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Perceptual resolution of color for multiple chromatically ambiguous objects

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Abstract

In a classic study, Kovács *et al.* [Proc. Natl. Acad. Sci. USA 93, 15508 (1996)] used an array of many disks presented dichoptically with half of the disks in one eye “red” and the other half “green;” disk chromaticities in the fellow eye were reversed, resulting in binocular color rivalry for every disk, thus creating color ambiguity. Surprisingly, the binocularly fused percept sometimes was all disks of the same color (red or green), which showed that perceptual resolution of the many ambiguous neural representations did not rely completely on monocular dominance or on independent resolution for each disk. The present study replicates and expands on the original with the aim to isolate binocularly driven neural mechanisms of perceptual resolution without contamination from monocular dominance. Observers viewed a color-rivalrous array with 16 disks presented either steadily to each eye, as in Kovács *et al.*, or with chromatic interocular-switch rivalry (CISR), which swaps the two images between the eyes every 133 ms. The total proportion of viewing time when the 16 disks were perceived to be all red or all green was measured. For three observers, the disks all appeared the same color more often with CISR than with steady rivalrous presentation, suggesting that monocular dominance interferes with grouped perceptual resolution of ambiguous stimuli in the Kovács paradigm. This conclusion was supported by an additional condition using CISR, but with every disk the same color in one eye at each instant (e.g., all “red” disks in one eye and all “green” in the other). This condition was never significantly different from the original CISR condition, as expected if CISR reveals only binocularly mediated perceptual resolution of the disks’ color, irrespective of monocular neural representations. In conclusion, chromatically tuned binocularly driven neurons account for perceptual resolution of CISR.

1. INTRODUCTION

The human visual system resolves the perceptual ambiguity implicit in visual scenes, yet the neural processes behind this resolution are still poorly understood and controversial (e.g.,

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[1–4]). While neural ambiguity in vision can occur for a number of reasons, in the laboratory it is often generated using rivalrous left-eye and right-eye images. What one sees while viewing the rivalrous images can help characterize neural processes of perceptual resolution. In standard binocular rivalry, dichoptic stimuli are presented in corresponding retinal locations of each eye, and the stimuli are presented steadily during the viewing period. A variant of this is interocular-switch rivalry [5], in which the rivalrous stimuli are exchanged between the two eyes several times a second. In either method of rivalry, the specific stimulus parameters for each eye, such as chromaticity, spatial frequency, or orientation can be individually controlled. This allows for testing hypotheses concerning specific representations of neural competition and also the neural level of ambiguity resolution.

A mainstream theory about competing neural representations posits competition between monocularly driven neurons with representations from a single eye's image. In this "eye-rivalry" view, the monocular representations compete for perceptual dominance [1,2,6]. The eye-rivalry approach can be extended to retinotopically local monocular competition in different parts of the visual field in order to account for meaningful cohesive percepts containing some elements presented to only the left eye and other elements presented to only the right. This can lead to an integrated percept with an amalgamation of pieces from the left-eye and right-eye images. These local monocularly resolved regions are not dominant or suppressed independently of one another but instead can be resolved according to the dominant activity in adjacent areas, perhaps facilitated by higher-level feedback or lateral connections in V1 that contribute to a cohesive percept [2,7,8].

An alternative to "eye-rivalry" is competition between binocularly driven neurons tuned for specific stimulus features, which results in alternating perceptual dominance [4,9,10]. This "stimulus-rivalry" theory assumes a continuous binocular-level representation of each stimulus by a neuron that can be driven by either eye. Much of the evidence for this theory comes from interocular-switch rivalry [4,5], though some evidence from standard binocular rivalry also supports stimulus rivalry [10,11].

Either binocularly driven neurons tuned to specific stimulus features, which result in stimulus rivalry, or monocularly driven dominance within local zones, which results in localized eye rivalry, might explain an integrated percept with multiple objects, some from the stimulus in the left eye and some from the stimulus in the right. How these multiple objects may become part of a single complete percept is a question considered 20 years ago [11]. Two types of dichoptic stimulus arrays were presented in standard binocular rivalry: conventional arrays [Fig. 1(a)] or patchwork arrays [Fig. 1(b)]. "Conventional" arrays used a rivalrous image in each eye with all 24 disks in each eye at the same chromaticity (say, all left-eye 24 disks at a chromaticity that appeared red, and all right-eye disks at a chromaticity that appeared green). "Patchwork" arrays, on the other hand, had half of the 24 disks in one eye at each of two chromaticities, and the retinotopically corresponding disk in the fellow eye had the other chromaticity [Fig. 1(b)]. Note that both types of arrays ensured chromatic binocular rivalry for all 24 disks. The primary importance of their experiments was that both types of steady dichoptic arrays sometimes gave a coherent percept with all 24 disks appearing the same color. For conventional arrays, such coherent percepts occurred about 60% of the time and for patchwork arrays 47% of the time (averaged over their three

observers). Note that for patchwork arrays, complete-eye rivalry predicts no coherent percepts, and even locally monocular independent competition among all 24 disks implies exceedingly rare coherent percepts (less than 1% of the time)—contrary to their measurements. These results are consistent instead with the resolution of neural ambiguity at the binocular stimulus-mediated level, at least in part.

At the same time, the difference in the frequency of perceived color coherence when viewing conventional versus patchwork arrays (60% versus 47%) supports some contribution from eye-specific dominance to the observer's percept. Eye-of-origin is a strong grouping cue that can lead observers to perceive what is presented to a single eye much of the time [12]. This grouping cue may promote perceptual coherence in the conventional-array condition beyond the coherency mediated by binocularly driven neurons observed in the patchwork-array condition. While the frequent coherent percepts found with patchwork arrays suggest that chromaticity is a strong grouping cue, the difference in frequency of perceived coherence between the patchwork and conventional conditions suggests that grouping by eye-of-origin was not entirely eliminated by Kovács *et al.* [11]. This is evidence that multiple mechanisms are involved in the resolution of ambiguity, a property of the visual system often invoked to explain seemingly conflicting results throughout the rivalry literature [13,14]. The present study aims to isolate rivalry mechanisms beyond those that are purely monocular.

Experiments here take as a working hypothesis that neural ambiguity caused by rapidly exchanging dichoptic images between the two eyes (interocular-switch rivalry) is resolved at only the binocular level; if so, then there can be no monocular influence, unlike what Kovács *et al.* found with standard binocular rivalry. Experiments here, therefore, test for a monocular influence on the resolution of ambiguity created by interocular-switch rivalry by comparing conventional and patchwork arrays. Of course, conventional and patchwork arrays always produce different monocular representations, but according to the binocularly driven stimulus-rivalry view, these monocular differences are irrelevant for perceptual resolution with interocular-switch rivalry. The measurements that follow test this.

2. METHODS

A. Apparatus

All conditions were presented on a calibrated Sony CRT, driven by a Mac computer. The CRT was viewed through a haploscope with eight mirrors used to display a different image to each eye (Fig. 2). The light path through the mirrors was approximately 115 cm, ensured by a chin rest. The last set of mirrors was adjustable such that observers could move it toward or away from themselves in order to achieve stable fusion of the two eyes' images. Four Nonius lines aided fusion of the two images. The top and left Nonius lines were shown to the left eye, and the bottom and right Nonius lines were shown to the right eye (Fig. 2). The two images were properly fused when the left and right lines were perceived to align horizontally and the top and bottom lines vertically.

B. Stimulus

Each condition used a 4.5 deg square containing a 4-4 array of 16 0.5-deg diameter disks, with each disk separated from its neighbors by 1.0 deg center-to-center. The whole stimulus was surrounded by black lines of a square with Nonius lines as described above, and had a black fixation cross in the center (Fig. 3). Aside from these components, necessary for fusion and fixation, the entire display was set to 5 cd/m². The disks could be either “red” or “green” with MacLeod and Boynton [15] chromaticities $[L / (L + M), S / (L + M)]$ of [0.71, 0.3] or [0.62, 0.3], respectively. The unit of $S / (L + M)$ is arbitrary and is set here to 1.0 for equal-energy-spectrum white. The background was set to the physical average of the two disk chromaticities: [0.665, 0.3], appearing yellowish. For the conditions presented in interocular-switch rivalry, the images were swapped between the two eyes at a frequency of 3.75 Hz. The conditions presented in standard binocular rivalry had steady, dichoptically presented images. For both methods, note that the disk at each retinotopic location was “red” in one eye and “green” in the other, always ensuring chromatic rivalry at all disk locations [see Figs. 3(a) and 3(b)]. Thus, in all conditions, the images were presented such that each disk was always chromatically ambiguous.

The conventional-rivalry and patchwork-rivalry conditions are defined by the chromaticities of the 16 disks presented within an eye at any given time. In the conventional-rivalry condition, all 16 disks in the left eye at any given time were one chromaticity, while all 16 disks in the right eye at any given time were the other chromaticity. In the patchwork-rivalry condition, eight randomly chosen disks were “red” and the remaining eight disks were “green” within an eye at any given time. The other eye also had eight “red” and eight “green” disks, though in the opposite locations. Figures 3(a) and 3(b) show these two conditions.

C. Procedure

Observers were instructed to hold down different buttons on a game pad that corresponded to three different coherent color percepts: (1) all 16 disks “red,” (2) all 16 disks “green,” and (3) all 16 disks “yellow” or appearing to disappear into the background. Observers held down a button for the entire duration of each percept, and were instructed to press a button only if they could keep up in time with the switches between percepts and if the percepts were of the same quality as shown on an instruction screen [images similar to Fig. 3(c)]. The dependent measures from this procedure were (i) the total proportion of viewing time each button was pressed during a trial and (ii) the mean duration each button was pressed continuously.

Observers came in on four different days to run the experiment, with the first day treated as practice and not included in any analyses. Each day, all four conditions were run in a random order. Each condition was run four times in a day for 70 s with 10 s between each 70-s trial. Button presses during the first 10 s of each trial were ignored due to the possibility of unequal adaptation between the two eyes caused by the initial 133 ms stimulus in the interocular-switch rivalry conditions. The same timing was maintained for the standard binocular-rivalry conditions. For the patchwork conditions, a new random array for each chromaticity was created for each trial. Thus, a total of eight different patchwork arrays were

created and run in a single day—four for the patchwork condition in standard binocular rivalry and four for the patchwork condition in interocular-switch rivalry. For the conventional-rivalry condition presented in standard binocular rivalry, the eye receiving all “red” disks was counterbalanced such that on each day, each eye was presented each chromaticity twice in a random order.

D. Observers

Four observers participated in the experiment: two male and two female, one of whom is author ES. The remaining three observers were naïve as to the purpose of the study. Prior to the start of the study, each observer was screened for normal color vision using the Ishihara Plates and Rayleigh matching using an anomaloscope, and for normal stereo vision using the Titmus Stereo Test. Once an observer passed the screening, heterochromatic flicker photometry (HFP) was used to ensure equiluminance for the chromatic stimuli for each individual observer. HFP was performed on at least four different days in order to get a stable measurement.

One observer was excluded due to a failure to replicate Kovács’ original finding. More detail about this observer is in Section 3.

3. RESULTS

Prior to the data analysis, the total amount of time observers perceived all 16 disks to be red or all 16 disks to be green was added together. This total time was then converted to a proportion of time out of the 60 s measurement interval. An arcsine transformation was applied to the data before conducting analyses of variance [16]. The all-yellow percept responses were analyzed separately, also as a proportion with the transformation applied. Separate analyses were conducted for each individual observer. One observer was excluded from analysis due to failure to replicate the main finding in Kovács *et al.* [11]: the summed time of all “red” and all “green” percepts in the patchwork-rivalry condition presented in standard binocular rivalry was close to zero (less than 1%).

For all other observers, planned, nonorthogonal Bonferroni-corrected contrasts were performed on four pairs of interest: (1) conventional-rivalry array in standard binocular rivalry versus patchwork-rivalry array in standard binocular rivalry; (2) conventional-rivalry array in interocular-switch rivalry versus patchwork-rivalry array in interocular-switch rivalry; (3) patchwork-rivalry array in standard binocular rivalry versus patchwork-rivalry array in interocular-switch rivalry; and (4) conventional-rivalry array in standard binocular rivalry versus conventional-rivalry array in interocular-switch rivalry. The results, separated by color percept in the stacked bars, are shown for each observer in Fig. 4.

All three observers showed a significant difference between the conventional-rivalry arrays and patchwork-rivalry arrays when presented in standard binocular rivalry (contrast 1, Obs. AE $p < 0.01$, Obs. ES $p < 0.01$, Obs. RH $p < 0.01$), such that coherent percepts of all red or all green were seen for higher proportions of time in the conventional-array condition. This corroborates the original Kovács *et al.* result showing that the patchwork-array condition yielded coherent percepts for a lower proportion of time than the conventional-array

condition. None of the three observers showed a significant difference between the conventional-rivalry array and patchwork-rivalry array conditions when they were presented in interocular-switch rivalry (contrast 2, all observers $p > 0.2$). These two results taken together are consistent with the prediction that monocular effects are present when the stimuli are presented in standard binocular rivalry but not with interocular-switch rivalry. All three observers showed also a significant difference in the patchwork-rivalry array condition when it was presented in standard binocular rivalry compared to when it was presented in interocular-switch rivalry (contrast 3, Obs. AE $p < 0.01$, Obs. ES $p < 0.01$, Obs. RH $p < 0.05$), such that coherent percepts were seen more often when the stimuli were presented in interocular-switch rivalry. This is further support for the hypothesis that a monocular neural representation influences perception when the stimuli are presented in standard binocular rivalry but not interocular-switch rivalry.

The final contrast revealed no consistent trend in how observers resolved ambiguity in the two conventional-rivalry array conditions. One observer (Obs. AE) showed no significant difference between the conventional-rivalry array condition presented in standard binocular rivalry and in interocular-switch rivalry ($p > 0.5$). The other two observers showed a significant difference, though in opposite directions: Observer ES had a significantly higher proportion of coherent percepts when the condition was presented in interocular-switch rivalry than when it was presented in standard binocular rivalry ($p < 0.05$), while observer RH had a significantly higher proportion of coherent percepts when the condition was presented in standard binocular rivalry ($p < 0.01$). In sum, there is no conclusion to draw from this contrast.

For the yellow percept, the same four Bonferroni-corrected planned nonorthogonal contrasts were tested as for the summed red and green results. All three observers showed an identical trend: no difference between proportions of time yellow percepts were seen between the conventional and patchwork conditions within each method ($p > 0.35$ for both conditions and observers). This result is consistent with the original Kovács work, which found no difference between the proportion of time yellow was seen for the two array conditions [11]. When comparing methods, however, two observers showed that the standard binocular rivalry conditions yielded a higher proportion of time when all yellow was seen, no matter the array condition ($p < 0.05$ for both conditions and observers). Observer RH showed no significant difference between proportions of time for yellow percepts in any condition or method ($p > 0.2$), though almost never saw yellow. In general, instances of chromatic fusion are not uncommon in standard binocular rivalry [17,18], though the yellow percept here was very rare except for Observer AE. The distance in color space between the two rivalrous, equiluminant chromaticities indicates that the yellow percept should be rare [19,20].

The same four Bonferroni-corrected planned nonorthogonal contrasts were performed on the mean dominance duration as for all previous analyses. The duration of button presses for “red” percepts and “green” percepts were averaged and analyzed separately from the “yellow” percepts. Analyses of the mean durations of sustained red and green percepts revealed results similar to the total dominance time results. All observers showed significantly longer durations of sustained red or green percepts from the conventional-rivalry arrays than from the patchwork-rivalry arrays when both were presented in standard

binocular rivalry ($p < 0.05$ for all observers). No observer showed a significant difference in mean duration from either array type when presented in interocular-switch rivalry ($p > 0.4$ for all observers). One observer showed significantly longer durations of sustained red or green percepts from the patchwork-rivalry array when presented in interocular-switch rivalry compared to the same array presented in standard binocular rivalry (Obs. ES, $p < 0.05$). One observer showed significantly longer durations of sustained red or green percepts from the conventional-rivalry array when presented in standard binocular rivalry compared to the same array presented in interocular-switch rivalry (Obs. RH, $p < 0.01$). These results are shown for each observer in Fig. 5.

The analyses of the mean durations of the yellow percept also followed the same trend as the total dominance time data. All observers show no difference in mean durations of yellow percepts when the two array types were presented using the same method ($p > 0.25$ for all observers for both methods). Two out of three observers show significantly longer durations of yellow percepts for the patchwork-rivalry array when it was presented in standard binocular rivalry compared to interocular-switch rivalry (Obs. AE and ES, $p < 0.05$). One observer showed a significantly longer duration of yellow percepts for the conventional-rivalry array when it was presented in standard binocular rivalry compared to interocular-switch rivalry (Obs. ES, $p < 0.01$). Observer RH showed no significant difference in the duration of yellow percepts for all methods and arrays ($p > 0.13$). The yellow-percept results are not considered further because two observers (ES and RH) saw yellow virtually never (at most one button press for all 24 trials in interocular-switch rivalry; Fig. 4).

4. DISCUSSION

Previous research shows that color is a strong grouping cue that can overcome grouping by eye-of-origin with steady dichoptic images. This work shows that the resolution of rivalry, at least partially, depends on binocularly driven neurons tuned to specific stimulus features [11]. The experiments reported here expand those findings to include dichoptic images that are swapped between the eyes in a method known as interocular-switch rivalry. According to the binocularly driven stimulus-rivalry theory, this method eliminates monocular-dominance effects and relies solely on binocularly driven neurons to resolve the ambiguity established by rivalry [4,5], though this theory is still controversial [1–3]. Results from this study support the stimulus-rivalry view and show also that monocular eye rivalry can interfere with grouping by color in standard binocular rivalry. Interocular-switch rivalry minimizes or eliminates the influence of the monocular-dominance mechanism.

Consistently across observers, differences in perceptual coherence between the two array types (conventional versus patchwork) were observed for stimuli presented in standard binocular rivalry, but there were no significant differences when they were presented in interocular-switch rivalry. This is as predicted if stimulus-specific binocularly driven neurons mediate perceptual resolution. Though the two arrays produce different monocular representations, this difference is irrelevant for binocularly driven resolution of ambiguity. With interocular-switch rivalry, the chromatic arrangement of the arrays presented to a single eye never had a significant effect on either the proportion of time perceptual coherence was

seen or on the mean duration of perceptual coherence, so there is no evidence for monocularly driven rivalry with interocular-switch rivalry.

For all observers, the proportion of time coherent percepts were seen in the patchwork-rivalry array conditions was significantly higher when the stimuli were swapped in interocular-switch rivalry than when they were presented steadily in standard binocular rivalry. This indicates that monocular interference can be minimized by presenting the stimuli in interocular-switch rivalry as opposed to standard binocular rivalry. Eye-specific grouping cues can decrease the amount of time perceptual color coherence occurs from patchwork arrays in standard binocular rivalry. The results indicate that when the stimuli are presented using interocular-switch rivalry, the eye-specific interference is minimized, while stimulus-specific information represented at the binocular level mediates coherent percepts.

These coherent percepts, grouped by color, may be formed by a chromatic mechanism representing a single integrated object. Previous studies examining feature misbinding with motion have found that stimuli with ambiguous motion but matched chromaticities can be grouped such that the observer perceives all dots of the same color to move in the same direction, despite the fact that some dots physically move in the opposite direction [21–23]. This illusion has been described as appearing as though two patterned sheets, one of red dots and the other of green dots, are moving in opposite directions. This implies that each individual colored stimulus is grouped such that it is now part of one, single-colored greater whole [21]. The same principles may be applied here to understand the predominance of coherent percepts. All 16 disks are chromatically ambiguous, either “red” or “green,” but instead of resolving each disk independently, they are all grouped into a single object, and the resolution of the chromatic ambiguity takes place at the object level. Of course, this is only a conjecture. Further experiments must be done to directly test this hypothesis of object-level chromatic resolution.

An alternative model for the resolution of ambiguity from interocular-switch rivalry is that monocular processes drive perception [3]. For the patchwork arrays used here, this would require that each area containing a single disk be resolved by a competing monocular representation, though not independently; instead, a top-down influence of grouping by color would create coherent percepts. This model, based on interocular-switch rivalry between differently oriented gratings rather than rivalrous, equiluminant colors, relies on fast flicker or a brief blank period between stimulus swaps to break inhibition between the two eyes’ monocularly driven neurons. The model uses the flicker to induce the eye dominance to swap at the same time as the perceived grating moves to the other eye, resulting in continued perception of the same grating despite it swapping eyes and exciting different monocular neural populations. The present study uses neither fast flicker nor blank periods. By matching chromatic stimuli in luminance, no flicker or blank period is needed to produce slow perceptual alternations, so this model does not directly apply to the experiments reported here.

The overall goal here was to investigate whether there are monocular influences on the resolution of chromatic ambiguity in standard binocular rivalry and in interocular-switch rivalry. Specifically, can the ambiguity created by interocular-switch rivalry be understood

based on only binocular, stimulus-driven neurons uninfluenced by differences in monocular representations? The results are consistent with the binocularly driven stimulus-rivalry theory, which posits that ambiguity is resolved by chromatically tuned binocularly driven neurons. This allows for coherent percepts, grouped by color, to be seen equally often with either conventional or patchwork arrays presented with interocular-switch rivalry.

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Fig. 1.

Stimuli from Kovács *et al.* [11]. The left [right] column represents what was presented to the left [right] eye. (a) “Conventional color rivalry condition” in which each disk was presented at the same chromaticity within each eye; (b) “patchwork color rivalry condition” in which half the disks in each eye were presented at one chromaticity and the other half at the other chromaticity.

Fig. 2.

Mirror haploscope display. The black rectangle represents the CRT monitor, the solid gray lines represent mirrors, and the dashed lines indicate the light paths.

Fig. 3.

(a) and (b) show the dichoptic stimuli used for both the standard binocular rivalry and interocular-switch rivalry conditions. (a) shows the conventional-rivalry condition, in which each disk is presented at the same chromaticity to a single eye at any given time; (b) shows the patchwork-rivalry condition, in which each disk is presented at one of two chromaticities to a single eye at any given time. In all conditions, the chromaticities presented to the two eyes are different at each corresponding disk location (e.g., where one disk is “green” in the left eye, the corresponding disk is “red” in the right eye); (c) shows three of the possible

percepts from (a) and (b). Only these three percepts were measured. Mixed or patchy percepts were excluded.

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Fig. 4.

Results from three observers. Graphed is the proportion of time each of the three measured percepts was seen out of the 60 s viewing time. The four different conditions are represented on the *x* axis by the method used to present the stimuli and the type of stimulus array. The brackets indicate significance for the red + green contrasts: * $p < 0.05$ and ** $p < 0.01$.

Fig. 5.

Results from three observers. Graphed is the mean duration of time all red and all green or all yellow was seen. The duration of time all red and all green percepts were seen is averaged, represented in gray. The four conditions are represented on the *x* axis by the method used to present the stimuli and the type of stimulus array. The brackets indicate significance for the averaged red and green contrasts: * $p < 0.05$ and ** $p < 0.01$.