thus, the early representation may be distinct from a separate representation of bound features that mediates integrated object perception. This is consistent with color-contingent motion after-effects from locally paired opposite-motion stimuli, which reveal an early stage of neural feature combinations that precedes a later representation that mediates perception of objects with integrated color and motion (Blaser, Papathomas, & Vidnyanszky, 2005). The early-stage representation may implicitly convey that color does *not* provide reliable information regarding direction of motion in the r/g random condition, leading to disambiguation of peripheral motion that takes no account of color.

Implications for neural processes mediating feature binding

Conjunctions of color and form reveal patterns of neural activity as early as primary visual cortex (Seymour, Clifford, Logothetis, & Bartels, 2010). The

particular areas associated with color-form conjunction representations are distinct from those associated with processing each feature alone (color *or* form; Seymour et al., 2010). Hence, it is probable that the experimental conditions in the studies here recruited neural activity in cortical areas V1 through V4, as they resulted in percepts with orientation-chromaticity conjunctions.

A neural representation of feature conjunctions in early visual cortex does not, of course, exclude contributions from higher cortical areas. For example, during the feature-binding process, peripheral objects may become linked to central objects that have common visual features in order to disambiguate the peripheral visual information (Barlow, 1981; Wu et al., 2004). This ambiguity results from the sparse neural representation in the periphery compared to the central visual field. As higher-level areas of the brain are posited to resolve ambiguous information (Leopold & Logothetis, 1996; Logothetis & Schall, 1989; Pack, Berezovskii, & Born, 2001; Shipp, Adams, Moutoussis, & Zeki, 2009; Sun, 2011; M. Wang, Arteaga, & He, 2013), an ambiguity-resolving process mediating feature binding may depend on neural mechanisms in these areas. Previous studies used visual stimuli with conflicting visual information (e.g., binocularly rivalrous stimuli causing bistable perception) to investigate cortical activity associated with resolving ambiguity. For example, monkey V4 neurons show patterns of activity corresponding to perceptual dominance during binocular rivalry established with orthogonally oriented gratings (Leopold & Logothetis, 1996). Also, neural activity in cortical area MT reflects the motion percept during motion rivalry, and correlates with the unambiguous motion percept derived from ambiguous motion features of a moving grid viewed through an aperture (Logothetis & Schall, 1989; Pack et al., 2001). Additionally, neurons in monkey inferotemporal cortex (IT) respond during the interpretation of ambiguous (morphed) images, and these responses correlate with how these images are interpreted (Liu & Jagadeesh, 2008). Thus, if an ambiguity-resolving process explains the feature-binding errors here, then these higher-level cortical areas involved in ambiguity resolution may contribute also to feature binding.

Whereas bottom-up processing is essential for a neural representation of a physical object, activity in higher-level cortical areas that mediate ambiguity resolution may reflect top-down processing in the form of neural feedback (Kanai et al., 2006; Logothetis & Schall, 1989; Pack et al., 2001; Seymour, Clifford, Logothetis, & Bartels, 2009; Whitney, 2009). In fact, such feedback has been posited to explain feature-binding errors. Recently, neural activity in V2 was reported to correlate with perceived color-motion binding errors (Zhang, Jiang, Zhang, Han, & Fang, 2014). Moreover, neurons in deep layers of V2 reveal

“combinatorial (dual) feature selectivity” (e.g., selectivity for a particular conjunction of orientation and color) via feedback connections from higher areas such as V4 and V5 (Bartels, 2009; Seymour et al., 2009; Shipp et al., 2009). Thus, erroneous feature combinations (that is, binding errors) may arise due to feedback from V4 and V5 to neurons in V2 (Zhang et al., 2014). Overall, there is evidence to suggest that peripheral binding errors may be explained by the influence of feedback representing the feature combinations presented in the central visual field to V2 neurons “dual-selective” for the *same* feature combinations in the periphery.

The experiments here may reveal a particular situation that increases the probability of nonveridical neural feedback to V2 neurons that are selective for stimuli presented within the periphery. Recall that when all of the objects were achromatic (all-achromatic condition), peripheral binding errors occurred more frequently compared to when all of the objects with one orientation were red and all of the other orientation were green (r/g chromatic condition). A possibility is that a larger degree of feature correspondence of *individual* (not joint) visual features in the center and periphery increases the likelihood that peripheral V2 neurons will receive nonveridical feedback from higher-level areas such as V4 and V5. In the case of peripheral binding errors, this nonveridical feedback could lead to more frequently perceived feature conjunctions in the periphery that correspond with the physically presented feature conjunctions in the central visual field.

Keywords: Color, motion, binding, feature integration

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