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Color-motion feature-binding errors are mediated by a higher-order chromatic representation

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Abstract

Peripheral and central moving objects of the same color may be perceived to move in the same direction even though peripheral objects have a different true direction of motion [Nature 429, 262 (2004)]. The perceived, illusory direction of peripheral motion is a color-motion feature-binding error. Recent work shows that such binding errors occur even without an exact color match between central and peripheral objects, and, moreover, the frequency of the binding errors in the periphery declines as the chromatic difference increases between the central and peripheral objects [J. Opt. Soc. Am. A 31, A60 (2014)]. This change in the frequency of binding errors with the chromatic difference raises the general question of the chromatic representation from which the difference is determined. Here, basic properties of the chromatic representation are tested to discover whether it depends on independent chromatic differences on the *l* and the *s* cardinal axes or, alternatively, on a more specific higher-order chromatic representation. Experimental tests compared the rate of feature-binding errors when the central and peripheral colors had the identical *s* chromaticity (so zero difference in *s*) and a fixed magnitude of *l* difference, while varying the identical *s* level in center and periphery (thus always keeping the *s* difference at zero). A chromatic representation based on independent *l* and *s* differences would result in the same frequency of color-motion binding errors at *every s level*. The results are contrary to this prediction, thus showing that the chromatic representation at the level of color-motion feature binding depends on a higherorder chromatic mechanism.

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1. INTRODUCTION

In natural viewing, the retinal stimulus is a mosaic composed from many distinct objects, each with its own shape, size, location, direction of motion, and color. We see unified objects with all features integrated together (say, a soaring inbound green Frisbee). Yet, despite advances from physiological and psychophysical studies of feature binding, e.g., [1–6], little is known about the neural representations of the features at the level of the feature-binding process.

Abundant evidence also shows that the features of color and motion are “prominent examples of functional specialization in the primate brain [7, p. 177].” Color and motion, therefore, provide an ideal pair of attributes for studying feature integration. While color is often cited as a prime example of an attribute that requires feature binding, most binding studies with color manipulate it at a categorical level (e.g., red versus green), which is too coarse to determine a chromatic neural representation [8–11]. The research here, in contrast, varies color systematically over a wide range and with knowledge of how each change of chromaticity alters photoreceptor excitation. This work also takes advantage of color-motion binding errors that are sustained for several seconds or longer and are induced simply and reliably [12], unlike some paradigms that give feature-binding errors that are brief (a fraction of a second) and infrequent, and/or observed under only highly constrained conditions. These aspects of the paradigm used here allow tests of specific hypotheses concerning the chromatic neural representation at the level where color and motion are bound.

An example of a stimulus arrangement giving sustained color-motion binding errors has “red” objects moving downward and “green” objects moving upward in the peripheral visual field, and “red” objects moving upward and “green” objects downward in the central visual field (Fig. 1). Observers veridically perceive the direction of motion of objects within the central field, but the perceived direction of motion in the peripheral field is often opposite to those objects’ physical directions. That is, peripheral “red” and “green” objects are seen to move in the same direction as the central objects of the same color, opposite to their real direction of motion in the periphery. This is a feature-binding error of color and motion in the periphery.

Recent work shows that peripheral color-motion binding errors occur without an exact color match between central and peripheral objects. Specifically, the rate at which featurebinding errors occur in the periphery is systematically related to the chromatic difference between the central and peripheral moving objects [13]. For example, with “red” moving objects in the center, the rate of peripheral binding errors is highest if peripheral objects are the same “red” chromaticity, somewhat less if “reddish-orange,” and lower still if “yellowish-orange.” That work considers chromatic differences along the L/M-cone axis alone and, separately, the S-cone axis alone. The results show that color-motion feature-binding errors in the periphery decrease in frequency monotonically as the difference between central and peripheral chromaticities increases, along either the *l* or *s* axis. Implicitly, this also reveals that the neural representation of color at the level of feature binding depends on signals from all three types of cone (L, M, and S).

The present study tests whether the chromatic difference regulating color-motion feature binding is determined by independent chromatic-difference representations along the I and the s axes or, alternatively, by a higher-order chromatic representation that combines signals from all three types of cone [14–17]. If the chromatic difference between the center and periphery depends on independent chromatic differences along each of the I and s axes, then, for example, the same chromatic difference in I should induce the same frequency of color-motion feature-binding errors whenever the s difference is held fixed at zero. This holds regardless of the *particular value of s* in center and periphery, as long as it is the same in both visual areas so the difference in s between center and periphery remains at zero. The same holds for any given chromatic difference on the s axis between center and periphery when the I difference between center and periphery is held at zero, regardless of the particular I value used for both the central and peripheral chromaticities.

A. Modeling

Well-defined models are useful for formalizing the hypothesis that color-motion feature binding depends on only independent chromatic-difference representations on the I axis and the s axis. Let the rate of feature-binding errors be R_{Error} , and assume R_{Error} decreases monotonically with an increase in the difference (D) in chromaticity between central and peripheral objects; thus, $R_{\text{Error}} = g(D)$, where function g is monotonically decreasing.

In general, the chromatic difference D is a function of the chromaticities of the objects in the center and periphery, labeled here C_c and C_p . A general form for D is

$$D = h(l_c, l_p, s_c, s_p), \quad (1)$$

where the chromaticities of central and peripheral objects are expressed in the equiluminant plane of the MacLeod and Boynton [18] I, s cone-excitation space. Function h has four parameters that completely specify the chromaticity in the center (l_c, s_c) and periphery (l_p, s_p), so it allows a chromatic representation based on either independent I and s -axis mechanisms or a higher-order chromatic mechanism. If the rate of binding errors depends on only independent I and s -axis differences, then central and peripheral chromaticities with an I difference but no s difference imply a special case of Eq. (1) such that

$$D = h(l_c, l_p, s^*, s^*) = k_1(l_c, l_p). \quad (2)$$

Note that the third and fourth parameters of function h have the identical value for $s(s^*)$, and, importantly, function k_1 depends on only the I values l_c and l_p (not the equal s^* value in center and periphery, whatever it may be). Similarly, if the frequency of binding errors depends on independent I and s -axis differences, then with only an s difference and no I difference between center and periphery Eq. (1) has the form

$$D = h(l^*, l^*, s_c, s_p) = k_2(s_c, s_p), \quad (3)$$

where function k_2 depends on only the s values (and not f^*). The primary goal of the experiments here is to test the model in Eqs. (2) and (3); that is, does $h(l_c, l_p, s^*, s^*) = k_1(l_c, l_p)$ regardless of the value of s^* , and does $h(l^*, l^*, s_c, s_p) = k_2(s_c, s_p)$ regardless of the value of f^* ? Note that no assumption is required about the metric to quantify the difference between l_c and l_p in Eq. (2) or between s_c and s_p in Eq. (3).

More specific forms than Eq. (1) are possible, of course, and can imply additional properties for the rate of feature-binding errors. For example, suppose the color difference D is

$$D = |W_c(C_c - C_{\text{Avg}}) - W_p(C_p - C_{\text{Avg}})|, \quad (4)$$

where weights W_c and W_p allow the central and peripheral chromaticities to have unequal influences on feature binding, and C_{Avg} is the average chromaticity of C_c and C_p ; at equiluminance, note that C_{Avg} is $(C_c + C_p)/2$ with C_c and C_p represented in an equiluminant plane (as for the stimuli here, where chromaticities are quantified in a MacLeod and Boynton cone-excitation space). In this case of equal luminance, rearranging terms in Eq. (4) gives

$$D = 0.5(W_c + W_p) |C_c - C_p|; \quad (5)$$

that is, Eq. (4) implies the difference D is directly proportional to the absolute difference between the central (C_c) and peripheral (C_p) chromaticities.

The model in Eq. (4) has four implicit properties: (i) D is directly proportional to the absolute difference between the central and peripheral chromaticities, *regardless* of the values of any fixed weights W_c and W_p ; (ii) when the central and peripheral chromaticities are the same ($C_c = C_p$), difference D is at its minimum (so the binding-error rate R_{Error} is at its maximum); (iii) for any two given chromaticities C_c and C_p , D is invariant with respect to which of the two chromaticities is presented in the center and which is in the periphery, even if weights W_c and W_p are unequal; and (iv) because binding-error rate R_{Error} is related to D by a function (g) assumed only to be monotonic, the above properties of Eq. (4) do not depend on the specific metric of chromaticity as long as the difference D increases with $|C_c - C_p|$.

Under the model in Eq. (4), if difference D (and thus the binding-error rate) depends on only independent chromatic differences on the l and the s axes, then

- i. given no difference in s between the central and peripheral chromaticities,

$$|C_c - C_p| = |l_c - l_p|; \quad (6)$$

- ii. given no difference in l between the central and peripheral chromaticities,

$$|Cc - Cp| = |sc - sp|. \quad (7)$$

Equations (2) and (3) as well as Eqs. (6) and (7) hold that with no s difference between center and periphery the rate of binding errors, R_{Error} , depends on only the magnitude of the I /chromaticity difference; and, similarly, with no I difference between center and periphery, the rate of binding errors depends on only the magnitude of the s difference. An empirical prediction from either Eqs. (2) and (3) or Eqs. (6) and (7), therefore, is that with an identical level of s in center and periphery, the rate of binding errors will always follow exactly the same quantitative relation as a function of Ic in the center and Ip in the periphery, regardless of the particular s value. Consider, for example, the frequency of feature-binding errors measured with a central (I, s) chromaticity of (0.80, 0.20), which appears red, and a peripheral chromaticity (0.70, 0.20), which appears yellowish. If binding-error rates depend on only independent I and s differences, then the same binding-error rate will be found with central and peripheral chromaticities (0.80, 1.00; now reddish-purple) and (0.70, 1.00; desaturated purple) because, in both cases, the difference between center and periphery in s is zero, $Ic = 0.80$ and $Ip = 0.70$. Similarly, the same binding-error rates as the s difference is varied between center and periphery should be found for *any* identical level of I in the central and peripheral fields, regardless of whether the common I value is, say, 0.80 (reddish) or 0.60 (greenish).

2. METHODS

A. Apparatus

The experimental stimuli were generated using an Apple iMac computer and presented on an NEC AccuSync 120 cathode ray tube (CRT) color display. The display was set to 1280 (×) 1024 pixel resolution at a refresh rate of 75 Hz noninterlaced, and was calibrated prior to beginning the experiments.

B. Stimulus

A schematic example of the experimental stimulus is shown in Fig. 1. The visual field (28 deg wide (×) 22 deg high) was separated into a central and two peripheral regions by four white vertical bars. The central region was 14 deg wide, and the left and right peripheral regions were each 7 deg wide. A white cross, metatmeric to an equal-energy-spectrum stimulus (EES), was presented in the center of the display as a fixation point. There were 320 moving open squares (each 0.3 deg wide) in the central region, and 160 moving squares in each of the left and right peripheral regions. In the central region, half of the squares moved in one vertical direction and had one color, while the other half moved in the opposite direction and had a different color (in Fig. 1, “red” squares move upward and “green” squares downward). In the periphery, the moving squares were similar but had opposite directions (in Fig. 1, “red” downward, “green” upward).

The chromaticity of the “green” squares was held constant in both center and periphery throughout the experiment. In the constant-periphery condition, the chromaticity of the peripheral “red” squares was held constant as well, while the chromaticity of the central

“red” (or, more appropriately, “non-green”) squares was changed on different trials. In the constant-center condition, the chromaticity of central “red” squares was held constant, while peripheral “non-green” squares were changed in chromaticity on different trials.

The chromaticity of all squares was specified in a cone-excitation color space: $I = L/(L + M)$, $s = S/(L + M)$ [18]. The unit of s , which is arbitrary, was set to 1.00 for EES “white.” In all the experiments, the chromaticity of the “green” squares was $I = 0.614$, $s = 0.17$, and the chromaticity for the “red” (or “non-green”) squares was varied. In the first experiment, the chromaticity of the “non-green” squares on different trials was set to one of six I -axis values (0.800, 0.775, 0.750, 0.725, 0.700, or 0.665), with s fixed at either 1.00 or at 0.20 [Figs. 2(a) and 2(b)]. In the second experiment, the chromaticity of the “non-green” squares on different trials was set to one of five s -axis values (0.20, 0.40, 0.60, 0.80, or 1.00), with I fixed at either 0.70 or 0.80 [Figs. 2(c) and 2(d)]. The luminance for all squares was fixed at 5 cd/m² in every condition, and the background was dark (<0.01 cd/m²).

Note that “green” squares always had the identical chromaticity in center and periphery (0.614, 0.17). A question to consider is whether feature-binding errors for “non-green” squares are affected by a substantial change in the chromatic difference between the “green” and “non-green” chromaticities. Measurements from a previous paper [13] show that this is not a concern. Figure 2 in that paper had the same “green” chromaticity as here and included “non-green” chromaticities of (0.665, 0.20) and (0.665, 1.00). These two chromaticities, one with $s = 0.20$ (nearly identical to $s = 0.17$ of the “green” chromaticity) and one with $s = 1.00$, had nearly the same rate of feature-binding errors. Therefore, the magnitude of chromaticity difference from the “green” squares is not a factor here.

C. Procedure

In the first experiment, “non-green” squares were changed among six different I chromaticities (described above) in only the center (constant-periphery condition) or only the periphery (constant-center condition). The level of s was fixed for half of the sessions at 1.00 [Fig. 2(a)] and for half at 0.20 [Fig. 2(b)]. For each of the six chromaticities within a session, there were 20 trials (counterbalanced, for example, with half having central “green” squares moving downward and the “non-green” chromaticity upward, and half having central “green” moving upward and “non-green” downward); thus for all six chromaticities there was a total of 120 trials in one session, randomly sequenced. Each trial lasted 20 s. Successive trials within a session were separated by a 5 s mask composed of “white” (EES) squares moving in random directions within the entire visual field. Each session began with 2 min of dark adaptation, and there was a 1 min break after each set of 50 trials. The constant-periphery and constant-center conditions were run in separate sessions, as were trials for the two different levels of s (1.00 or 0.20). Each condition was repeated three times on separate days, so there were 12 sessions in all. The second experiment was similar to the first one except that the “non-green” squares in either the center or periphery were changed among five different s chromaticities (described above), with I fixed for half of the sessions at 0.70 and half at 0.80. Thus there were 100 trials in each session. Each observer completed 24 separate sessions in total (12 for each experiment), in addition to performing

heterochromatic flicker photometry (HFP) for luminance matching before the binding experiments began.

The observer's task was always to fixate in the center of the visual field (white cross, Fig. 1) and report the motion direction of the majority of the peripheral "non-green" squares by pressing preassigned buttons on a game pad. Observers' possible button-press responses were limited to "up," "down," or "neither," and were recorded at 200 ms intervals. A color-motion feature-binding error was defined as a response of "up" or "down" inconsistent with the physical direction of motion of the judged peripheral squares. For example, when the "non-green" squares in the peripheral region moved upward physically but the observer's response was "down," the illusory percept (downward) was classified as a binding error. The binding-error rate was calculated as the proportion of time with a binding-error response during each 20 s trial.

D. Observers

Three observers participated in the study. Each observer had normal color vision as tested with a Neitz anomaloscope. Observer #1 was one of the authors and had prior experience with color-motion feature-binding experiments. Observers #2 and #3 were naïve as to the design and purpose of the experiments. Consent forms were completed in accordance with the policy of the University of Chicago's Institutional Review Board.

3. RESULTS

A. Chromatic Differences along the I Axis, at Two Different Levels of s

Color-motion binding-error rates are shown in Fig. 3 (vertical axis) as a function of the "non-green" squares' chromaticity, which was varied along the I /chromatic direction (horizontal axis in Fig. 3). Results are shown for the constant-center condition [Fig. 3(a)] and the constant-periphery condition [Fig. 3(b)]. Each pair of touching bars shows results at a given level of I (horizontal axis) and with s at two different levels: $s = 1.00$ (left bar) or $s = 0.20$ (right bar). For example, the leftmost pair of bars in each panel of Fig. 3(a) is for conditions with "non-green" squares in the periphery at I, s chromaticities (0.80, 1.0) (left bar) and (0.80, 0.20) (right bar). The color of each bar is the approximate appearance of the "non-green" squares varied in chromaticity. Each panel shows results for one observer.

First, color-motion binding errors in the periphery were found at every chromaticity for each observer. In the constant-center condition [Fig. 3(a)], the "non-green" squares in the center were at fixed chromaticity (0.80, 1.0) for the left bar of each touching pair of bars, and at (0.80, 0.20) for the right bar of each pair. The leftmost pair in each panel, therefore, is for conditions with the identical "non-green" chromaticity in center and periphery [that is, in Eq. (1) the chromatic difference $D = 0$]. These chromaticities had the highest rate of binding errors within each panel, as expected, and are in accord with earlier results [13]. As the I -chromaticity difference between center and periphery increased (from left to right in each panel), the rate of binding errors decreased, with s held fixed at either 1.00 or 0.20.

Second, consider the critical question of whether binding is regulated by independent chromatic differences on the I and s axes. If so, then the same decline in binding-error rate

should be observed as I decreased (from left to right), regardless of whether the value of s in both center and periphery is 1.0 (left bar of each touching pair) or 0.20 (right bar of each pair). Thus, for each pair of touching bars, both measurements should be identical within measurement error because each member of a pair is for a difference in s between center and periphery of zero and a difference in I (horizontal axis) that is the same. This was tested with a three-way analysis of variance. The measurements of binding-error rates are proportions and thus were subjected to an inverse sine transformation before performing the analyses [19]. For the I axis (Fig. 3), the three ANOVA factors were the common s chromaticity in center and periphery (1.0 or 0.20, two levels), the “non-green” I chromaticity (horizontal axis, six levels), and the constant-periphery versus constant-center conditions [Fig. 3(a) versus Fig. 3(b), two levels].

Results from each observer were analyzed separately. The analyses showed that the rate of binding errors did indeed depend on the s -chromaticity value (1.0 or 0.20) even though there was no difference in s level between the central and peripheral squares ($F(1, 48) = 20.2$ ($p < 0.001$), 13.0 ($p < 0.001$), and 15.1 ($p < 0.001$) for observers #1, #2, and #3, respectively). This is contrary to the hypothesis that binding depends on a chromatic representation at the level of independent chromatic differences on the I and s axes. The analyses also showed an effect of I chromaticity (horizontal-axis value in Fig. 3), as expected from prior work [13] and the model in Eq. (4) ($F(5, 48) = 209.5$ ($p < 0.001$), 109.0 ($p < 0.001$), and 70.9 ($p < 0.001$) for the three observers). There was never a significant effect of the constant-periphery versus constant-center conditions ($p > 0.05$ for all nine tests as a main effect or an interaction); this is also consistent with the model in Eq. (4).

B. Chromatic Differences along the s Axis, at Two Different Levels of I

Similar results were found when the “non-green” squares’ chromaticity was varied along the s chromatic direction (horizontal axis, Fig. 4), in both the constant-center [Fig. 4(a)] and constant-periphery conditions [Fig. 4(b)]. Each pair of touching bars now shows results at a given level of s (horizontal axis) and with I at one of two levels: $I = 0.70$ (left bar) or $I = 0.80$ (right bar). For example, the leftmost pair of bars in each panel of Fig. 4(a) is for conditions with “non-green” squares in the periphery at I, s chromaticities (0.70, 0.20) (left bar) and (0.80, 0.20) (right bar). Again, the color of each bar is the approximate appearance of the “non-green” squares that were varied in chromaticity. Each panel shows results for one observer.

As before, color-motion binding errors in the periphery were found at every chromaticity for each observer. The leftmost pair in each panel, which represents stimuli with the identical chromaticity in center and periphery (so $D = 0$), tended to have the highest rate of binding errors within each panel, and as the s -chromaticity difference between center and periphery increased (left to right in each panel) the frequency of binding errors tended to decrease, whether I was held fixed at 0.70 (left bar of each touching pair) or 0.80 (right bar of each pair).

For the s axis (Fig. 4), the three factors in the ANOVAs were the common I chromaticity in center and periphery (0.70 or 0.80, two levels), the “non-green” s chromaticity (horizontal axis, five levels), and the constant-center versus constant-periphery conditions [Fig. 4(a)

versus Fig. 4(b), two levels]. The binding-error rate depended on the level of I for each of the observers ($F(1, 40) = 110.5, 42.7$, and 15.5 for observers #1, #2, and #3, $p < 0.001$ in every case), which again rejects the hypothesis, for each observer, that binding depends on independent chromatic differences on the I and s axes. As expected, the effect of the s chromaticity (horizontal axis) was also significant for every observer ($F(4, 40) = 185.8, 23.8$, and 28.2 for the three observers, all $p < 0.001$).

Unlike the results for varying the I chromaticity (Fig. 3), varying the s chromaticity (Fig. 4) revealed a significant difference between the constant-periphery and constant-center conditions for two of the three observers ($F(1, 40) = 0.07$ (ns), 18.4 ($p < 0.001$), and 44.6 ($p < 0.001$) for observers #1, #2, and #3). Thus, for a *given* chromaticity difference between center and periphery, the binding-error rate depended on which member of the pair was presented in the center and which in the periphery. This is contrary to an implicit property of the model in Eq. (4). This point is taken up in Section 4.

4. DISCUSSION

This study tested whether the chromatic representation that regulates color-motion feature binding depends on independent chromatic differences along the I and the s axes, or instead on a higher-order chromatic representation. Changes in the observed rate of color-motion binding errors with various strategically chosen central and peripheral chromaticities were not consistent with independent chromatic differences on the I and s axes. Therefore, the neural representation of color at the level of binding depends on a higher-order chromatic representation.

A higher-order representation implies, for example, that the s chromaticities in center and periphery may *not* be ignored even if they are equal (so have zero difference). In this context, the influence on feature binding from the unequal I chromaticities in center and periphery depends on the particular (identical) level of s in both visual areas.

A. Implications from the Constant-Center and Constant-Periphery Conditions

The model in Eq. (4) requires, for any pair of central and peripheral chromaticities C_c and C_p , the same rate of binding errors regardless of which of the two chromaticities is presented in the periphery [see Eq. (5)]; thus, reversing the retinal locations of two chromaticities should not affect the results. This was explicitly tested by comparing two experimental conditions, one with the central chromaticity fixed and the peripheral chromaticity varied (the constant-center condition) and one with the peripheral chromaticity fixed and the central chromaticity varied (constant-periphery condition). In the first experiment with chromatic differences along the I axis (at each of two different levels of s), there was never a significant difference between the constant-center and constant-periphery conditions (neither a main effect nor interaction), for any of the three observers. This is consistent with Eq. (4). In the second experiment (chromatic differences along the s axis, at each of two different levels of I), however, two of the three observers showed a significant difference between the constant-center and constant-periphery conditions, which is further evidence against the model in Eq. (4). The alternative model [Eqs. (1)–(3)] does not require the same results from the constant-center and constant-periphery conditions.

Another important conclusion from the constant-periphery condition is that it eliminates any concern that different peripheral chromaticities affect the difficulty of making direction-of-motion judgments. Recall that the observer's task was always to judge the motion direction of peripheral "non-green" objects, so if this judgment were influenced by the specific chromaticity of the "non-green" objects, then changing their chromaticity might affect the difficulty of the judgment task used to measure the rate of feature-binding errors. This is not a factor, of course, in the constant-periphery condition, in which the peripheral "non-green" objects always had the same fixed chromaticity. Therefore, separate ANOVAs were completed using measurements from only the constant-periphery condition. They confirmed that (1) for two given I chromaticities I_c and I_p , a change in the equal s chromaticity in center and periphery altered the rate of color-motion feature-binding errors ($F(1, 24) = 7.17, 7.13, \text{ and } 8.25$ for observers #1, #2, and #3, respectively; $p < 0.02$ for every observer), and also (2) for two given s chromaticities s_c and s_p , a change in the equal I chromaticity in center and periphery altered the rate of color-motion feature-binding errors ($F(1, 20) = 78.5, 73.3, \text{ and } 9.24$ for observers #1, #2, and #3; $p < 0.01$ for every observer). Therefore, the constant-periphery results alone reaffirm that color-motion binding depends on a higher-order chromatic representation.

B. Is the Neural Locus of Higher-Order Chromatic Mechanisms Consistent with Known Neural Representations of Binding Errors?

Neural representations from independent I and s pathways are found in the input layers of V1, but psychophysical and physiological evidence shows that signals from the two chromatic pathways combine to establish multiple "higher-order" chromatic responses with many different chromatic preferences [14,15]. Importantly, many neurons in V1 have chromatic-tuning peaks that vary over a broad range of directions [20,21]. Thus, some (though not all) neurons in area V1 have a representation of color based on higher-order chromatic mechanisms.

Color-motion feature binding has been localized as early as V1 [7], and fMRI results reveal neural activity in V2 that corresponds with perceived (not physical) color-motion feature binding [22]. Thus, a representation of perceived feature conjunctions, including binding errors, is within V2. Further, color-motion binding errors may be due to feedback from V4 and V5/MT + to specific layers of V2 [22,23]. Thus, V2 has representations of both perceived color-motion binding errors and higher-order chromatic responses.

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Fig. 1.

Schematic of the experimental stimulus. In this example, the central visual field has red objects that move upward and green objects that move downward; in the peripheral visual field, red objects move downward and green objects move upward. All objects are open squares. A white fixation cross is located in the center of the display. Symbols above the schematic show the direction of motion of red and green squares within each area for clarity of exposition (they are not presented during experiments).

Fig. 2.

Schematic of chromaticities used in constant-periphery conditions: peripheral chromaticities held fixed while one central chromaticity (see dashed circles) was changed on different trials. (a) l changed to one of six different values on different trials (top panel) with s fixed at 1.00 (schematic stimulus in bottom panel is with l at 0.70); (b) as in (a) but with s fixed at 0.20; (c) s changed to one of five different values on different trials (top panel) with l fixed at 0.70 (schematic stimulus in bottom panel is with s at 0.80); (d) as in (c) but with l fixed at 0.80. Note that a trial could have a difference in chromaticity between center and periphery of either only l [in (a) and (b)] or only s [in (c) and (d)]. The critical comparisons are between (a) and (b), and between (c) and (d). Colors show approximate appearance of stimuli but are imperfect reproductions.

Fig. 3.

(a) Average binding-error rate for l -chromaticities of “non-green” squares for the constant-center condition. For each touching pair of bars, the left one shows results with $s = 1.00$ and the right one with $s = 0.20$. (b) As in (a) but results are for the constant-periphery condition.

Fig. 4.

(a) Average binding-error rate for s chromaticities of “non-green” squares for the constant-center condition. For each touching pair of bars, the left one shows results with $I = 0.70$ and the right one with $I = 0.80$. (b) As in (a) but results are for the constant-periphery condition.