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Binocular rivalry between identical retinal stimuli with an induced color difference

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Abstract

An open question in color rivalry is whether alternation between two colors is caused by a difference in receptoral stimulation or a difference in the neural representation of color appearance. This question was examined with binocular rivalry between physically identical lights that differed in appearance due to chromatic induction. Perceptual alternation was measured between gratings of the same chromaticity; each one was presented within a different patterned surround that caused the gratings, one to each eye, to appear unequal in hue because of chromatic induction. The gratings were presented dichoptically with binocular disparity so the rivalrous gratings appeared in front of the surround. Perceptual alternation in hue was found for the two physically identical chromaticities. Stereoscopic depth also was perceived, corroborating binocular neural combination despite color rivalry (Treisman, 1962). The results show that color rivalry is resolved after color-appearance shifts caused by chromatic context, and that color rivalry does not require competing unequal cone excitations from the rivalrous stimuli.

Keywords: Chromatic induction; Color rivalry; Neural representation of color appearance

Introduction

Perceptual alternation between two colors occurs when two sufficiently different chromaticities are presented dichoptically to the same part of the visual field. This is the phenomenon of binocular color rivalry (Ikeda & Sagawa, 1979; de Weert & Wade, 1988). The perceptual alternation results from competing chromatic signals, but are competing receptoral signals from the two eyes necessary for binocular color rivalry?

Two physically identical lights can appear unequal in hue due to different surrounding context (reviewed by Shevell, 2003). An induced difference in color appearance might cause binocular color rivalry. If so, this would indicate that color rivalry does not require competing unequal cone excitations, but instead can result from rivalrous neural representations of color. The experiments here test whether binocular color rivalry can occur between identical physical lights with an induced appearance difference.

Unlike previous studies (Wallach & Adams, 1954; Andrews & Lotto, 2004), the rivalrous chromatic targets were induced by the identical chromatic context in each eye. Thus, the alternations in color appearance during dichoptic viewing could not be due to alternation between competing chromatic contexts.

In the present study, the difference in color appearance between two physically identical stimuli was caused by chromatic induction, inferred to be cortically mediated (Monnier & Shevell, 2003, 2004; Shevell & Monnier, 2005). The chromatic inducing pattern varied in only S-cone stimulation (see Materials and methods for detail). Color-appearance shifts caused by this type of S-cone patterned background are accounted for by a receptive field with S-cone spatial antagonism, such as +S center and −S surround, and such receptive fields are first found at the cortical level. No known neural mechanism at the retinal or lateral geniculate nucleus (LGN) level can explain these induced color shifts. Various levels of the visual processing hierarchy are proposed as a neural locus for resolving rivalry (Blake & Logothetis, 2002): LGN (Wunderlich et al., 2005; Haynes et al., 2005), V1 (Polonsky et al., 2000; Lee & Blake, 2002, 2004; Tong & Engel, 2001), and beyond (Logothetis & Schall, 1989; Logothetis et al., 1996; Sheinberg & Logothetis, 1997; Tong et al., 1998). If the rivalrous chromatic representations at the cortical level cause binocular rivalry, this would imply that rivalry can be triggered by a neural process beyond the LGN.

Materials and methods

Apparatus

Stimuli were generated using a Macintosh G4 computer and presented on a calibrated Sony color display (GDM-F520). Sepa-

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rate stimuli on the cathode ray tube (CRT) screen were projected to the left and right eye using a haploscope. The haploscope was composed of eight front-surface mirrors. Two of the mirrors were attached to a saddle on a triangular rail so observers could adjust their position to achieve precise binocular fusion. The CRT display had 1360 × 1024 pixel resolution and a refresh rate of 75 Hz non-interlaced. The red, green, and blue guns of the color CRT were linearized using 10-bit lookup tables.

Stimuli

Perceptual alternation during dichoptic presentation of rivalrous stimuli was measured in two different conditions. In the main "physically identical" condition (Fig. 1a), rivalrous targets were presented within an inducing background that was the same in both eyes. The inducing background was a 4 cpd vertical square-wave pattern with two chromaticities that differed in only S-cone stimulation. Their chromaticities in a cone excitation space (MacLeod & Boynton, 1979) were ($L/(L + M) = 0.667$, $S/(L + M) = 3.30$), which appeared purple, and ($L/(L + M) = 0.667$, $S/(L + M) = 0.2$), which appeared lime (circles, Fig. 1b). Chromaticities for the inducing pattern were chosen to cause relatively large shifts in the appearance of the test bars, based on a previous study (Monnier & Shevell, 2003). The luminance of the inducing background was 8 cd/m^2. The rivalrous target presented to each eye was three vertical bars, 7.5 min of arc wide and 1° high. The chromaticity of the target bars was metameric to a "white" equal-energy-spectrum stimulus ($L/(L + M) = 0.667$, $S/(L + M) = 1.0$; square Fig. 1b) and had luminance 12 cd/m^2. Note that the unit of $S/(L + M)$ is arbitrary and scaled here to 1.0 for an equal-energy spectrum. The width of each target bar was the same as the width of each stripe of the inducing background. The rivalrous targets, one to each eye, were on stripes of different chromaticity in the same inducing pattern. The location of target bars, therefore, differed in the two eyes by 7.5 min of arc, which provided binocular disparity so that the target bars, when fused, appeared in front of the inducing pattern. The binocular disparity allowed an induced color-appearance difference between the two rivalrous targets while maintaining identical inducing backgrounds in each eye.

In a second "physically different" condition, two rivalrous targets of different chromaticities were presented within a uniform equal-energy-spectrum surround (Fig. 1c). The chromaticities of the target bars in the uniform surround were set to match the *appearance* of the target bars in the purple/lime inducing patterns (Fig. 1a) by asymmetric color matching (see Monnier & Shevell, 2004, for detail). When the target bars were on top of "purple" stripes in the inducing pattern, the bars appeared greenish (Fig. 1b, inverted triangle). When the target bars were on top of "lime" stripes in the inducing pattern, the bars appeared purplish (Fig. 1b, upright triangle). These chromaticities of bars within the uniform surround (Fig. 1c) gave the same difference in color appearance as the physically identical bars in the purple/lime inducing patterns (Fig. 1a).

Procedure

Percepts were measured during 1 min of presentation of rivalrous targets. Observers used a game pad to report their percept by

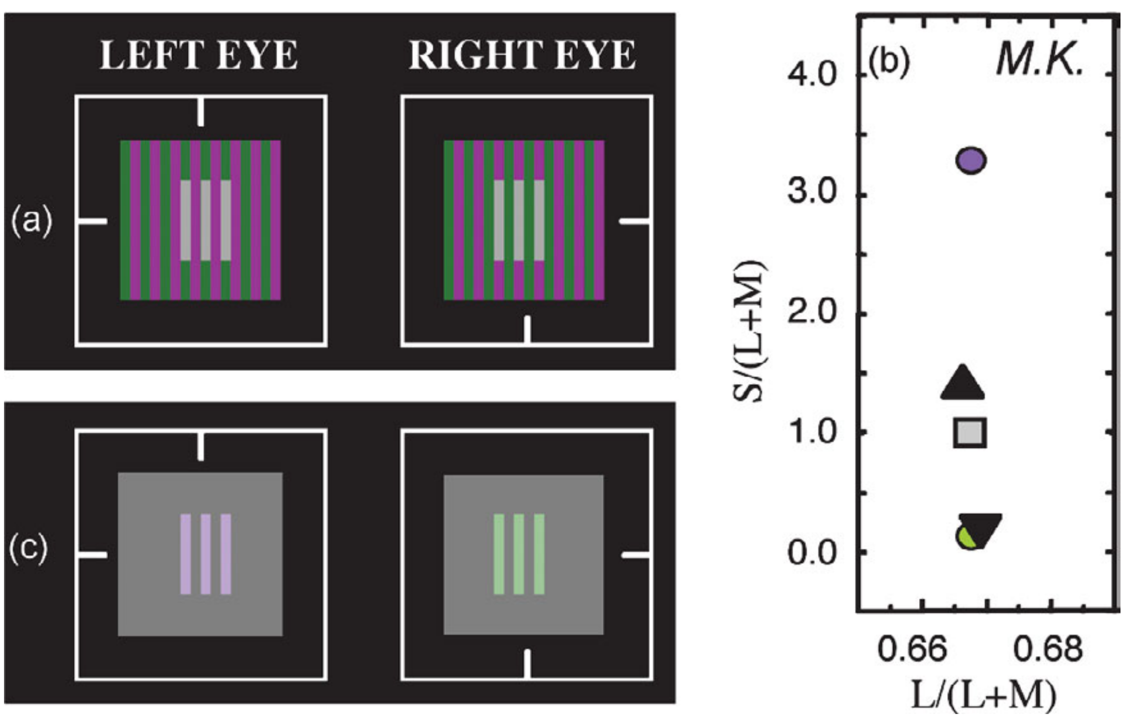

Fig. 1. (**a**) Stimuli for the "physically identical" condition. All target bars were identical and metameric to an equal-energy-spectrum "white." (**b**) Chromaticities of stimuli used in experiments, shown in a cone excitation diagram (MacLeod & Boynton, 1979): target bars (square), stripes in background (circles). One observer's asymmetric matches to the perceived color of target bars within the pattered background are shown by triangles. (**c**) Stimuli for the "physically different" condition with target bars on a uniform background. The appearance of the target bars in each eye is the same for the two conditions (see text).

pressing separate buttons. When the complete stimulus presented to the left eye was perceived, observers held a particular button until the percept changed. When a complete stimulus presented to the right eye was perceived, observers held a different button. An additional button was assigned to the percept of binocular color mixture. The percentage of the total duration of perceptual alternation and of color mixture was used for analysis, as in recent studies of binocular rivalry (Blake et al., 1998; Andrews & Blakemore, 2002; Paffen et al., 2006). Each experiment was repeated three times on different days.

Observers

Three observers participated in the study. All had normal color vision as tested with a Neitz anomaloscope. Author H.S.W. was knowledgeable about the experimental design and had prior experience making brightness matches. Observers M.K. and J.L. were naïve. Consent forms were completed in accordance with the policy of the University of Chicago's Institutional Review Board.

Results

Rivalry between two physically identical chromaticities that appeared different due to chromatic induction was compared to rivalry between two physically different chromaticities. Recall that the appearance difference between the two rivalrous targets was the same in both conditions (within measurement error).

The percentage of the total duration of perceptual alternation and of color mixture in the two conditions is shown in Fig. 2. The horizontal axis indicates each percept, and the vertical axis shows the percentage of the total duration. Open bars are measurements with rivalrous targets that were physically identical but appeared

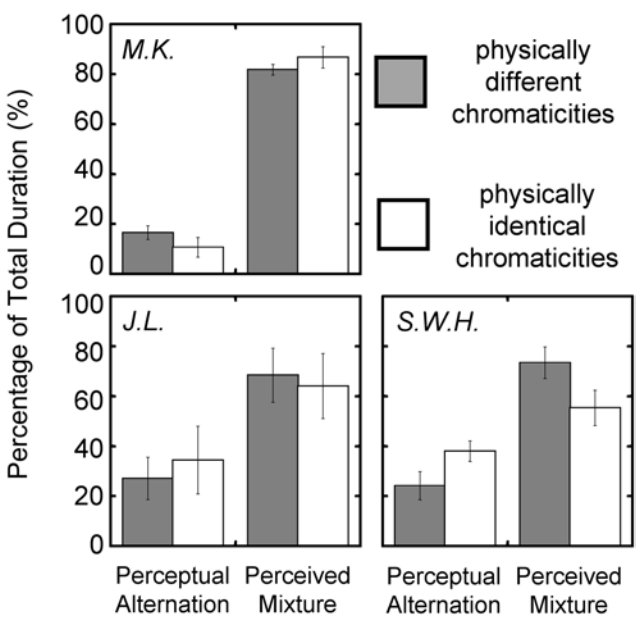

Fig. 2. Perceptual alternation (color rivalry) and color mixture were perceived by each observer, whether rivalry was between physically identical chromaticities that appeared different due to chromatic induction (open bars) or between physically different chromaticities (filled bars). The vertical axis shows the percentage of the total duration during one minute of stimulus presentation.

unequal in hue because they were on different stripes of the patterned inducing field. Filled bars are measurements with the physically different rivalrous targets presented within the equal-energy-spectrum surround.

Perceptual alternation ("rivalry") between two color percepts was perceived with targets that were either physically identical (open bars) or physically different (filled bars), though binocular color mixture was perceived predominantly during the one minute of presentation. The duration of color alternation was comparable in both conditions for all three observers. Stereoscopic depth was perceived consistently during color alternation, indicating neural combination of signals from the two eyes despite color rivalry (Treisman, 1962).

Discussion

The perceptual alternation between two identical chromaticities that appeared different due to chromatic induction shows that color rivalry can be resolved after shifts in color appearance caused by chromatic context. This result implies that rivalrous chromatic representations, not the physical differences in stimuli, cause binocular rivalry.

The predominant percept of binocular color mixture is due to the modest difference in color appearance between the rivalrous stimuli. Binocular color mixture was the predominant percept also in the "physically different" condition in which the chromaticities of the rivalrous targets were chosen to match the induced colors from the patterned fields. Small differences in dichoptically presented chromaticities tend to give binocular color mixture instead of rivalry (Ikeda & Sagawa, 1979).

The results shed light on the question of where in the visual processing stream binocular color rivalry can be resolved. Recent funtional magnetic resonance imaging (fMRI) studies show that activity in the LGN tracks perceptual alternation during binocular rivalry between two gratings that are defined by both luminance and color (Wunderlich et al., 2005; Haynes et al., 2005). These studies, however, cannot distinguish the source of the inhibitory modulation of LGN activity during rivalry, which may be due to direct interactions between LGN layers or to feedback from visual cortex. Unlike rivalry between two different forms (e.g., orientation), binocular color rivalry theoretically could be resolved by inhibitory interactions among monocular, chromatically selective neurons in the LGN because about 90% of neurons within the parvocellular pathway of LGN are monocularly driven and color opponent (Lennie, 2003). Inhibitory binocular interactions have been reported in the monkey LGN (Schroeder et al., 1990; but see Rodieck & Dreher, 1979). The rivalry here between two physically identical stimuli, however, strongly suggests that color rivalry does not require competing signals at the receptors, retina or LGN. If binocular color rivalry and its resolution depended exclusively on neural processes prior to cortical processing, then color rivalry would not be expected between the physically identical rivalrous stimuli here, because their color difference is thought to be mediated by a cortical neural receptive field with S-cone spatial antagonism (e.g., $+$S center and $-$S surround; Monnier & Shevell, 2003, 2004). The results, therefore, suggest that binocular color rivalry can be resolved when competing neural representations first emerge at a cortical level.

If suppressive interaction at the cortical level causes perceptual alternation in color, the suppression must be selective to neural signals that drive central processes of color perception, not the whole eye or even the target-stimulus region, because in both of our conditions, the three-bar target always appeared in a different depth plane than its surround. This corroborates simultaneous binocular integration of spatial information and interocular suppression of (physical) color differences (Treisman, 1962), and is consistent with a distinct neural binding process that integrates color with depth.

In sum, the results show that color rivalry is resolved after color-appearance shifts caused by chromatic context. Color rivalry does not require competing unequal cone excitations, but instead can result from rivalrous neural representations that mediate color appearance. The "physically different" rivalrous stimuli have unequal neural representations at all levels of visual processing (receptoral, retinal, LGN, and cortical) but the "physically identical" stimuli are thought to first differ at the cortical level. Both conditions give rise to comparable color rivalry, suggesting that rivalry can be triggered at the cortical level.

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References

Andrews, T.J. & Blakemore, C. (2002). Integration of motion information during binocular rivalry. *Vision Research* **42**, 301–309l.

Andrews, T.J. & Lotto, R.B. (2004). Fusion and rivalry are dependent on the perceptual meaning of visual stimuli. *Current Biology* **14**, 418–423.

Blake, R. & Logothetis, N.K. (2002). Visual competition. *Nature Review Neuroscience* **3**, 1–11.

Blake, R., Yu, K., Lokey, M. & Norman, H. (1998). Binocular rivalry and motion perception. *Journal of Cognitive Neuroscience* **10**, 46–60.

de Weert, C.M.M. & Wade, N.J. (1988). Compound binocular rivalry. *Vision Research* **28**, 1031–1040.

Haynes, J.D., Deichmann, R. & Rees, G. (2005). Eye-specific effects of binocular rivalry in the human lateral geniculate nucleus. *Nature* **438**, 496–499.

Ikeda, M. & Sagawa, K. (1979). Binocular color fusion limit. *Journal of Optical Society America* **69**, 316–321.

Lee, S.-H. & Blake, R. (2002). V1 activity is reduced during binocular rivalry. *Journal of Vision* **2**, 618–626.

Lee, S.-H. & Blake, R. (2004). A fresh look at interocular grouping during binocular rivalry. *Vision Research* **44**, 983–991.

Lennie, P. (2003). The physiology of color vision. In *The Science of Color*, ed. Shevell, S.K., pp. 217–246. Oxford: Elsevier.

Logothetis, N.K., Leopold, D.A. & Sheinberg, D.L. (1996). What is rivaling during binocular rivalry? *Nature* **380**, 621–624.

Logothetis, N.K. & Schall, J.D. (1989). Neural correlates of subjective visual perception. *Science* **245**, 761–763.

MacLeod, D.I.A. & Boynton, R.M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America* **69**, 1183–1186.

Monnier, P. & Shevell, S.K. (2003). Large shifts in color appearance from patterned chromatic backgrounds. *Nature Neuroscience* **6**, 801–802.

Monnier, P. & Shevell, S.K. (2004). Chromatic induction from S-cone pattern. *Vision Research* **44**, 849–856.

Paffen, C.L.E., Tadin, D., te Pas, S.F., Blake, R. & Verstraten, F.A.J. (2006). Adaptive center-surround interactions in human vision revealed during binocular rivalry. *Vision Research* **46**, 599–604.

Polonsky, A., Blake, R., Braun, J. & Heeger, D.J. (2000). Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nature Neuroscience* **3**, 1153–1159.

Rodieck, R.W. & Dreher, B. (1979). Visual suppression from nondominant eye in the lateral geniculate neucleus: A comparison of cat and monkey. *Experimental Brain Research* **35**, 465–477.

Schroeder, C.E., Tenke, C.E., Arezzo, J.C. & Vaughan, H.G., Jr. (1990). Binocularity in the lateral geniculate neucleus of the alert macaque. *Brain Research* **521**, 303–310.

Sheinberg, D.L. & Logothetis, N.K. (1997). The role of temporal cortical areas in perceptual organization. *Proceedings of the National Academy of Sciences USA* **94**, 3408–3413.

Shevell, S.K. (2003). Color appearance. In *The Science of Color*, ed. Shevell, S.K., pp. 149–190. Oxford: Elsevier.

Shevell, S.K. & Monnier, P. (2005). Color shifts from S-cone patterned backgrounds: contrast sensitivity and spatial frequency selectivity. *Vision Research* **45**, 1147–1154.

Tong, F. & Engel, S.A. (2001). Interocular rivalry revealed in the human cortical blind-spot representation. *Nature* **411**, 195–199.

Tong, F., Nakayama, K., Vaughan, J.T. & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrstriate cortex. *Neuron* **21**, 753–759.

Treisman, A. (1962). Binocular rivalry and stereoscopic depth perception. *Quarterly Journal of Experimental Psychology* **14**, 23–37.

Wallach, H. & Adams, P.A. (1954). Binocular rivalry of achromatic colors. *The American Journal of Psychology* **67**, 513–516.

Wunderlich, K., Schneider, K. & Kastner, S. (2005). Neural correlates of binocular rivalry in the human lateral geniculate neucleus. *Nature Neuroscience* **8**, 1595–1602.