

Chromatic interocular-switch rivalry

Jens H. Christiansen

Center for Autisme, Herlev Hovedgade, Herlev, Denmark

Anthony D. D'Antona

Department of Psychology, The University of Chicago,
Chicago, IL, USA

Steven K. Shevell

Department of Psychology,
Department of Ophthalmology & Visual Science,
and Institute for Mind & Biology,
The University of Chicago, Chicago, IL, USA

Interocular-switch rivalry (also known as stimulus rivalry) is a kind of binocular rivalry in which two rivalrous images are swapped between the eyes several times a second. The result is stable periods of one image and then the other, with stable intervals that span many eye swaps (Logothetis, Leopold, & Sheinberg, 1996). Previous work used this close kin of binocular rivalry with rivalrous forms. Experiments here test whether chromatic interocular-switch rivalry, in which the swapped stimuli differ in only chromaticity, results in slow alternation between two colors. Swapping equiluminant rivalrous chromaticities at 3.75 Hz resulted in slow perceptual color alternation, with one or the other color often continuously visible for two seconds or longer (during which there were 15+ eye swaps). A well-known theory for sustained percepts from interocular-switch rivalry with form is inhibitory competition between binocular neurons driven by monocular neurons with matched orientation tuning in each eye; such binocular neurons would produce a stable response when a given orientation is swapped between the eyes. A similar model can account for the percepts here from chromatic interocular-switch rivalry and is underpinned by the neurophysiological finding that color-preferring binocular neurons are driven by monocular neurons from each eye with well-matched chromatic selectivity (Peirce, Solomon, Forte, & Lennie, 2008). In contrast to chromatic interocular-switch rivalry, luminance interocular-switch rivalry with swapped stimuli that differ in only luminance did not result in slowly alternating percepts of different brightnesses.

viewing angles. Normally, our visual system fuses the two images to give a three-dimensional percept, but in some cases, the images are too different to fuse. This can result in binocular rivalry, with the image in the left eye and the image in the right eye competing (“rivaling”) to reach conscious vision. In the simplest example of rivalry, the competition is between a percept driven entirely by the stimulus representation from the left eye alternating with a percept driven entirely by the stimulus representation from the right (Levelt, 1965).

In general, binocular rivalry can be more complex than competition between the whole image representation from each eye. For example, resolution of binocular rivalry can differ for specific stimulus features seen simultaneously. Lights of a different chromaticity in each eye may rival in color percept even when the two eyes’ stimuli are integrated to give stereoscopic depth (Treisman, 1962), although the depth may be compromised relative to the depth experience without rivalry (Blake, 2012). Also, different chromaticities in each eye may combine to give a steady color percept even while differences in spatial form between the eyes rival (Creed, 1935). As an example, a reddish-appearing vertically oriented grating in one eye and a bluish-appearing horizontally oriented grating in the other eye may combine to give a percept of a purplish (red-blue) grating that switches back and forth between a vertical and a horizontal orientation (Holmes, Hancock, & Andrews, 2006). Thus, colors may rival while forms combine to give depth, or forms may rival while colors combine.

Many, but not all, findings within the binocular rivalry literature have been explained by reciprocal inhibition between left and right eye monocular neurons that causes binocular neurons to receive information from only one eye at a time (Alais, 2011;

Introduction

In natural viewing, the two eyes’ retinal images are not exactly the same because the eyes have different

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Blake, 1989). Other work, however, suggests competition between binocularly driven neurons that sum signals from monocular neurons over time, for example, when rivalry is induced by orthogonal gratings swapped between the two eyes at 1.5 Hz (Logothetis, Leopold, & Sheinberg, 1996). Despite the physical swapping three times each second, much slower perceptual alternations persist with stable periods of one orientation spanning many eye swaps. The percept is similar to what is perceived during classic binocular rivalry with a steady stimulus in each eye. The swapping paradigm will be referred to here as *interocular-switch rivalry* (also known as *stimulus rivalry*). If a single binocular neuron receives information from the left eye as well as the right, then a rapid exchange of monocular information should result in a continuous binocular neural response.

Neural mechanisms at multiple levels of the visual system determine the resolution of rivalry (Tong, Meng, & Blake, 2006), so it is not surprising to find monocularly mediated contrast adaptation during interocular-switch rivalry (Brascamp, Sohn, Lee, & Blake, 2013). The monocular contrast adaptation, however, does not exclude competition between binocular neurons preferring one or the other orientation of a grating.

To date, interocular-switch rivalry has been explored in the feature domain of form (referred to here as *form interocular-switch rivalry*). Most models explain how the visual system produces the perceived slow alternations between two percepts by assuming that binocular neurons receive input from left-eye and right-eye monocular neurons with matched orientation tuning (Dayan, 1998; Freeman, 2005; Wilson, 2003); see Brascamp et al. (2013) for an exception). Because the preferred orientation of monocular neurons from each eye driving a particular binocular neuron typically is well matched (Bridge & Cumming, 2001; Skottun & Freeman, 1984), binocular neurons plausibly can sum signals from monocular neurons over time (as a given orientation is swapped between the two eyes) and produce a stable response. Once stable responses are established by these binocular neurons, their outputs can be used to model rivalrous fluctuations. In Wilson's (2003) model, for example, inhibitory connections between self-adapting binocular neurons lead to the perception of alternating orientations.

Does known neurophysiology provide evidence for binocularly driven neurons that could support slowly varying *color* percepts from stimuli that rapidly exchange the chromaticity presented to each eye (*chromatic interocular-switch rivalry*)? That is, are monocular neurons driving a particular binocular color-preferring neuron matched in chromatic selectivity, analogously to the orientation-tuned monocular neurons driving a binocular orientation-preferring neuron? To answer this question, Peirce et al. (2008)

recorded from binocular neurons in V1 and V2 of macaque while presenting to each eye a spatially uniform field that alternated between two equiluminant chromaticities. They found that binocular neurons classified as preferring chromatic modulation had receptive fields with chromatic tuning remarkably well matched between the two eyes (figures 3A and 3B in Peirce et al., 2008).

In analogy to Wilson (2003) and others, the results from Peirce et al. (2008) underpin the possibility of slowly alternating color percepts during chromatic interocular-switch rivalry due to binocular neurons. Stable periods of perceptual dominance of only one or the other color could occur because, when switching chromaticities between eyes, the response from binocular neurons preferring one chromaticity will be fairly stable. Inhibitory connections between these binocular neurons combined with self-adaptation (similar to the mechanisms envisioned by Wilson, 2003) could cause the slow perceived color alternations.

Experiments reported here show that slowly alternating color percepts from *chromatic interocular-switch rivalry* do in fact occur. Participants were presented with a spatially uniform disc in each eye at a corresponding retinal location. Each eye's disc alternated many times per second between the same two equiluminant chromaticities (with a time-average chromaticity metameric to equal-energy-spectrum [EES] "white") or, in separate runs, between two achromatic (EES) luminances. Temporal oscillation in both eyes was always at the identical frequency (e.g., 3.75 Hz) but opposite in temporal phase to maintain rivalry throughout the viewing period. The two chromaticities were along one of the cardinal color directions (Derrington, Krauskopf, & Lennie, 1984; Krauskopf, Williams, & Heeley, 1982)—either L/(L + M) or S/(L + M) in MacLeod and Boynton (1979) chromaticity space—or along an intermediate chromatic direction. Equiluminant chromatic square wave modulation resulted in remarkably slow perceptual color alternation, with one or the other color remaining continuously visible for several seconds or longer (equivalent to 20 or more chromaticity switches in each eye at 3.75 Hz). With achromatic stimuli at different luminances, on the other hand, observers virtually never experienced slow perceptual alternation between brightnesses from the two achromatic luminances.

Methods

Equipment

All experiments were done at the University of Chicago. A chin rest was used to provide head

stabilization. Stimuli were displayed on a Sony color cathode ray tube (CRT) display (Model GDM-F520) with a resolution of $1,280 \times 1,024$ and a refresh rate set to 75 Hz (noninterlaced) in an otherwise dark room. A Macintosh G4 computer controlled the CRT via a Radius video board supplying 10-bit resolution for each gun. All stimuli were viewed through a custom-built eight-mirror haploscope using large front-surface Beral-coated mirrors. Viewing distance along the light path was 1.18 m.

Calibration

Unless stated otherwise, calibration was done for light directly from the CRT rather than through the haploscope. The relative radiance of the light from each of the R, G, and B guns of the CRT was linearized using a 10-bit lookup table. The spectral distribution of each of the three phosphors was measured at the maximal output using a PhotoResearch PR-650 spectroradiometer. Each phosphor was measured directly and also through the haploscope to verify that the spectral reflectance of the haploscope's mirrors did not alter a gun's chromaticity. As expected, these two sets of measurements showed excellent agreement within a measurement error of 0.003 or less for any CIE x, y chromaticity value.

Heterochromatic flicker photometry at 12.5 Hz was used to determine equiluminance for each participant (details in Christiansen, D'Antona, & Shevell, 2009).

Color space

All chromatic stimuli were expressed using coordinates from the l - and s -axes of the MacLeod and Boynton (1979) chromaticity space, where $l = L/(L + M)$ and $s = S/(L + M)$, and L , M , and S refer to the activation of the (L)ong-, (M)iddle-, and (S)hort-wavelength sensitive cones, respectively. The unit of the s -axis is arbitrary and was set here so that s was 1.0 for EES "white." The Smith and Pokorny (1975) cone fundamentals were used to calculate the L , M , and S values used in the MacLeod-Boynton chromaticity diagram.

Observers

Five observers participated in the experiments. Two were authors (A.D.D. and J.H.C.), and the others were naïve as to the hypotheses being tested. Rayleigh matches, obtained with a Neitz anomaloscope, were normal. Participation by all observers was in accord with the policies of the University of Chicago's Institutional Review Board.

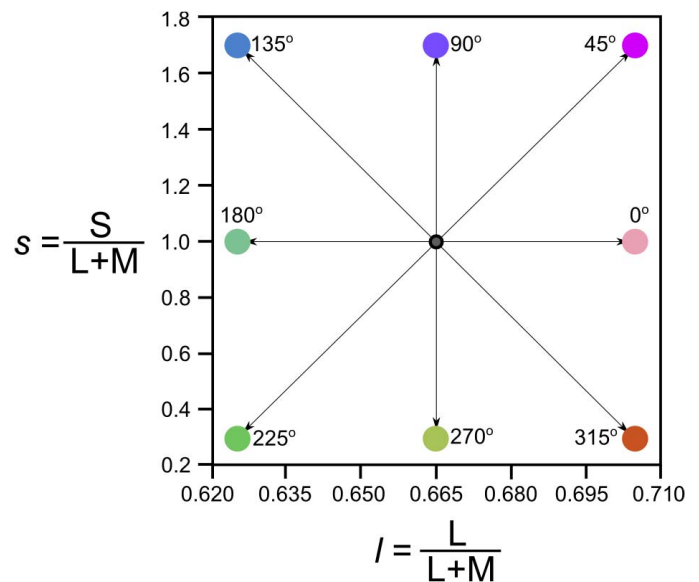


Figure 1. The equiluminant plane of the MacLeod-Boynton chromaticity space showing chromaticities used in the experiments. Circles at the ends of a single line represent chromaticities of the square wave modulation used in the experiments (always symmetric around equal-energy-spectrum "white" at the center of the diagram). Four axes of chromatic modulation are shown. The vertical and the horizontal axes are referred to as cardinal axes (Derrington et al., 1984). The two diagonals are referred to as intermediate axes.

Stimuli

Chromaticity values used in Experiments 1, 2, 3, and 5 are depicted in Figure 1 as circles at the endpoints of the vertical, horizontal, and diagonal lines crossing the central EES point. In Experiments 1, 3, and 5, the chromaticities were at the endpoints of the lines on either the l -axis or the s -axis (the cardinal directions: 0° – 180° or 90° – 270° axes). In Experiment 2, the chromaticities were at the endpoints of lines in intermediate directions (along the 135° – 315° or 45° – 225° axis). In Experiment 4, stimulation consisted of pure luminance exchanges at the EES chromaticity (see specific luminance values in Experiment 4).

The basic stimulus paradigm for Experiments 1–5 is shown in Figure 2a. The background surrounding both the annulus and test discs was dark (i.e., close to 0 cd/m^2). All stimuli were surrounded by a white fixation square ($6^\circ \times 6^\circ$) with two thin Nonius crosshairs used to aid binocular fusion. Test discs were always 2.5° in diameter and presented with a surrounding annulus of outer diameter 3.5° .

In the experiments using chromatic stimuli (Experiments 1–3 and 5), the surrounding annulus was EES "white" with a fixed luminance of 23 cd/m^2 . The luminance of the test discs was always constant at 20 cd/m^2 . In Experiment 4, the luminances of the

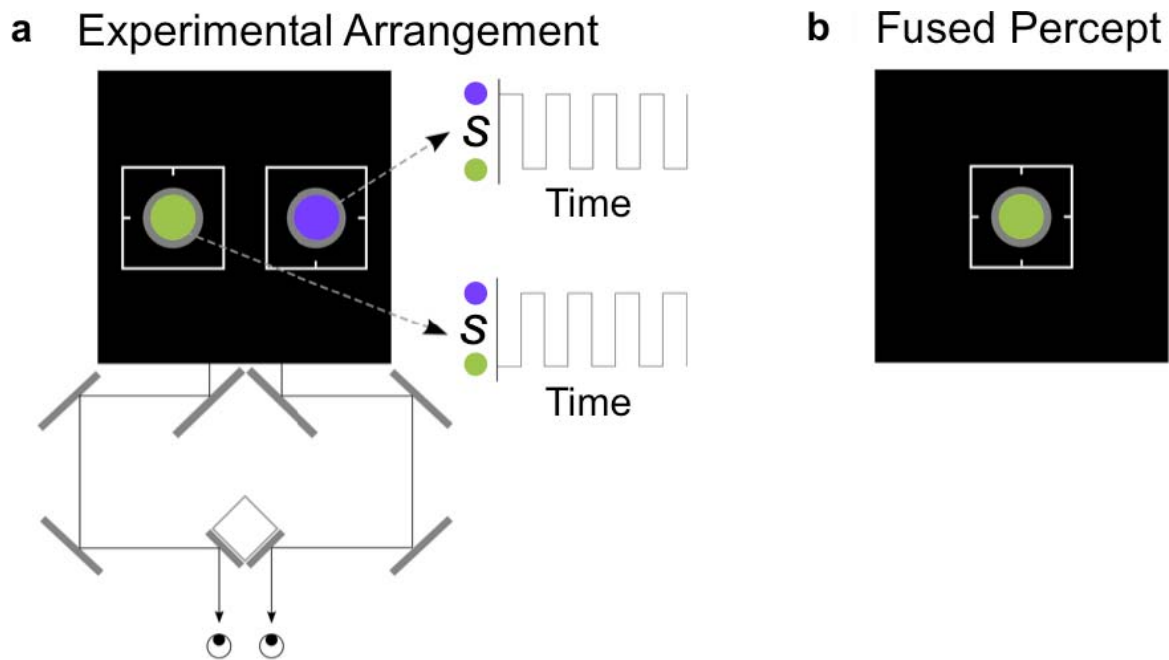


Figure 2. (a) Schematic diagram of the experimental arrangement. (b) Example of a possible fused percept with stable perception of a lime-colored disc (corresponding to the chromaticity at 270° in the MacLeod and Boynton chromaticity space in Figure 1).

surrounding annulus and test discs were systematically varied. These variations are described with Experiment 4. Note that all luminances reported here were measured at the CRT display. With four front-surface Beral-coated mirrors in the light path to each eye, luminance at the cornea was lower by about 30%.

Test discs were modulated at 3.75 Hz (i.e., the two chromaticities swapped every 133 ms), except in Experiment 3, in which the modulation frequency was varied, and in Experiment 5, which used classic binocular rivalry without interocular switching or temporal modulation. Note that all experiments here with interocular-switch rivalry (1–4) had successive stimulus swaps without a gap or blank period as often used in paradigms with interocularly switched gratings (Logothetis et al., 1996; van Boxtel, Knapen, Erkelens, & van Ee, 2008).

In all experiments, the different conditions were presented in random order within each session.

Procedure

The observer viewed the stimuli through a haploscope (Figure 2a). A button press initiated each trial, after which two 2.5° spatially uniform test discs of differing chromaticities (or luminances) were presented, one to each eye. Surrounding each disc was an annulus 1° wider in diameter than the colored test discs. This annulus was included to aid stable fusion.

The participant could adjust two of the mirrors of the haploscope to aid binocular fusion. The Nonius

lines depicted in Figure 2a were seen as collinear (Figure 2b), ensuring that the two binocularly fused discs fell on corresponding retinal areas in each eye. Beneath the white squares, two small colored discs could be presented (0.5° diameter), one to the left and one to the right (not shown in Figure 2a). The small disc to the left had the same chromaticity as the test disc in the left eye, and participants were instructed that when this color was seen, the left button on a game controller was to be pressed. Likewise, the small disc beneath the white square and to the right had the same chromaticity as the test disc in the right eye, and when this color was seen, the right button on a game controller was to be pressed. When the participant had adjusted for optimal fusion and become acquainted with which button to press when seeing a given color, a button press on the controller caused the two small discs to disappear, and the chromaticities of the two test discs began to modulate temporally (except in Experiment 5 with classic binocular rivalry, in which the chromaticities were not modulated). At this stage of preparation for a trial, the participant was again able to adjust the mirrors of the haploscope for optimal fusion of the temporally modulating stimuli. Once the observer comfortably fused the temporally modulating stimuli, another button press caused a trial to begin. A trial lasted 70 s, but during the first 10 s, no data were collected to avoid any possible effect from the unequal onset transient in the two eyes, which, of course, viewed a different chromaticity in the first 133-ms interval. After 60 s of data collection, the screen went blank, and no responses were collected

for five seconds. The participant then pressed a button to make the discs reappear and repeated the procedure described above for the next trial.

Within each trial, the periods were measured during which participants experienced only one or the other color. To measure these periods unambiguously, participants were instructed to press a left or right button only when experiencing a spatially uniform disc color, comparable in hue to one of the small colored discs shown below the white square at the beginning of each trial. If the hue was desaturated, but still had the right hue, the button was also to be pressed. If a sensation of flicker was superimposed upon the perception of a stable spatially uniform color in the test disc, the button was also to be pressed. Participants were instructed *not* to press a button if (a) experiencing rapid switching between the two colors (faster than one could reasonably alternate button presses—this is the percept expected for perceptual dominance of stimuli in only one eye—(b) experiencing rapid switching between only one spatially uniformly colored disc and a colorless disc, (c) experiencing a spatial compound of the two colors (similar to what is called *mosaic* or *piecemeal rivalry* in classic binocular rivalry), (d) the two test discs fused and presented themselves as a third and different color, or (e) the test disc appeared too desaturated to judge in color.

Results

Experiment 1: Chromatic interocular-switch rivalry along cardinal chromatic directions

Overview of Experiment 1

This experiment tests whether chromatic interocular-switch rivalry results in long periods of perceiving one and then the other rivalrous color.

Procedures specific to Experiment 1

Chromatic interocular-switch rivalry was measured with square wave modulation along the cardinal *l*-axis or *s*-axis shown in Figure 1 (see circles at the endpoints of the horizontal and vertical lines in Figure 1 at 0° – 180° or 90° – 270°). Each observer ran 10 trials of each condition over several different days for a total of 10 min of rivalrous presentation time for each chromaticity pair. Measurements along the two cardinal directions were made within the same sessions as the measurements in Experiment 2 and part of Experiment 4.

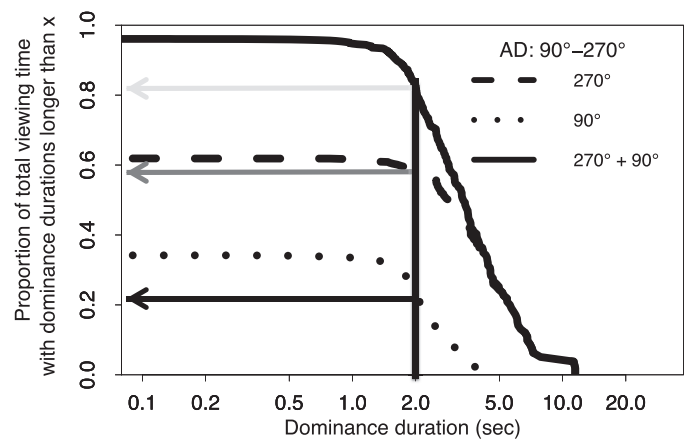


Figure 3. Didactic graph with a cumulative survival-style plot that will be used to present results from Experiment 1 (and 2 and 5). The plot above is for one participant (A.D.D.) with chromaticities switching along the S/(L + M) axis in Experiment 1. See the main text for an explanation of how to interpret the plot.

Introduction to the cumulative survival-style plots used to present results

Figure 3 shows a didactic graph introducing the cumulative survival-style plot used for displaying results from Experiment 1 (and later Experiments 2 and 5). This graph shows one participant's measurements for only the S/(L + M) axis. The value on the horizontal axis indicates the length of time a single button was pressed without interruption. Pressing a button meant that the observer perceived one of the spatially uniform colors, not fast flicker or other possible percepts (see the Procedure section). A value on the vertical axis is the proportion of total viewing time (during 10 min, from 10 trials of 60 s each) during which a participant perceived a given color *continuously* for as long or longer than the value on the horizontal axis. In Figure 3, the dotted or dashed line represents one of the two rivalrous colors (from the chromaticity at either 90° or 270° , respectively). The solid line combines dominance durations for both colors. Consider, for example, the dotted line for 90° , which is based on intervals when the participant reported seeing the color corresponding to the chromaticity at 90° in the MacLeod-Boynton chromaticity space. From Figure 3, it can be seen that at a horizontal-axis value of 0.5 s, this participant perceived a uniform field corresponding to the color at 90° for 0.5 s or longer for about 35% of the total viewing time (vertical axis). Moving further out along the horizontal axis shows the participant perceived the same color continuously for two seconds or longer during about 23% of the total viewing time (black arrowhead). For the dashed line, signifying perception of the color corresponding to the chromaticity at 270° , the participant perceived this color for two seconds or

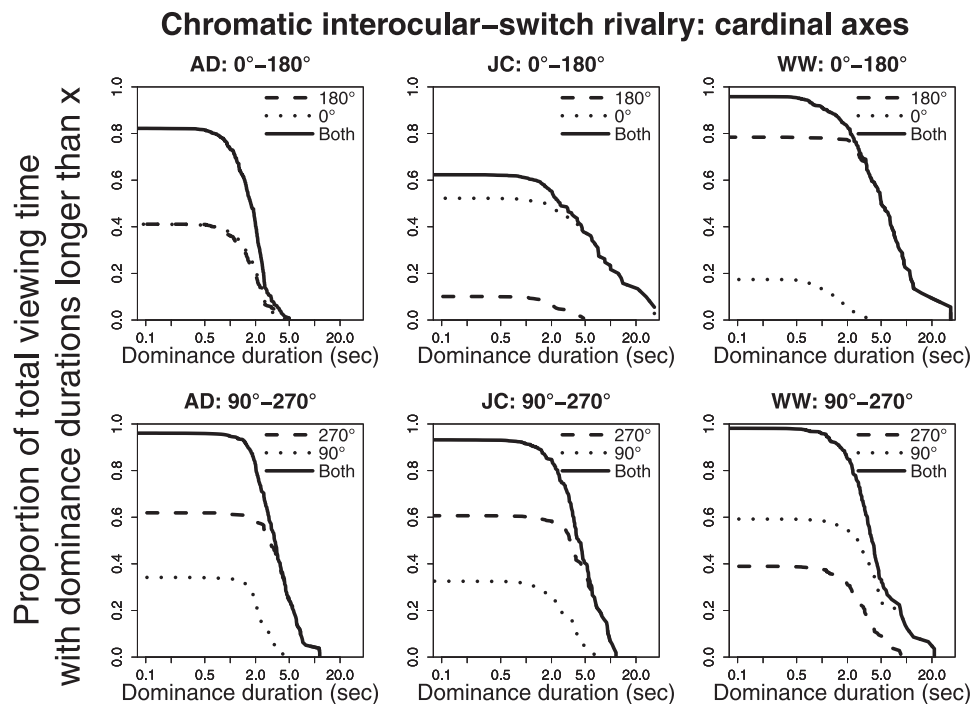


Figure 4. Results from the experiment with chromatic interocular-switch rivalry along cardinal axes, plotted using the conventions in Figure 3. All measurements with modulation along each of the cardinal directions are shown, for each of the three observers (A.D.D., J.H.C., and W.W.). The top panels are for modulation between chromaticities at 0° and 180° (*l*-axis). The bottom panels are for modulation between chromaticities at 90° and 270° (*s*-axis). Each of the six panels contains three cumulative survival-style plots showing the proportion of time that the dominance duration of a uniformly colored disc was as long or longer than a given value on the horizontal axis.

longer during about 58% of the total viewing time (darker gray arrowhead). Finally, the solid line, based on seeing either uniform color (90° or 270°), shows that one of these colors was perceived for two seconds or longer for about 82% of the total viewing time (lighter gray arrowhead) and for five seconds or longer for about 24% of the time.

Results and interpretation of Experiment 1

The top (bottom) row in Figure 4 shows results for chromaticities switched along the $L/(L + M)$ [$S/(L + M)$] axis at 0° – 180° [90° – 270°] for three observers (A.D.D., J.H.C., W.W.). Notice the high proportion of total viewing time (solid lines) during which a stable color was perceived for several seconds or longer, despite swapping colors between eyes at 3.75 Hz. For the three participants in condition 0° – 180° , a stable color was perceived for two seconds or longer for 40%, 55%, and 82% of the total viewing time for participants A.D.D., J.H.C., and W.W., respectively.

Looking at the dashed and dotted lines, for the 0° – 180° condition for participants J.H.C. and W.W. (Figure 4, upper panels), the high proportion of time perceiving a stable color is driven more by one than the other of the two chromaticities. That is, one chroma-

ticity predominated. The balance between the chromaticities at 0° and 180° for dominance durations over two seconds was 21% and 19%, 48% and 7%, and 6% and 76% for participants A.D.D., J.H.C., and W.W., respectively. Thus, for J.H.C., the chromaticity at 0° was predominant, but for W.W., the chromaticity at 180° was predominant. Although individual differences are not a focus of this study, the one seen here is found again in later experiments. In contrast, for participant A.D.D., the chromaticity pair along the *l*-axis (0° – 180°) was almost perfectly balanced for the two chromaticities. Overall, the mean dominance duration of a stable percept was 1.6 (standard error of the mean $SEM = 0.14$), 3.9 (0.57), and 3.3 (0.47) s for A.D.D., J.H.C., and W.W., respectively.

In the 90° – 270° condition (Figure 4, lower panels), the solid line shows for all three participants that, as a percentage of the total viewing time, a stable color was perceived for two seconds or longer for 83%, 84%, and 84% for participants A.D.D., J.H.C., and W.W., respectively. Looking at the dashed and dotted lines for the *s*-axis (90° – 270° condition), at the two-second mark on the *x*-axis, the dominance durations at 90° and 270° were 24% and 59%, 26% and 58%, and 54% and 30% for participants A.D.D., J.H.C., and W.W., respectively. With modulation on the *s*-axis, the overall mean

dominance durations were 3.0 ($SEM = 0.19$), 3.5 (0.21), and 3.2 (0.29) s for A.D.D., J.H.C., and W.W. In this condition, participants experienced some very prolonged dominance durations for each color, occasionally continuously reporting perception of the color corresponding to the chromaticity at 90° for as long as 5, 6, and 20 s and the color corresponding to the chromaticity at 270° for as long as 11, 12, and 9 seconds (A.D.D., J.H.C., and W.W., respectively).

Overall, chromatic interocular-switch rivalry results in extended periods of perceiving a single color. Every participant saw *each* of the colors as stable and had occasions of continuously experiencing each color for two seconds or longer.

A hallmark of the percepts resulting from chromatic interocular-switch rivalry is the slow perceptual alternation between two colors. A quantitative assessment of how often “slow alternation” occurred requires a specific definition of it, and here a very broad and inclusive one is used: Slow alternation occurs within a trial of duration 60 s if the color corresponding to *each* chromaticity is seen as stabilized for one second or longer. This sets a very low bar for slow alternation because, in an extreme case, one second of continuously seeing one color at the beginning of a trial, followed by 58 s of no button presses indicating no stable percept, and then a final second of continuously seeing the other color, would satisfy the criterion for slow alternation. As discussed later, this weak criterion is useful for identifying conditions that *fail* to cause slow alternation. Unsurprisingly, according to this definition, all three participants experienced slow alternation during *all* 60 trials in Experiment 1.

Experiment 2: Chromatic interocular-switch rivalry along intermediate chromatic axes

In Experiment 2, the two chromaticities were modulated along chromatic directions intermediate to the cardinal directions. A basic question is whether chromatic interocular-switch rivalry along intermediate directions also results in sustained color percepts and whether the temporal dynamics of rivalrous colors along intermediate directions are systematically related to the temporal dynamics of rivalrous colors along the cardinal directions.

Procedures specific to Experiment 2

Two different pairs of chromaticities were modulated along intermediate directions in MacLeod-Boynton chromaticity space (see circles at the endpoints of the diagonal lines in Figure 1 at 135° – 315° and 45° – 225°). Each observer ran 10 trials of each condition over several different days for a total of 10 min of rivalrous

presentation time for each chromaticity pair. Measurements along the intermediate directions were made within the same sessions as the measurements in Experiment 1 and are separated here for clarity of presentation.

Results and interpretation of Experiment 2

Chromatic interocular-switch rivalry results in long-lasting color percepts when chromatic stimuli are modulated along intermediate directions (Figure 5). For one of the participants (J.H.C.), however, one color strongly predominates. Looking at the solid lines for all three participants in condition 135° – 315° (upper panels), it can be seen that, as a percentage of the total viewing time, a stable color was perceived for two seconds or longer for 28%, 50%, and 82% of the viewing time for participants A.D.D., J.H.C., and W.W., respectively. In this condition, the overall mean dominance duration was 1.4 ($SEM = 0.22$), 4.4 (5.89), and 3.2 (0.63) s for A.D.D., J.H.C., and W.W. For the 45° – 225° condition, a stable color was perceived for two seconds or longer for 16%, 34%, and 70% of the time (see solid lines in lower panels). The overall mean dominance durations were 1.3 (0.13), 2.7 (1.16), and 2.2 (0.18) s for A.D.D., J.H.C., and W.W., respectively.

In terms of the proportion of total viewing time for each alternating color, the balance between the two colors on an intermediate axis is closely related to the balance between the two colors modulated on only the *l*-axis. This holds for all three participants and for both intermediate directions. For participant A.D.D., for example, when modulation was on only the *l*-axis (Figure 4), the proportion of total viewing time for each color was almost perfectly balanced. As can be seen in Figure 5, the proportion of total viewing time for each of the two colors on each intermediate direction is also almost perfectly balanced (despite an unbalanced proportion of total viewing time for each color when modulation was on only the *s*-axis; see bottom left panel of Figure 4). For participant J.H.C., on the other hand, when modulation was on only the *l*-axis (Figure 4), the proportion of total viewing time for each color was not well balanced. Instead, the color corresponding to the chromaticity at 0° was seen for most of the time. When the modulating colors were on an intermediate axis, the intermediate color seen for most of the time was the color with the same *l*-axis component as the color corresponding to the chromaticity at 0° (i.e., the intermediate colors corresponding to the chromaticities at 45° and at 315°). The balance between colors with modulation on only the *s*-axis did not correspond with the balance between colors with modulation on the intermediate axes. To see that this is so, consider the very low proportion of total viewing time for the intermediate color corresponding to the chromaticity at

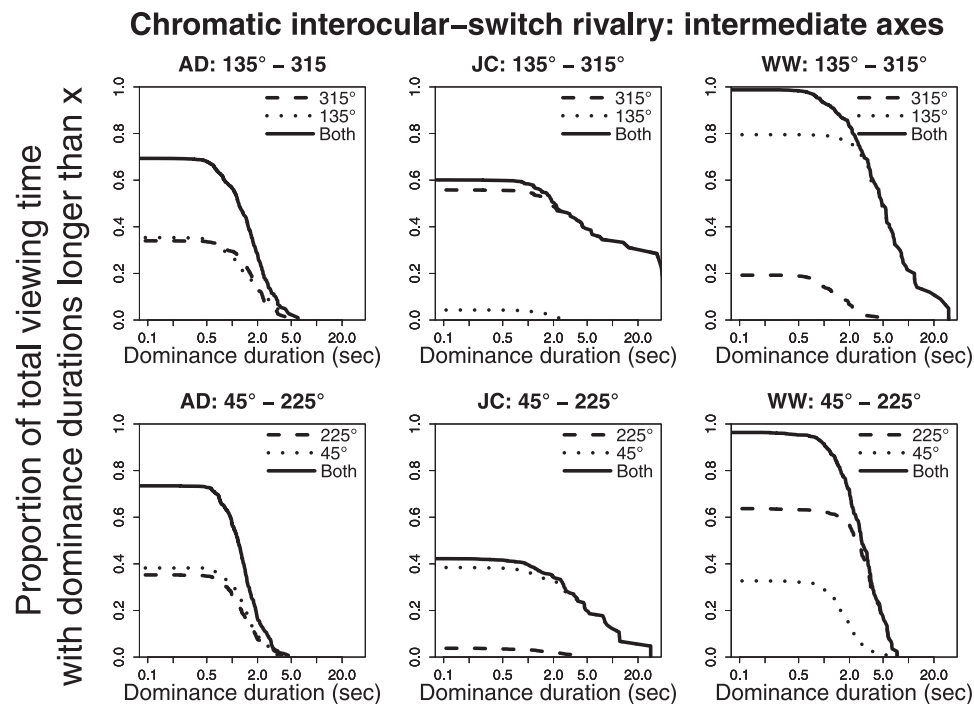


Figure 5. Results from Experiment 2. As Figure 4 but with chromaticities modulated along noncardinal intermediate directions (either 135° – 315° or 45° – 225°).

225° for participant J.H.C. The s -axis component for the intermediate color at 225° is the same as the s -axis component for the cardinal color at 270° (see Figure 1). For participant J.H.C., the cardinal color at 270° was seen for most of the time with modulation on only the s -axis, but this did not carry over to the intermediate color at 225° . Thus, the s -axis component of a color on an intermediate direction cannot account for the imbalance of total viewing time for colors on intermediate directions. A similar but instructive result holds also for participant W.W. The proportion of total viewing time for each color with modulation on only the l -axis was also unbalanced but, contrary to participant J.H.C., now the color corresponding to the chromaticity at 180° was seen for most of the time (Figure 4). Results for W.W. with modulation along intermediate directions followed the same pattern as for J.H.C.: The intermediate colors with the highest proportion of total viewing time (Figure 5) were those corresponding to the chromaticity coordinates at 135° and at 225° , again showing that the l -axis component of these colors corresponds to the same l -axis component for the color predominantly seen in the cardinal L/(L + M) condition (180°).

In sum, chromatic interocular-switch rivalry results in slowly alternating color percepts when chromatic modulation is along an intermediate direction. The overall proportion of total viewing time perceiving a uniform field of a particular color correlates with its l -axis component, suggesting the influence of a chromatic

neural representation originating at a level of the visual system where there are distinct L/(L + M) and S/(L + M) signals.

Experiment 3: Chromatic interocular-switch rivalry along cardinal chromatic directions at four different temporal modulation frequencies

Procedures specific to Experiment 3

The two previous experiments used interocular-switch rivalry with disc chromaticities changing at 3.75 Hz (i.e., the two chromaticities swapped every 133 ms). In Experiment 3, four temporal frequencies were tested: 3.13, 3.75, 4.69, and 6.25 Hz. Measurements were made along the cardinal l -axis and s -axis as in Experiment 1. Two new naïve observers were tested. Each observer ran five trials at each frequency on five different days. Each frequency was tested in a separate session.

Results and interpretation of Experiment 3

Results from Experiment 3 are summarized by the proportion of total viewing time during which each particular stable color percept was perceived, rather than by a great many individual survival-style plots (a separate one would be required for every combination of frequency, chromatic direction, and observer). The proportion of total viewing time is represented in survival-style plots by the vertical-axis intercept of the

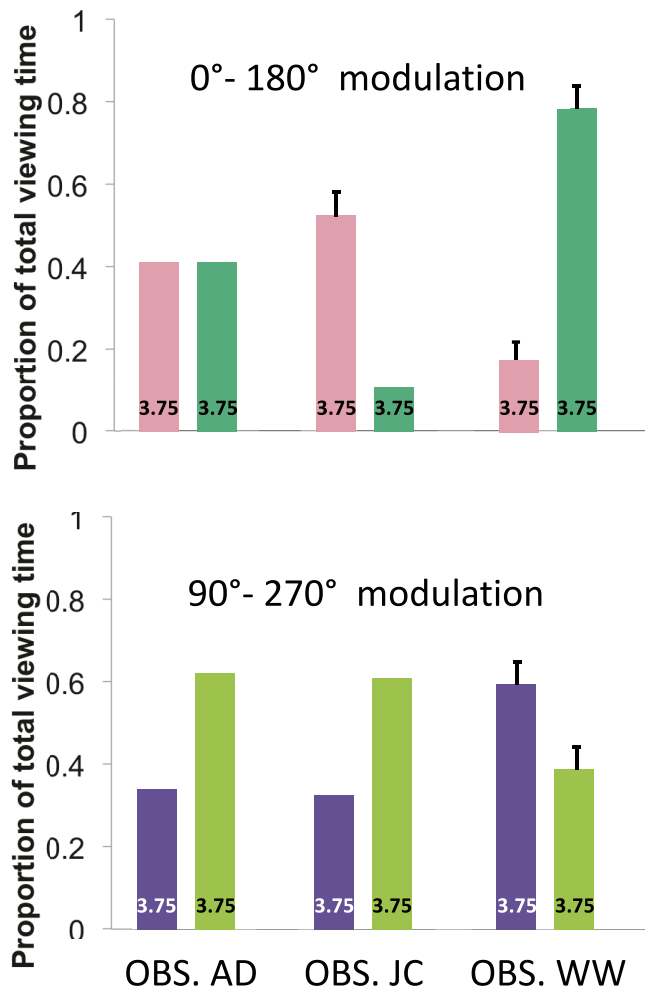


Figure 6. The proportion of total viewing time perceiving a particular stable uniform color percept, with chromatic modulation along each of the cardinal directions (above, 0°–180 for three observers; below, 90°–270 for three observers). The interocular-switch frequency was 3.75 Hz, as indicated within each bar. The approximate perceived stable color is indicated by the bar's color. Error bars show *SEMs* (*SEM* less than 0.02 where not plotted). Values replotted from Figure 4.

curves in each panel of Figures 4 and 5. For comparison, the results from Experiment 1 are replotted in this format in Figure 6.

Results with four different interocular-switch frequencies show there was little effect of the frequency of temporal modulation (Figure 7). Sustained color percepts occurred with interocular-switch rivalry at every frequency tested at every chromaticity. These results show that the specific frequency is not critical within the range from 3.13–6.25 Hz. There is, however, a limit to the frequency range that is useful for understanding the neural representation from chromatic interocular-switch rivalry. Above about 10 Hz, the two alternating chromaticities in each eye would be perceived as a single continuous intermediate hue, a

well-known phenomenon exploited in heterochromatic flicker photometry. At substantially lower frequencies, a switch in perceived color could occur faster than the chromatic stimulus-alternation rate, and thus, the results would be contaminated by perceptual switching that occurs in classical (nonswitch) binocular color rivalry.

The similar results at every frequency in Figure 7 from each of the participants attest also to the replicability of the measurements within an observer.

Mean dominance durations also showed sustained periods of perceiving a single color at every modulation frequency and for each observer. Across all chromaticities, the mean dominance durations for participant E.U. at 3.13, 3.75, 4.69, and 6.25 Hz were 4.61 s (*SEM* = 0.28), 3.79 s (0.09), 3.41 s (0.87), and 3.81 s (0.31), respectively, and for participant I.W. were 2.33 s (0.21), 2.50 s (0.28), 2.30 s (0.31), and 2.47 s (0.27), respectively. A detailed inspection of within-trial results showed that the criterion for slow alternation was met in every one of the 80 trials (2 observers × 2 chromatic directions × 4 frequencies × 5 replications).

Experiment 4: Brightness percepts with luminance interocular-switch rivalry

Overview of Experiment 4

Does interocular-switch rivalry result in slowly alternating percepts of different brightnesses when the binocularly rivalrous stimuli in the two eyes differ in only luminance? This is considered in Experiment 4.

A preliminary question is the magnitude of luminance modulation to be tested. Chromatic interocular-switch rivalry, always at equiluminance in previous experiments, causes only modest L- and M-cone contrast when the two chromaticities are exchanged. This is a consequence of the overlap of the L- and M-cone relative spectral sensitivity functions, which constrains the maximal L and M contrast. S-cone contrast is much less constrained on a typical video display, as used here, and there is no constraint on the magnitude of luminance contrast. If luminance interocular-switch rivalry is tested using luminances with higher cone contrasts than in Experiments 1 and 2, then perhaps the higher cone contrasts alone may interfere with the formation of stable percepts such as those found with chromatic interocular-switch rivalry. This concern was addressed by using two contrast levels of luminance modulation. The first luminance pair, for the “high luminance-contrast condition,” had achromatic stimuli that modulated between 18 and 28 cd/m² (Michelson contrast of 22%). In the “low luminance-contrast condition,” luminance levels were 21.5 and 24.5 cd/m² (Michelson contrast of 6.5%). The low luminance-contrast condition had pooled cone con-

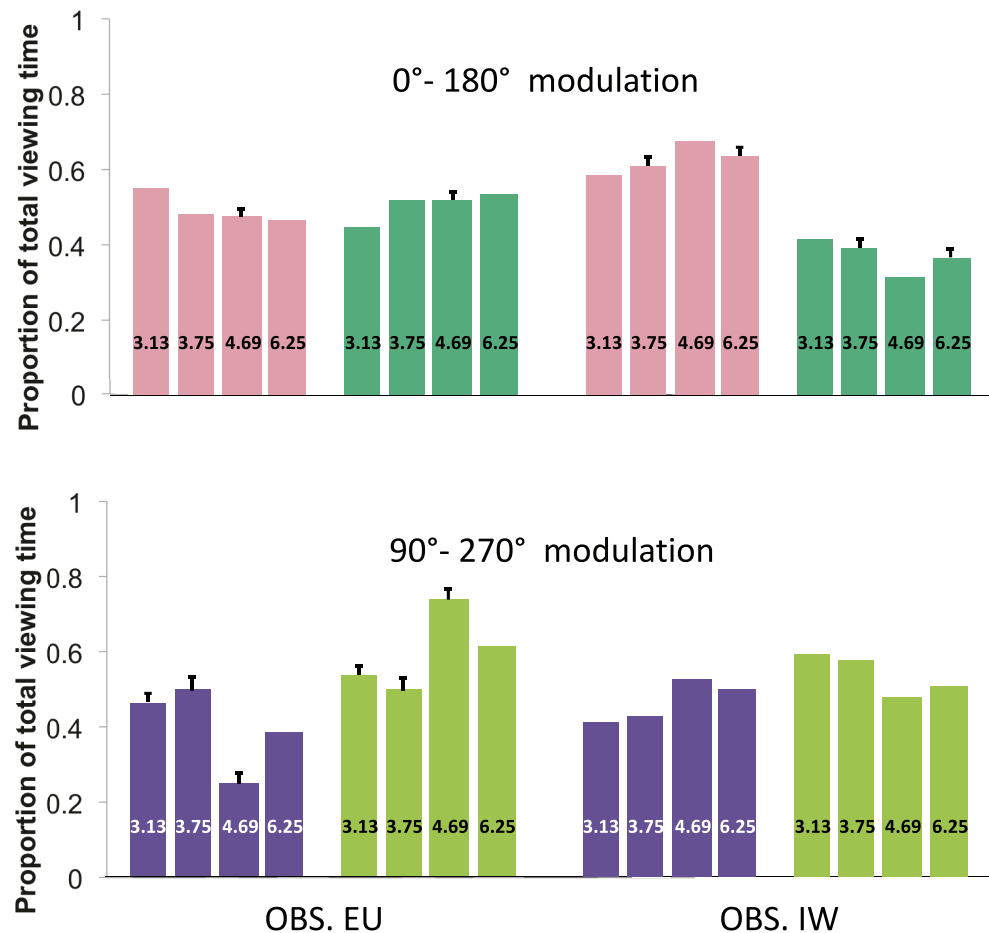


Figure 7. The proportion of total viewing time for which each stable uniform color was perceived (approximate perceived hue shown by bar color), with chromatic modulation along each of the cardinal directions (0° – 180° above, 90° – 270° below). Measurements for two observers were taken at 3.13, 3.75, 4.69, and 6.25 Hz (frequency indicated by label within each bar). Error bars show SEMs (SEM less than 0.02 where not plotted).

trast¹ very close to that from modulation along the cardinal direction at 0° – 180° .

Procedures specific to Experiment 4

Luminance interocular-switch rivalry was tested with pure luminance modulation of achromatic lights metameric to the equal-energy spectrum ($l = 0.665$, $s = 1.0$). With the surrounding annulus at 23 cd/m^2 , the higher (lower) alternating luminance was an increment (decrement) with respect to the surround. Over several different days, each observer ran ten 60-s trials for each of the high and low luminance-contrast conditions with the 23 cd/m^2 surrounding annulus. These measurements with luminance interocular-switch rivalry were made within the same sessions as the measurements in Experiment 1 and are separated here for clarity of presentation.

In separate sessions, the luminance of the surround was changed from 23 cd/m^2 to either 16 or 30 cd/m^2 , so that the 21.5 and 24.5 cd/m^2 (low contrast) and 18 and

28 cd/m^2 (high contrast) stimuli were surrounded by an annulus that kept luminance-modulation levels either entirely above or below the surround level. That is, with a 16 (30 cd/m^2) surround, all modulating lights were increments (decrements) with respect to the surround. These four conditions were repeated in eight trials on a single day; thus, total viewing time was eight minutes per condition.

Results and interpretation of Experiment 4

For all participants and conditions, luminance interocular-switch rivalry rarely gave a stable brightness percept. The measurements, therefore, are not plotted here as cumulative survival-style plots as in Experiments 1 and 2 because most plots would be a nearly flat line close to zero on the vertical axis. Instead, a summary of the measurements (Table 1) shows the percentage of total viewing time when a stable brightness was perceived. There are 36 values represented in the table (two contrast conditions \times two

	Participant					
	A.D.D.		J.H.C.		W.W.	
Levels of modulating achromatic discs (cd/m ²)	21.5/24.5	18.0/28.0	21.5/24.5	18.0/28.0	21.5/24.5	18.0/28.0
Level of annulus (cd/m ²) surrounding the modulating achromatic discs						
23	*/*	*/3%	*/*	*/*	*/*	*/*
16	*/*	*/*	*/*	*/*	*/4%	*/5%
30	*/*	*/*	10%/*	16%/*	*/*	21%/2%

Table 1. Percentage of total viewing time with one or the other achromatic stimulus perceived as stable during luminance interocular-switch rivalry. Note: *Less than 1% of viewing time.

luminance levels for each contrast \times three surround levels \times three observers). Twenty-nine of these 36 measurements were less than 1% (represented by an asterisk), indicating a stable brightness percept for less than 600 ms during a 60-s viewing period so negligible (and possibly an accidental button press).

With the surrounding annulus at the intermediate luminance (23 cd/m², first row of Table 1), slow perceptual alternations between two brightnesses virtually never occurred. Very rarely, a participant would press a button meant to indicate stabilization of one or the other brightnesses, but none of these button presses ever exceeded one second in duration and usually were shorter than 500 ms.

When luminance interocular-switch rivalry stimuli were either entirely above or entirely below the luminance of the surrounding annulus (second and third rows of Table 1), slow perceptual *alternation* between two brightnesses still was nearly absent. Rarely, participant J.H.C. or W.W. pressed a button indicating a stabilized brightness percept *associated with the luminance closest to the surrounding annulus*. The most extreme example of this was participant W.W. with the surrounding annulus at 30 cd/m² (bottom row of table) and the luminance of the discs oscillating between 18 and 28 cd/m². Here, participant W.W. occasionally made button presses indicating seeing the higher brightness (corresponding to 28 cd/m²), and these summed to 2% of the total viewing time (on average, a total duration of 1.2 s during a 60-s run of this condition). Importantly, the mean duration of pressing the button in this case was about 600 ms, and no single button press lasted longer than one second. The same was found for all other cases when participant J.H.C. or W.W. pressed the button that indicated seeing the brightness as stabilized at the level for the luminance closest to the surrounding annulus: The mean button press duration was less than 500 ms, and no single button press lasted longer than one second.

The most common stabilized brightness percept occurred for the *luminance most different from the surround* level. When the surround was 16 cd/m², occasionally the brightness for 24.5 cd/m² or 28 cd/m² stabilized, especially for participant W.W.; when the

surround was 30 cd/m², the brightness from 21.5 cd/m² or 18 cd/m² sometimes stabilized, reaching up to 21% of the viewing time for W.W.

A critical question is whether these relatively rare stable percepts reflected the brightnesses of the two alternating stimuli. Considering all conditions and participants in Table 1, the clear answer is no. Achromatic switch stimuli were viewed for a total of 156 sixty-second trials. On 154 of these 156 trials, there was no slow alternation according to even the minimal definition of it used for slowly alternating colors in Experiment 1 (that is, slow alternation during a 60-s trial required only that the brightness corresponding to each alternating stimulus was seen as stabilized for at least one second). Therefore, *luminance* interocular-switch rivalry almost never caused slow perceptual alternation.

Moreover, the two of 156 trials that did meet the slow-alternation definition had the 30 cd/m² annulus surrounding the achromatic disc modulating between 18 and 28 cd/m². In both of these trials, the dark percept for the 18 cd/m² luminance (the one most different from the surround level and a 25% Michelson-contrast decrement) predominated while the other brightness percept for the 28 cd/m² level (3% Michelson-contrast) was seen for little more than a second during a 60-sec trial, barely reaching the slow-alternation criterion.

Overall, luminance interocular-switch rivalry almost never resulted in slowly alternating brightness percepts analogous to the slow alternating color percepts found in Experiments 1, 2, and 3. Note that this holds for both the low and the high level of luminance contrast for interocular-switch stimuli, as shown in the columns of Table 1.

Experiment 5: Classic binocular color rivalry along cardinal chromatic directions

Overview of Experiment 5

Experiment 5 was performed to compare classic binocular color rivalry to chromatic interocular-switch rivalry. In classic rivalry, a stimulus of one chromaticity is continuously presented to one eye and a rivalrous

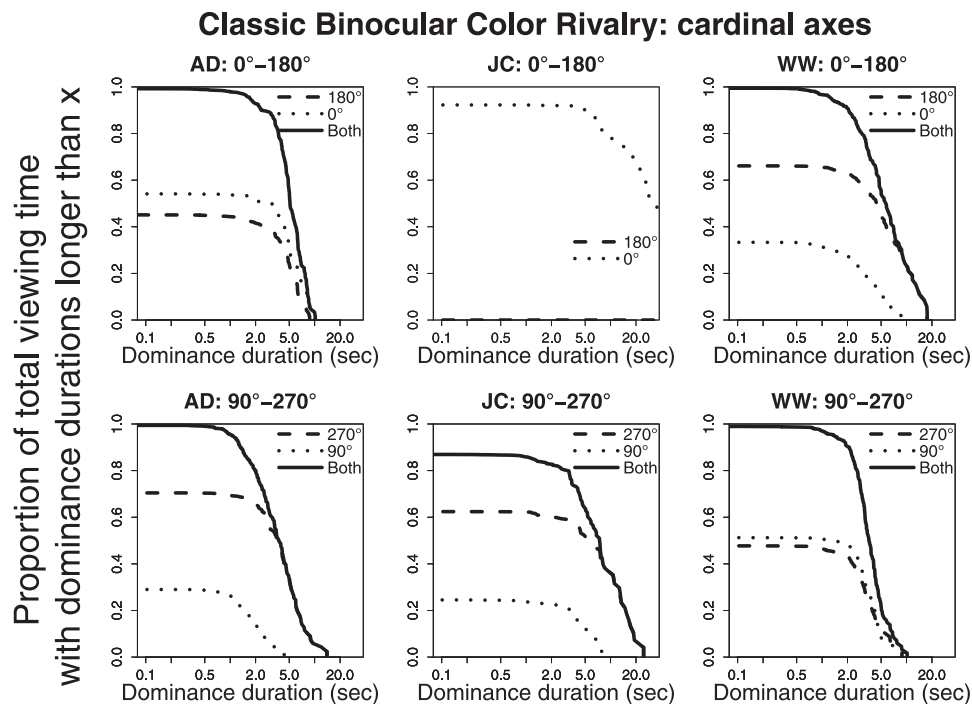


Figure 8. Results from Experiment 5. As Figure 4 but for classic binocular color rivalry. Note that participant J.H.C. never experienced the color corresponding to the chromaticity at 180° , so there is no plot for that chromaticity in the top middle panel.

chromaticity continuously to the other eye at the corresponding retinotopic location. Otherwise, the methods and analysis used here were the same as in Experiment 1.

Procedures specific to Experiment 5

Classic binocular color rivalry was measured with chromaticities from the cardinal l -axis or s -axis shown in Figure 1 (the 0° – 180° or 90° – 270° axis). The two rivalrous chromaticities for each axis were counterbalanced for the left and right eyes. This produced four unique conditions, each of which was presented five times. Because measurements on each trial were taken for 60 s, a total of 600 s of measurements were taken for each cardinal axis. Each observer completed Experiment 5 in one session.

Results and interpretation of Experiment 5

Qualitatively, the results from chromatic interocular-switch rivalry (Figure 4) are similar to those with classic binocular color rivalry (Figure 8). First, the relative stimulus strengths of the two chromaticities on the l -axis or s -axis are comparable in chromatic interocular-switch rivalry and classic binocular color rivalry. That is, for all three participants and for both the l - and s -axes, the chromaticities that predominated during chromatic interocular-switch rivalry also predominated during classic binocular rivalry ($p < 0.04$ by two-tailed

sign test for six binary outcomes). This is true even for participant A.D.D. with modulation along the l -axis (top left panel), for whom the chromaticity at 0° during chromatic interocular-switch rivalry gave results very similar to the chromaticity at 180° but with marginally higher predominance at 0° , just as is the case for classic color rivalry. Second, and just as for chromatic interocular-switch rivalry, there is a high proportion of total viewing time during which a stable color is seen. Looking at the solid lines for participants A.D.D. and W.W. in condition 0° – 180° (Figure 8), it can be seen that, as a percentage of the total viewing time, a stable color was perceived for two seconds or longer for 92% and 90%, respectively.

There is no solid line for the 0° – 180° condition for participant J.H.C. because only one of the colors was perceived stably with classic rivalry at 0° – 180° . This is reminiscent of the finding for J.H.C. in the 0° – 180° condition for chromatic interocular-switch rivalry (Figure 4), in which this participant predominantly perceived the 0° chromaticity. Participants A.D.D. and W.W., on the other hand, frequently perceived both colors corresponding to the chromaticity pair at the endpoints of the l -axis (0° – 180°). As was the case for chromatic interocular-switch rivalry, the dominance durations for the two colors were not equal (dominance durations at 0° [180°] at or above two seconds were 51% [41%], 92% [0%], and 27% [63%] for participant A.D.D., J.H.C., and W.W., respectively). Overall mean dominance duration was 4.1 ($SEM = 0.12$), 17 (4.93),

and 3.8 (0.33) s for participant A.D.D., J.H.C., and W.W.

Looking at the solid line in Figure 8 for condition 90° – 270° , for all three participants it can be seen that, as a percentage of the total viewing time, a stable color was perceived for two seconds or longer for 80%, 82%, and 90% (participants A.D.D., J.H.C., and W.W., respectively). The balance between chromaticities at 90° (270°) for dominance durations at or greater than two seconds was 15% (65%), 22% (60%), and 47% (43%) for participant A.D.D., J.H.C., and W.W., respectively. For the *s*-axis, the overall mean dominance duration was 2.7 ($SEM = 0.08$), 5.6 (0.36), and 3.1 (0.13) s (A.D.D., J.H.C., and W.W., respectively).

Using the definition of “slow alternation” given above, the three participants experienced slow alternation during 20 of 30 trials for the 0° – 180° condition (not all 30 because participant J.H.C. experienced only one of these colors and therefore never saw slow alternation) and 29 of 30 trials for the 90° – 270° condition.

In sum, the total time perceiving a stable uniform color and the number of trials with slow alternation is high for both chromatic classic and interocular-switch rivalry. Further, the relative strength of each chromaticity within a pair is comparable for both kinds of rivalry, for all three participants.

Discussion

In chromatic interocular-switch rivalry, equiluminant binocularly rivalrous colors are presented to the two eyes. The two rivalrous colors are kept constant but are swapped between the eyes several times a second, for example, at 3.75 Hz. If an observer closes one eye, the percept is a rapidly changing sequence of one color and then the other, as expected. Viewing with both eyes, however, results in a surprising percept: One of the colors often is seen steadily for two seconds or longer (that is, during 15 or more left-eye/right-eye color swaps at 3.75 Hz), and then the steady appearance changes to the other color. These sustained color percepts are a bistable phenomenon with conspicuously slow perceptual alternation between two colors. Slow bistable perceptual alternation was found in *every* condition with chromatic interocular-switch rivalry (all conditions in Experiments 1, 2, and 3) for *every* observer.

Chromaticities on only the L/(L + M) axis, only the S/(L + M) axis, or on intermediate axes

Chromatic interocular-switch rivalry caused bistable sustained color percepts, regardless of whether the

chromatic rivalry was along the L/(L + M), S/(L + M), or an intermediate axis. Swapping chromaticities along intermediate axes (Experiment 2) involves a simultaneous change in both L/(L + M) and S/(L + M) so they can be used to assess whether intermediate-axis color percepts are dominated by either the L/(L + M) or the S/(L + M) swap component. Results show the L/(L + M) swap is dominant. With rivalry along an intermediate axis, the predominant stable color percept was from the chromaticity with an *l*-axis value equal to that for the predominant percept with cardinal *l*-axis-only modulation and not the predominant percept with cardinal *s*-axis-only modulation. This suggests that swapping chromaticities along intermediate chromatic directions establishes a predominant color percept regulated by a neural representation that maintains separate L/(L + M) and S/(L + M) signals.

Luminance interocular-switch rivalry

In contrast to chromatic interocular-switch rivalry, *luminance* interocular-switch rivalry in Experiment 4 shows that achromatic luminance modulation virtually never results in slow perceptual alternations between spatially uniform fields differing in brightness. In classic binocular rivalry between uniform stimuli differing only in luminance, the percept can be slowly alternating achromatic percepts (Fox & Herrmann, 1967; Levelt, 1965, 1966). In these studies, rivalry was between small uniformly white or black discs, where white was an increment on a black background and black a decrement on a white background. The stimulus parameters were similar to those used here in the first part of Experiment 4, where the surround was 23 cd/m^2 and a central circular luminance increment was in one eye and a decrement in the other eye. Why then do the swapped luminance stimuli in Experiment 4 not cause slow alternation of perceived brightness (or lightness)?

This question is intriguing because purely chromatic differences instigate bistability for both types of rivalry (Experiments 1–3 and 5). A finding by E. L. Smith, Levi, Harwerth, and White (1982) may partly explain why *luminance* interocular switches do not result in slowly alternating achromatic percepts whereas *chromatic* interocular-switch rivalry gives slowly changing colors. E. L. Smith et al. instigated classic binocular rivalry between two orthogonal achromatic gratings and then pulsed a small spot of light (a probe) on one of the gratings when it was either dominating perceptually or suppressed perceptually. By systematically varying the radiance and wavelength of the spot of light, they determined the spectral sensitivity to the probe during both dominance and suppression. When the test was presented on a dominating grating, the

spectral sensitivity of the probe had three peaks corresponding well to the three sensitivity peaks of the L, M, and S cones. This indicates that sensitivity was poorer in the luminance pathway than a chromatic pathway. During suppression, however, they found a different result: The spectral sensitivity had a single broad peak at 555 nm (the peak of the human luminosity function), indicating sensitivity was better in the luminance than chromatic pathway during perceptual suppression. If the transients of the test probes used by E. L. Smith et al. are akin to transients implicit in luminance interocular-switch rivalry when the stimuli are swapped between eyes, then during luminance interocular-switch rivalry, the transients may disturb a stable percept via the luminance pathway, overcoming any suppression, whereas transients created by equiluminant modulation along a chromatic direction cannot trigger a luminance response.

As discussed above, the predominant bistable color perceived during *chromatic* interocular-switch rivalry implicates responses from a level of the visual system where $L/(L + M)$ and $S/(L + M)$ signals are separate (cf. Christiansen et al., 2009). It is therefore plausible that the mechanism limiting the perception of slowly alternating achromatic percepts during *luminance* interocular-switch rivalry also resides at this level of the visual system. If so, the differences between luminance and chromatic interocular-switch rivalry, found here, mirror work on *form* interocular-switch rivalry. Only under particular circumstances will *form* interocular-switch rivalry result in slowly alternating percepts (Lee & Blake, 1999). In a more recent study, Denison and Silver (2012) examined the hypothesis that these circumstances are those that favor activation in the parvocellular pathway over the magnocellular pathway. Note that the parvocellular and magnocellular pathways are widely thought to subserve chromatic and luminance processing, respectively. Although S-cone isolating stimuli, as included here, are thought to activate the koniocellular pathway (Conway et al., 2010), Denison and Silver's results suggest that the magnocellular pathway may play the main role in disrupting stable percepts from interocular-switch rivalry.

Individual differences with interocular-switch rivalry

Individual differences are well known in classic binocular rivalry with a stimulus of one orientation continuously presented to one eye and a competing orientation to the fellow eye. The temporal rate of alternation between perceiving each of the two orientations varies substantially among observers, as demonstrated in two studies with a good number of

participants ($n = 61$ in Carter & Pettigrew, 2003; $n = 20$ in Hancock, Gareze, Findlay, & Andrews, 2012).

Further, individual differences in the temporal dynamics of fluctuating orientations in classic binocular rivalry correlate well with individual differences in the dynamics found with *form* interocular-switch rivalry ($n = 21$ in Patel, Stuit & Blake, 2014). This indicates a link between classic and interocular-switch rivalry and, of course, documents individual differences in switch rivalry.

Are there individual differences in *chromatic* interocular-switch rivalry? The sample size here was not intended to investigate individual differences, but it is worth noting obvious differences among the participants tested and, moreover, the consistency of these individual differences with both chromatic interocular-switch rivalry and classic binocular color rivalry. With chromatic interocular-switch rivalry along the 0° – 180° axis (*l*-axis; Figure 4, top panels), one observer (J.H.C.) predominantly perceived the color at 0° , another (W.W.) the color at 180° , and the third (A.D.D.) saw the two colors nearly equally; along the 90° – 270° axis (*s*-axis; Figure 4, bottom panels), two observers predominantly perceived the color at 270° (A.D.D. and J.H.C.) and the third at 90° (W.W.). Importantly, for every observer, the same pattern of dominance by one color or the other was found with classic binocular color rivalry (Figure 8). Despite the small sample size, these individual differences, and especially their correspondences across classic and interocular-switch rivalry, are unlikely to reflect chance.

Neural models

The predominant explanation for *form* interocular-switch rivalry is based on inhibition between orientation-tuned binocular neurons (see the Introduction), but a recent alternative approach (Brascamp et al., 2013) shows monocular neurons theoretically could cause the rivalrous dynamics from *form* interocular-switch rivalry with orthogonal gratings. The monocular model of Brascamp et al. deliberately ignores the binocular-processing level and instead adds two new monocular neural mechanisms to the classic binocular rivalry model, in which reciprocal inhibition between left- and right-eye monocular neurons causes binocular neurons to receive information from one eye at a time. With the addition of the two extra monocular mechanisms, Brascamp et al. were able to model computationally the percepts from *form* interocular-switch rivalry as a monocularly driven phenomenon.

One of their added mechanisms is between-eye same-orientation inhibition. The authors use this mechanism to explain why 18-Hz on-off flicker or a single blank interval inserted between monocular switches (Denison

& Silver, 2012; van Boxtel et al., 2008) is necessary during *form* interocular-switch rivalry. *Chromatic* interocular-switch rivalry, however, does not require flicker (or blank intervals); in fact, rapid on-off flicker or a blank interval was never used in the experiments here. Thus, this monocular mechanism is not an account for *chromatic* interocular-switch rivalry.

The other monocular mechanism in Brascamp et al. is within-eye cross-orientation inhibition. The monocular model posits continuous inhibition, within each eye and between the two orthogonal orientations, with inhibition from the perceptually dominating orientation stronger than the inhibition from the perceptually suppressed orientation. When the two orientations are swapped between eyes, say a perceptually dominating vertical orientation is swapped from the left to right eye, the neurons in the right eye that are driven by a stimulus with a vertical orientation will be less inhibited compared with the neurons in the left eye that are driven by a stimulus with a horizontal orientation, because, in the right eye, the immediately preceding inhibition was mediated by neurons preferring the horizontal stimulus, which was perceptually suppressed and therefore inhibiting less than the dominating vertically oriented stimulus. This results in a tendency for perceptual dominance to switch in synchrony with the physical swapping. Thus, *form* interocular-switch rivalry might be understood as alternating eye dominance across eye swaps. Applying the same type of mechanism to the chromatic domain, however, would require a monocular neural mechanism for color having within-eye inhibition between differently colored stimuli. Although this is a theoretical possibility, we are not aware of evidence to support it.

Without evidence of a *chromatic* counterpart to within-eye cross-orientation inhibition, we are swayed by the chromatic neural responses discovered by Peirce et al. (2008), which are in accord with a model of *chromatic* interocular-switch rivalry analogous to the binocular neural model for *form* proposed, for example, by Wilson (2003). This model holds that alternating sustained periods of perceptual dominance of only one or the other color occur because the responses from binocularly driven neurons, preferring one chromaticity, will fluctuate very little when chromaticities are swapped between the two eyes.

Keywords: binocular rivalry, color perception, stimulus rivalry

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Corresponding author: Steven K. Shevell.

Email: shevell@uchicago.edu.

Address: Department of Psychology, The University of Chicago, Chicago, IL, USA.

Footnote

¹ Pooled cone contrast was calculated using the equation in Kaiser and Boynton (1996). The L-cone excitation for each of the central discs was calculated by multiplying the chromaticity value on the *l*-axis, for the central disc, by the luminance (cd/m^2) of the central disc. The M-cone excitation, for each central disc, was calculated by subtracting the chromaticity value on the *l*-axis from 1 and then multiplying this result by the luminance (cd/m^2) of the central disc. The S-cone excitation was calculated by multiplying the chromaticity value on the *s*-axis by the luminance (cd/m^2) of the central disc.

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