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Fusion and Rivalry Are Dependent on the Perceptual Meaning of Visual Stimuli

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Summary

We view the world with two eyes and yet are typically only aware of a single, coherent image. Arguably the simplest explanation for this is that the visual system unites the two monocular stimuli into a common stream that eventually leads to a single coherent sensation [1]. However, this notion is inconsistent with the well-known phenomenon of rivalry; when physically different stimuli project to the same retinal location, the ensuing perception alternates between the two monocular views in space and time [2]. Although fundamental for understanding the principles of binocular vision and visual awareness, the mechanisms underlying binocular rivalry remain controversial [3, 4]. Specifically, there is uncertainty about what determines whether monocular images undergo fusion or rivalry. By taking advantage of the perceptual phenomenon of color contrast, we show that physically identical monocular stimuli tend to rival—not fuse—when they signify different objects at the same location in visual space. Conversely, when physically different monocular stimuli are likely to represent the same object at the same location in space, fusion is more likely to result. The data suggest that what competes for visual awareness in the two eyes is not the physical similarity between images but the similarity in their perceptual/empirical meaning.

Results and Discussion

Binocular rivalry presents a unique opportunity to correlate transitions in visual awareness with changes in neural activity [5]. Given their importance, the mechanisms that underlie fusion and rivalry have not surprisingly been debated for many years [6]. However, an issue that is often overlooked in this debate is the question of what actually determines whether two monocular images will rival when viewed dichoptically, which is fundamental for understanding how and why we see what we do. Is it the physical differences between two monocular images or the differences in the perception elicited by each image? In Figure 1, for example, do the spectral differences between the light that falls on the right and left eyes determine whether the two images will rival, or is it the difference in the perception of a yellow and blue surface that is most important? A key to understanding how one might resolve this issue may be found in previous studies that show that changing the context of a stimulus can alter perceptual dominance [7–11]. But why does context have such an effect on cyclopean vision?

To answer this question, we took advantage of the well-known phenomena of color contrast [12] and color constancy [13]. In the first experiment, subjects viewed physically identical monocular stimuli that (when consigned to specific chromatic contexts) were able to elicit different chromatic perceptions (color contrast). In the second experiment, we placed physically different monocular stimuli into contexts that elicited comparable chromatic perceptions (color constancy). Our prediction was that, if binocular integration was dependent on physical differences between the two eye views, the context in which the stimuli were viewed should have no effect on whether the targets fuse or rival. On the other hand, if binocular vision were contingent on the probable source, and thus on perceptions elicited by the stimulus, the context in which the stimuli are viewed should influence whether they fuse or rival.

Color Contrast: Inducing Rivalry between Physically Identical Targets

Subjects were first presented dichoptically with two sets of spectrally identical (control) surfaces (Figure 2A). In this condition, subjects readily fused the two images and reported a cyclopean image that was identical to each of the monocular images. Subjects were then presented with the same surfaces within two different chromatic contexts (shown in Figure 2B). These panels were created to provide spectral information that would change the probable sources (i.e., reflectance). Specifically, in Figure 2B, the neutral returns from the surfaces in the left panel are relatively consistent with the experience of longer wavelength-reflecting surfaces under shorter-wavelength light, whereas the same neutral returns from surfaces in the right panel are consistent with relatively short wavelength-reflecting surfaces under longer-wavelength light. In accordance with this difference in their probable sources, the surfaces appear to be very different, blue on the left and yellow on the right (given the strength of this illusion, some may want to confirm the underlying identity of the tiles by masking the surfaces' surrounds). What happens when subjects attempt to fuse these physically identical surfaces under these conditions?

Again, if rivalry is simply the result of physical similarity between binocular spectra, then no rivalry should be experienced between the target surfaces. However, if rivalry arises when the binocular information implies that one is viewing different surfaces at the same location in visual space, then perception should alternate be-

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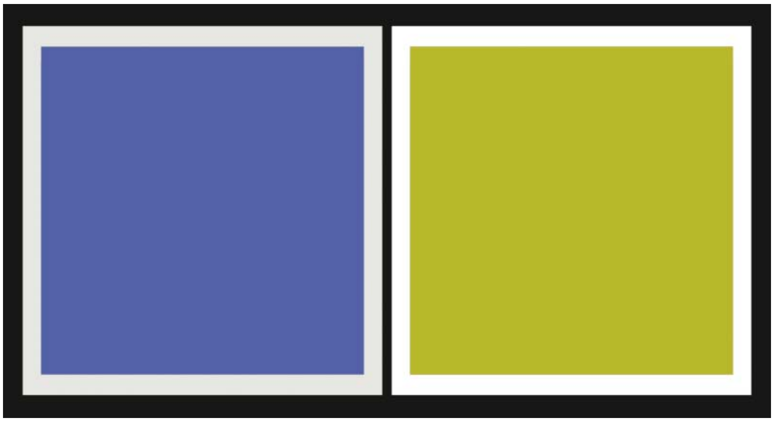

Figure 1. A Demonstration of Color Rivalry
When these two differently colored panels are fused, perception in any particular location in space alternates between the two eye views.

tween the two possible sources of the stimulus. Subjects reported experiencing an alternation in perceptual dominance in which the achromatic surfaces were, from time to time, perceived as blue or yellow. A histogram summarizing the durations of individual periods of dominance is shown in Figure 2C. Consistent with previous reports, individual dominance durations conform to a gamma distribution [3]. This finding is consistent with a report by Wallach and Adams [11] in which the illusion of simultaneous brightness contrast was used to show that rivalry of achromatic colors is triggered by surface appearance rather than local differences in spectral return. Together these findings suggest that physically identical retinal images can compete for perceptual

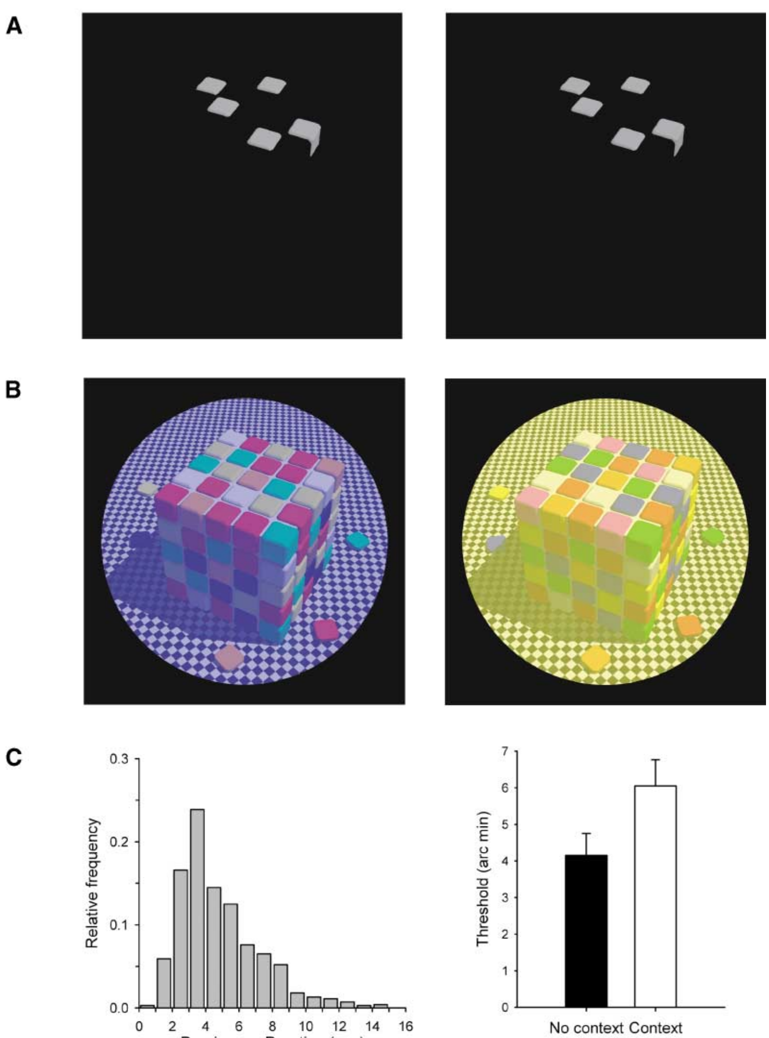

Figure 2. Inducing Rivalry between Identical Spectra
Subjects viewed the two different chromatic stereograms in (A) and (B). In all cases, the same five gray surfaces were presented in both panels. (C) The left graph represents the data from one subject viewing the stimulus in (B) and reporting changes in perceptual dominance of the blue and yellow surfaces. The right graph represents the average threshold (n = 7) for discriminating the sizes of two probes that were briefly presented to the suppressed eye. Subjects found that detecting a difference in size between the two probes was easier under the conditions in (A) than when the same targets were viewed under the conditions in (B). Scale bars represent one standard error.

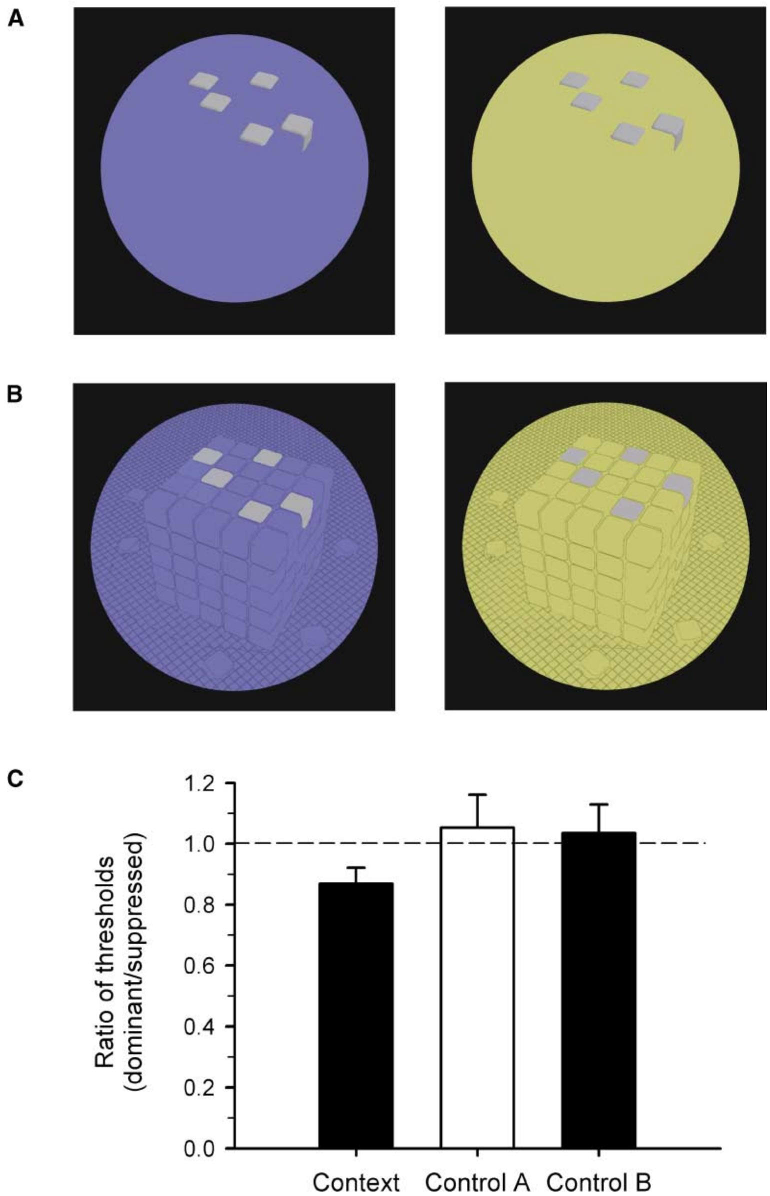

Figure 3. Control Conditions for Color Contrast Experiment

Control (A) The target surfaces in Figures 2A and 2B are superimposed on uniform surrounds that have the same average chromaticity as the corresponding panels in Figure 2B. Control (B) The same target surfaces are superimposed on the same averaged spectral backgrounds but also include the structural outlines of the elements that are apparent in Figure 2B. (C) The average ratio of thresholds ($n = 6$) for the size-matching task when the probes were routed to either the dominant or suppressed eye in the control (A and B) conditions or context (Figure 2B) stereograms. Scale bars represent one standard error.

dominance if the context in which they are viewed suggests that they arise from different objects.

An alternative explanation for these observations, however, is that the physically identical targets fused while the surrounds competed for perceptual dominance; the perceptually dominant surround then influenced the perception of the fused targets, thereby giving the impression that the targets were competing for perceptual dominance. To address this issue, we determined the degree of suppression that occurred when subjects viewed these stimuli. Two probes were briefly superimposed on two of the target surfaces in the suppressed eye, and the subjects' task was simply to indicate which of the probes was larger (see Experimental Procedures). The results shown in Figure 2C demonstrate that, under these conditions, the ability to discriminate the probe size was attenuated when subjects viewed the images in Figure 2B compared to Figure 2A, despite the spectral identity of the surfaces upon which the probes were presented ($t = 3.3$; $p < 0.01$). During the experiment, subjects were only asked to perform the size-matching task and not to indicate whether they were aware of the probes. However, subjects did report that the visibility of the probes was more difficult in some stimulus configurations. Presumably, this affected performance by producing psychometric functions with a shallower slope and thus higher thresholds.

Another possible confounding factor was that the differences in spatial complexity and spectral contrast that were evident between the context and noncontext conditions could have influenced performance in this task. Accordingly, we created control stimuli that contained the same average chromaticity and spatial complexity but that had a diminished illusion of color contrast [14, 15]. In addition, we compared relative performance when the probes were routed to either the dominant or

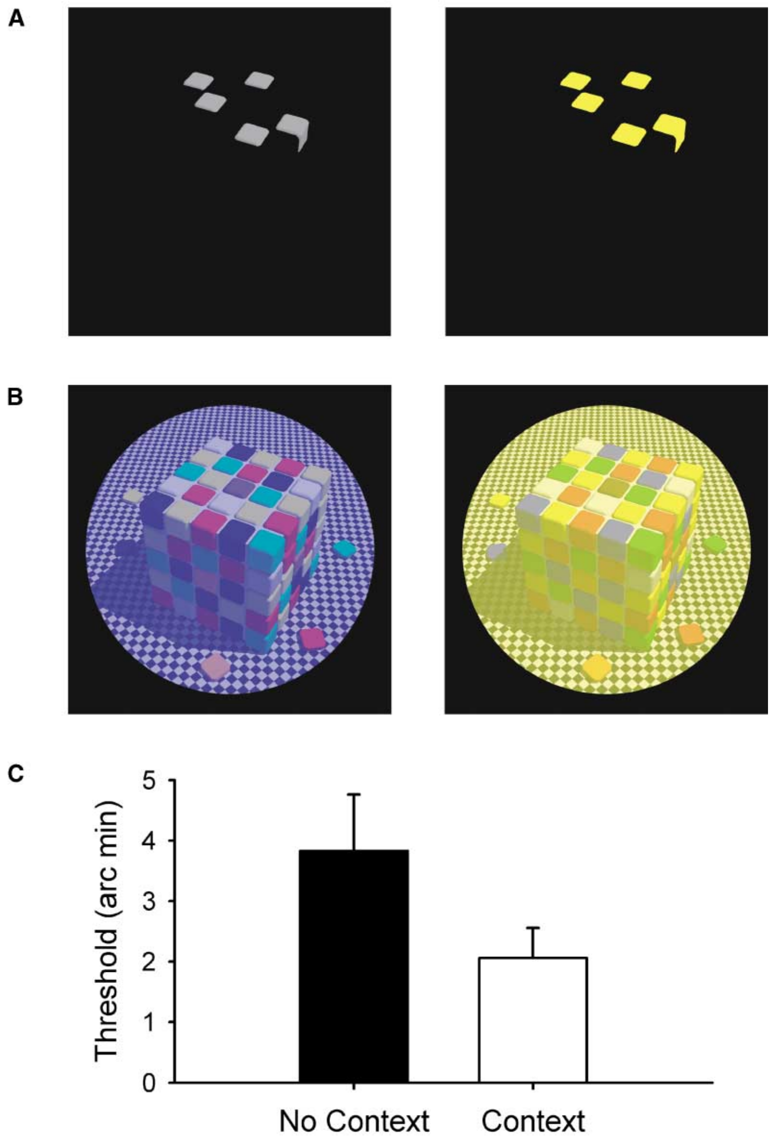

Figure 4. Inducing Fusion between Different Spectra

For determination of whether context can also enhance chromatic fusion, subjects were presented with the two stereograms shown in (A) and (B). The results for these experiments are presented in (C). The graph represents the average threshold ($n = 7$) for the size-matching task for all participants. The results show that the ability to detect physical differences between the test probes was significantly better in condition (B) than in condition (A). Scale bars represent one standard error.

the suppressed eye. To control for whether the difference in performance in the size-matching task involving the probes on the target surfaces in Figure 2A versus 2B could be explained by the addition of different spectral surrounds, we presented subjects with two further stereograms (Figure 3). In Figure 3A, the target surfaces in Figures 2A and 2B are superimposed on uniform surrounds that have the same spatial chromatic average as the corresponding panels in Figure 2B. In Figure 3B, the targets are superimposed on the same averaged spectral backgrounds but also include the structural outlines of the elements that are apparent in Figure 2B. Importantly, although these changes in chromatic structure maintain the average spectral difference between the target surfaces and their surround, reducing the information in the stimulus makes the surfaces less likely to represent differently reflective objects (and as a result, the illusion of color contrast is much reduced) [14, 15]. In this experiment, we measured size difference thresholds during the suppression and dominance phases of rivalry. Despite the similarity in the physical contrast between the target surfaces and surround, the suppression/dominance ratio of the size-matching task was significantly reduced when subjects viewed the panels in Figure 2B compared to Figures 3A and 3B ($F = 3.4$; $p < 0.05$). Thus, the attenuation in probe discrimination during the suppression phase of rivalry was only apparent when the context was consistent with the achromatic panels giving rise to the perception of blue or yellow objects rather than being a function of lower-level changes to the surround.

Color Constancy: Inducing Fusion between Physically Different Targets

If chromatic rivalry can be induced by the addition of spectral context that increasingly concords with an identical spectral return arising from different surfaces occupying the same location in space, then fusion should be augmented between physically different target surfaces when the spectral context is consistent with different monocular spectra arising from similar surfaces at the same location in space. To test this possibility, we embedded gray and yellow surfaces in contexts that implied they had the same chromatic reflectance (Figure 4). Subjects were again asked to perform a size-matching task. The spectrally different target surfaces viewed in isolation (on the same black surround) appeared gray in the left panel and yellow in the right panel (Figure 4A). However, when subjects viewed the stereogram in Figure 4B, the left and right surfaces from Figure 4A all appeared yellow. Importantly, the ability to differentiate between the test probes was facilitated (presumably as a result of the targets fusing more readily) when the targets were perceptually more similar (Figure 4C), than in the stereogram in Figure 4A ($t = 2.0$; $p < 0.05$). Thus, when different spectra signify the same object in space (as in Figure 4B), fusion can be augmented between spectrally physically dissimilar stimuli. Together, these results further demonstrate that the determinant of chromatic integration is the perceptual meaning (or empirical significance) of spectral stimuli [16].

So where might the underlying neural processes take place for the binocular integration of chromatic signals? One possible location, based on neuropsychological studies of achromatopsia, is the fusiform gyrus [17] because activity in this area can be correlated with sensations of surface color independent of changes in illumination [18, 19]. Although this possibility is consistent with the idea that rivalry involves neuronal competition in extrastriate visual cortex [20–22], a recent study has suggested that perceived color could be represented by neurons in the primary visual cortex [23]. Consequently, we speculate that the neural processes that underlie chromatic rivalry—and sensations of color generally—do not reduce to any one area but represent a distributed pattern of neural events that emerge from interactions between cortical areas whose principle aim is to resolve the inherent ambiguity of spectral stimuli.

Experimental Procedures

Stimuli were created with Adobe Photoshop 5.0 software with the standard color palette and were displayed with a VSG graphics card (CRS, Rochester, England) linked to a high-resolution, calibrated, color monitor (Vision Master 17, Ilyama) at 110 Hz. Subjects viewed the monitor from an adjustable chin rest and forehead bar, at a distance of 1.5 m through Ferro-Electric Shutter Goggles (CRS, Rochester, England) that alternately occluded the two eyes at the same frequency as the frame rate of the monitor (110 Hz). The display alternated on successive frames between the pairs of images shown in Figures 2 and 3, so that each was seen by only one eye with no perceptible flicker at this high alternation rate. Superimposing a fixation dot on the two images (approximately 8° in diameter) aided vergence. Cross talk was minimized by the 3 log unit contrast ratio of the shutter goggles and by the fast phosphor decay. All participants in this experiment had normal or corrected to normal vision and good stereopsis.

In the size-matching task, both eyes initially viewed one of the left-hand images in Figures 2–4 for 500 ms. The image in one eye was then replaced by the corresponding right-hand image while the other eye continued to view the original image. This sequence of image presentation resulted in an immediate and complete switch in perception to the new stimulus on the right—a phenomenon known as flash suppression [24]. To measure the degree to which the target surfaces fuse or rival, probes were briefly presented (50 ms) on the two spectrally neutral surfaces to the right or left of fixation in either the suppressed or the dominant eye. The suppressed eye was the eye that continued to view the original image throughout the presentation sequence, whereas the dominant eye switched from the original image to the new stimulus. The eye receiving the probe stimuli was randomized from trial to trial. The probes were filled circles (4.5–9.0 arc min in diameter) and were optically superimposed on the image in one eye. The subjects were instructed to press one of two buttons to indicate which of the two probes (left or right) was larger. Previous studies have shown that, during rivalry, test flashes in the suppressed eye often go undetected by the observer [25]. For generation of the stereograms in Figures 2 and 3, a blue probe that matched the perceived color of the test tiles in the right image of Figure 2B was used. Correspondingly, in the stereograms from Figure 4, a yellow probe that matched the apparent color of the test tiles in the right image of Figure 3B was used. (The logic of using colored probes is that their onset would be more difficult to detect during rivalry if they were color-matched to the dominant target.) Thus, when monocular targets rival, and the test probes are presented to the suppressed eye, then the ability to discriminate between the probes will be reduced. If, however, the targets fuse, then the test probes will be more easily discriminated. For threshold determination, cumulative-Gaussian curves were fitted to the forced-choice data. The difference between performance at 0.5 and 0.82 on the fitted Gaussian was taken as the threshold. Statistical comparisons were only possible within each condition because different groups of subjects were used in different experiments.

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