



Binocular fusion of luminance, color, motion and flicker – Two eyes are worse than one

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ARTICLE INFO

Article history:

Received 7 October 2011

Received in revised form 8 November 2011

Available online 22 November 2011

Keywords:

Color

Luminance

Motion

Binocular vision

Stereo

Visual search

Afterimages

ABSTRACT

How much information is conserved, or discarded, as it travels through the visual system? A target (an oriented bar) was defined by dark grey spots embedded in light spots for the left eye, and by light grey spots embedded in dark spots for the right eye. With one eye open, the target bars were clearly visible, but with both eyes open the light and dark spots fused binocularly into medium grey and the target vanished. Results were similar for color; the target comprised greenish spots embedded in reddish spots for the left eye, and by reddish spots embedded in greenish spots for the right eye (somewhat like an Ishihara color plate).

Result: The colored targets were invisible when both eyes were open but reappeared when one eye was closed. Small targets that moved in opposite directions in the two eyes were visible to each eye alone by common fate, but motion averaging made them disappear when both eyes were open.

Conclusion: Opposed retinal luminances or colors were averaged out by binocular fusion, but could be retrieved by a special afterimage technique in Experiment 6. Conversely, in Experiment 7 dichoptic target spots flickered in counterphase but background spots flickered in-phase to the two eyes.

Result: The targets were invisible monocularly but became visible as reduced-flicker when fused binocularly. We conclude that two eyes were worse than one eye when opposite colors or movements were fused (Experiments 1–6) but were better than one when binocular correlations could be extracted (Experiment 7). These experiments show how much of the visual information gets transmitted, gets discarded, can still be retrieved, or reaches conscious awareness.

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1. Introduction

How much information is conserved as it travels through the visual system, and how much is discarded? A well-designed information transmission system will transmit only the information it is going to use and will discard everything else. For this reason one might expect that information will travel up the visual system as far as necessary but no further. Here is a cartoon account of the stimuli we used: Imagine a field of colored random spots, something like an Ishihara (1980) color-testing plates. Each eye sees spatially congruent spots (no disparities) but in different colors. One eye sees a cross made of yellow spots, embedded in reddish spots. The other eye sees the same yellow cross, but embedded in greenish spots. When fused binocularly, all the spots look yellow and the cross vanishes. In this paper we study how the monocular and binocular color information is transmitted through the visual system.

It is already known that some information is transmitted part-way through the visual system to some unknown location where its salient features can be filtered out and accepted, while its inessential features are discarded. For instance, our ability to tell which of two eyes sees a single flash of light (utrocular discrimination) is poor or non-existent (Martens et al., 1981; Ono & Barbeito, 1985; Templeton & Green, 1968), for both normal and stereoblind observers (Barbeito et al., 1985; Blake, 1982; Porac & Coren, 1986). Yet stereo vision “knows” which eye is which, otherwise we would be unable to see stereo depth (Julesz, 1971). Clearly the eye-signature information is available to stereo computations but not to conscious awareness, rather as a driver is aware of the position of the steering wheel and the direction of the car’s travel, but not of the inner workings of the servo steering. We know only what we need to know.

Tyler and Cavanagh (1991) reported that two eyes are as sensitive as one for the perception of motion in depth. Conversely, in a random-dot stereogram a central square is seen in depth, which does not exist within either monocular pathway, but exists only binocularly as a correlation between the eyes (Julesz, 1971). In this case, the depth information is missing early on but is created at the

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binocular level. Consequently, we asked whether information available at the monocular level would remain available or might sum linearly to become invisible at the binocular level. Sherrington (1904) and Thomas (1954) measured the flicker thresholds for a binocularly fused flickering disk, and found that the relative phase of the flicker in the two eyes made almost no difference to the thresholds. Thus, counterphase flicker in the two eyes did not cancel out; but we wondered whether such cancelation might be obtainable by a different paradigm. To anticipate, we did find such dichoptic cancelation.

Our experiments used a form of rapid visual search. It is easy to see a row of red spots hidden among green spots, or of light grey spots hidden among dark grey spots. It is also easy to see a row of spots that move to the left when surrounding spots move to the right. In general, targets that are embedded among distractors “pop out” visually and can be seen immediately if they differ from the distractors in some primary visual quality such as color, luminance, motion or disparity (Treisman 1986). (More complex differences such as +’s hidden among L’s take much longer to see). We presented briefly a target row of clustered spots that differed from distractors in color or luminance (Anstis, Ramachandran-Rogers, & Ramachandran, 1994); or that differed in motion or flicker. Observers had to discriminate the orientation of this row – horizontal, vertical, left-oblique or right-oblique.

2. Methods

2.1. Display

We studied the binocular fusion of luminance or color by means of dichoptic displays. Each eye saw 400 irregularly arranged spots that were spatially congruent (no disparities) but differed across eyes in luminance or color. The displays looked somewhat like Ishihara’s (1980) pseudo-isochromatic plates. For ease of computation, the array consisted of 5×5 tiles, with each tile containing 16 irregularly arranged spots ($5 \times 5 \times 16 = 400$), each tile being of side 0.55° (33 min) and separated by their widths, so that they tessellated the surface. Spot sizes ranged from 5 to 10 min arc. A subset of these tiles defined a target; instead of a complete cross, our targets were either the horizontal or the vertical bar of a cross, or else a left-oblique or right-oblique bar, which the observer had to report. To aid fixation, each eye’s display was centered in a square speckled picture frame of side 6.5° . The two displays were binocularly fused with the aid of a mirror stereoscope. Brief presentations (<1 s) helped to minimize binocular rivalry (Wolfe, 1983).

For luminance, we presented figures defined by light gray spots (200 cd m^{-2}) against a background of dark gray spots (120 cd m^{-2}) to one eye, and a congruent fig. of dark spots against a background of light spots to the other eye (Fig. 1). For color, the dark and light were replaced by greenish-yellow and reddish-yellow spots (not illustrated). These greenish and reddish hues could be fused binocularly into an intermediate hue (yellow). We used two types of experiment. In Experiments 1–5, monocular information about luminance, color or motion that specifies a target would normally reach consciousness but here was suppressed or discarded during binocular viewing. In this case the target information was present early on but was missing at the binocular level. In Experiment 7, on the other hand, the quality (here, depth of flicker) specifying the target did not exist at the monocular level, but existed only as a correlation between the two eyes that was then revealed by means of binocular fusion. Here the targets flickered in counterphase, but the surround flickered in-phase, across the two eyes, giving deeper dichoptic flicker to the surround. Experiments 1–5 contrasted with Experiment 7 demonstrated respectively that two eyes could be worse, or better, than one.

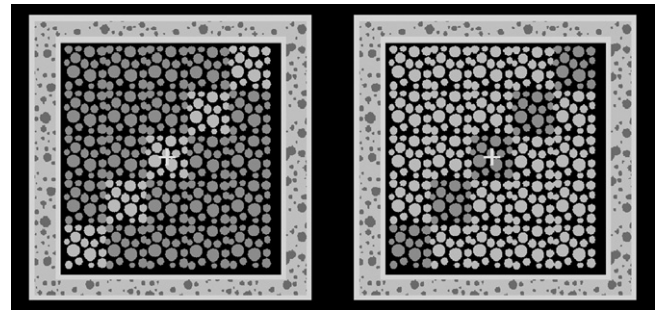


Fig. 1. Sample stimulus from Experiment 1, condition 3. Target is a right-oblique bar, here defined by light grey in the left eye and dark grey in the right eye. In a staircase procedure, observers adjusted these grey levels to reach detection threshold for the target. Results showed higher thresholds for binocular targets (as here) than for monocular targets (close one eye). (This reproduction may not accurately depict actual stimulus grey levels.)

2.2. Promoting binocular fusion

Grey spots of different luminance levels readily fuse binocularly (Anstis & Ho, 1998; Ding & Sperling, 2006a; Ding & Sperling, 2006b; Legge, 1984; Levelt, 1965). For colored spots we chose conditions that would encourage binocular fusion. Such fusion is best when the patches seen by the two eyes are small ($<2^\circ$) (Grimsley, 1943; Gunter, 1951; Thomas, Dimmick, & Luria, 1961) or textured (de Weert & Levelt, 1976; de Weert & Wade, 1988) and of similar hues (Ikeda & Sagawa, 1979). Hovis (1989) and Howard and Rogers (2002) have reviewed the literature on binocular color mixing.

Ding and Sperling (2006a, 2006b) have produced an impressive model of binocular luminance combinations in which each eye (i) exerts gain control on the other eye’s signal in proportion to the contrast energy of its own input and (ii) additionally exerts gain control on the other eye’s gain control. We shall not discuss this model further since we are studying not the computations that achieve binocular combination but rather the perceptual results of such computations.

The background behind all our spots was black, so that all spots in our stimuli were spatial increments. This was because we have found (Anstis & Ho, 1998) that spatial increments presented one to each eye summate linearly, whereas spatial decrements behave in a nonlinear winner-take-all fashion. If each eye were to see a different gray on a white surround, the binocularly combined percept would accept the luminance of the higher-contrast (darker) target and completely ignore that of the lower-contrast (lighter) target. To avoid this nonlinear behavior we always used spatial increments. In addition, this uniform contrast polarity of all the spots helped to block unwanted binocular rivalry. (Note that even if binocular rivalry did occur, it would have a conservative effect, tending to make binocular targets more visible and militating against the results we obtained.)

3. Experiments

3.1. Binocular fusion of luminance

The targets were defined by luminance, as rectangular regions of light gray spots against a surround of dark gray spots or vice versa. On each trial the computer randomly selected one of the four bar orientations (horizontal, vertical, left-oblique or right-oblique). It also chose whether the targets were lighter or darker than the surround, and which eye was to be stimulated – a total of six possibilities, as follows:

#	Left eye	Right eye
1	–	Dark
2	Light	–
3	Light	Dark
4	–	Light
5	Dark	–
6	Dark	Light

In this table, “Light” refers to a light gray target on a dark gray surround, and “Dark” refers to a dark gray target on a light gray surround. “–” means that this eye saw nothing. Thus conditions 1, 2, 4 and 5 were Monocular, whilst conditions 3 and 6 were Binocular, with the two eyes seeing the same targets but with opposite luminance values.

3.1.1. Procedure

The experiments were designed with six randomly interleaved staircases running concurrently (Cornsweet, 1962). On each trial the computer randomly selected one of the six conditions. If the observer reported the target correctly, the computer remembered this and slightly reduced the contrast for that condition on the next trial. If s/he failed to report it, the contrast was slightly increased for that condition on the next trial. In this design, which made the stimulus in each condition depend upon the previous response, the stimulus contrast homed in automatically on the observer’s visual threshold, for each of the six conditions independently. The last six reversals of each staircase were averaged to give the threshold for that condition.

3.1.2. Results

Results were averaged for all four monocular conditions, and for both binocular conditions, across all three observers. The final results gave the Michelson contrasts that were just at threshold. These threshold contrasts were 0.173 for the monocular conditions, and 0.377 for the binocular conditions ($p < 0.005$). Thus the contrast thresholds were twice as high (bad) for the binocular trials. So two eyes were much worse than one, and the opposite contrast information from the two eyes was being canceled out and never reached conscious awareness.

3.2. Colored targets

We now introduced color. Instead of grey spots, the targets were now composed of reddish spots against a background of greenish spots in one eye, and of greenish spots against a background of reddish spots in the other eye. The initial hues were a reddish yellow, which we shall call orange, and a greenish yellow, which we shall call lime. As we shall see, the CIE x and y values of these hues were variables that changed during the running of the experiment. Each stimulus was presented for 1000 ms, and eight observers were run.

The six conditions were as follows:

#	Left eye	Right eye
1	–	Orange
2	Lime	–
3	Lime	Orange
4	–	Lime
5	Orange	–
6	Orange	Lime

This is the same table as for Experiment 1, but with Orange substituting for Dark and Lime substituting for Light. In this table, “Lime” refers to a lime-colored target on an orange-colored surround, and “Orange” refers to an orange-colored target on a lime-colored surround. “–” means that this eye saw nothing. As before, conditions 1, 2, 4 and 5 were Monocular, whilst conditions 3 and 6 were Binocular, with the two eyes seeing the same targets but in opposite colors.

3.2.1. Procedure

The staircase procedure was the same as before, except that the program adjusted the hues, instead of the luminances, of the stimulus spots. In Experiment 1, light and dark gray spots had been coded by $rgb(hi, hi, hi)$ and $rgb(lo, lo, lo)$. In Experiment 2, orange and lime spots were now coded by $rgb(hi, lo, 0)$ and $rgb(lo, hi, 0)$. The computer controlled the variables hi and lo , which moved further apart to make the light and dark spots (or the lime and orange spots) more different, and moved them closer together to make them more similar.

As before, the six final reversals of each staircase were taken as the final values of the lime and orange. Results were pooled for all monocular conditions (1, 2, 4 and 5) and for both binocular conditions (3 and 6). The final results were the just noticeable differences in hue, in other words the hues of lime and orange that lay at the *chromatic threshold* for monocular and binocular conditions.

3.2.2. Results

The results are plotted in Fig. 2. The threshold hues for lime and orange are plotted in CIE coordinates for the monocular and binocular conditions. Fig. 2 shows that the monocular targets could be successfully discriminated when the orange and lime were close together in CIE space, with respective ordinates of $x = 0.454$, $y = 0.448$ for orange and $x = 0.440$, $y = 0.452$ for lime. For the binocular viewing conditions, on the other hand, the lime and orange had to be no less than 6.5 times as far apart in color space, with coordinates of $x = 0.485$, $y = 0.425$ for orange and $x = 0.412$, $y = 0.474$ for lime ($p < 0.0001$).

Thus, in the color domain as in the luminance domain, two eyes were much worse (here about six times worse) than one. This shows that binocular color averaging canceled out color information, as it did luminance information, when opposite information was fed to the two eyes.

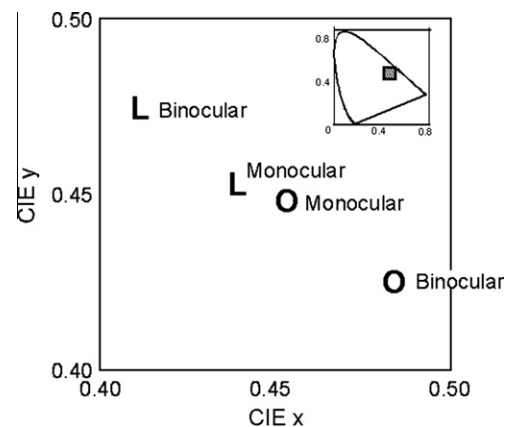


Fig. 2. Inset shows position of main diagram in the 1931 CIE color triangle. Hue thresholds at which lime (L) could just be discriminated from orange (O) were close together in monocular conditions, but were six times further apart (worse) when opposite hues were presented to the two eyes and binocularly averaged. Mean of eight observers.

3.3. Experiment 3: percent correct for colors

Next, Experiment 3 shows that the differences in color thresholds just established in Experiment 2 were reflected in a percent-correct task. The hues of lime and orange were set to fixed values of CIE $x = 0.627$, $y = 0.667$ for lime and $x = 0.894$, $y = 0.608$ for orange. Conditions 1–3 from Experiment 2 were presented in random order, and on each trial the observer identified the target orientation, if s/he could.

#	Left eye	Right eye
1	–	Orange
2	Lime	–
3	Lime	Orange

The hues and saturations were fixed on each trial, but dynamic luminance noise was applied to make the stimuli twinkle randomly, in order to rule out any cues from inadvertent differences in luminance. Corresponding spots in the two eyes always had the same luminance, but there was no spatial correlation between spots within one eye. The observers simply reported the target, and the success rate was scored separately for each condition.

3.3.1. Results

Results were striking (mean of four observers). The success rate (percent correct) was 90% for the left eye alone, 92% for the right eye alone, but only at chance (25%) for the two eyes combined ($p < 0.001$). Thus the monocular success rate was more than three times higher than the binocular, showing that two eyes were very much worse than one. Binocular averaging canceled out the opposite color information from the two eyes, which was never transmitted into conscious awareness.

3.4. Experiment 4: yellow targets

This was like Experiment 2, except that the targets were yellow in both eyes, whilst the surrounding spots were orange in one eye and lime in the other. The purpose was to show that orange and lime hues viewed separately by the two eyes could fuse binocularly into a true cortical yellow that was indistinguishable from a directly viewed yellow stimulus.

3.4.1. Procedure

This was the same as in Experiment 2. As before, there were six conditions:

#	Left eye Targets/surround	Right eye Targets/surround
1	–	Yellow/orange
2	Yellow/lime	–
3	Yellow/lime	Yellow/orange
4	–	Yellow/lime
5	Yellow/orange	–
6	Yellow/orange	Yellow/lime

There were six concurrent, randomly interleaved staircases, one for each condition. In this table, “Yellow/Orange” refers to a target of yellow spots against a surround of orange spots. Since it was technically difficult to ensure that the lime/orange combination exactly matched the luminance of the yellow, any inadvertent clues from luminance were ruled out by making all the spots flicker randomly in luminance, as in Experiment 3.

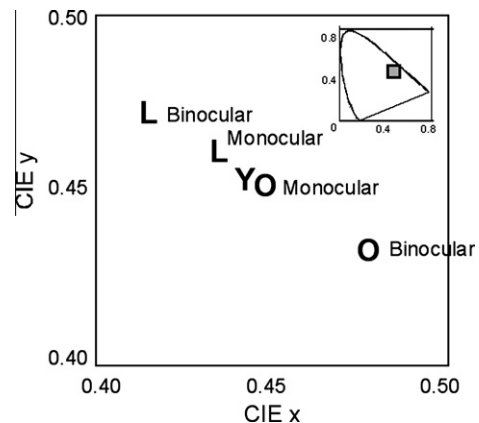


Fig. 3. Inset shows position of main diagram in the 1931 CIE color triangle. As in the previous figures, binocular hue thresholds were 4.67 times further apart (worse) than monocular ones, when opposite hues were presented to the two eyes and binocularly averaged. Y shows the yellow targets. See text. Mean of seven observers.

3.4.2. Results

The results are plotted in Fig. 3. Results are qualitatively similar to Experiment 2 (Fig. 2) but with the yellow stimulus added. The fixed yellow hue of the targets, and the final threshold hues for lime and orange in the background, are plotted in CIE coordinates for the monocular and binocular conditions. In Fig. 3, the fixed yellow targets had CIE coordinates $x = 0.444$, $y = 0.453$. The monocular targets could be successfully discriminated when the orange and lime were each close to yellow in CIE space, with respective ordinates of $x = 0.448$, $y = 0.452$ for orange and $x = 0.433$, $y = 0.462$ for lime. For the binocular viewing conditions, on the other hand, the lime and orange had to be 4.67 times as far apart in color space, with coordinates of $x = 0.477$, $y = 0.434$ for orange and $x = 0.415$, $y = 0.472$ for lime ($p < 0.0001$).

Experiments 2 and 4 gave similar results, and both show that two eyes were much worse than one. But in addition, Experiment 4 shows that the lime and orange background spots could combine binocularly into a perceptual yellow that was metameric with (indistinguishable from) a simple yellow target presented to each eye. So the “cortical yellow” of the surround was indistinguishable from the “retinal yellow” of the targets, implying the presence of true binocular color fusion.

In Experiments 2–4, the different colors in the spots seen by the two eyes could have provided an unwanted additional cue of binocular luster. This would not be a problem in Experiment 2, in which the target and background regions would have similar lusters. But in Experiment 4, the surround could have been more lustrous than the target, so the threshold elevation that was nevertheless found is the evidence for dichoptic fusion despite any luster cues.

3.5. Experiment 5: motion-defined shapes

Observers can readily identify shapes that are defined by motion (Regan, 2000, chap. 5). To define our targets by apparent motion instead of by luminance or color, the tiles were replaced by an array of small white x's, each subtending $0.25^\circ \times 0.25^\circ$ and separated by 0.75° (Fig. 4). A subset of these, forming a horizontal, vertical or oblique row, as before, now moved opposite to the direction of the remaining x's, which formed the background. On half the trials, the x's comprising the target moved up-down-up-down while the background x's moved down-up-down-up. On the other half of trials, the targets moved left-right-left-right while the background moved right-left-right-left. The motion,

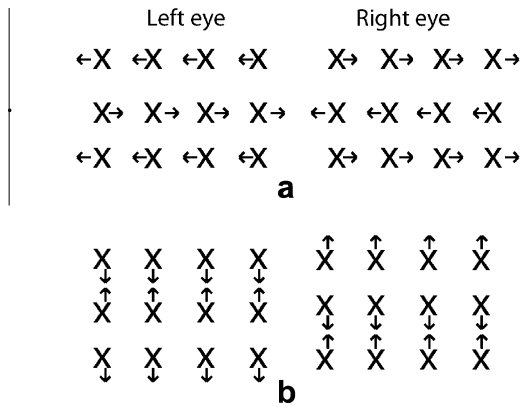


Fig. 4. Cartoon of stimuli in Experiment 5. x's move in opposite directions in the two eyes: (a) Horizontal movements generate disparities which may aid detection. (b) Vertical movements are probably canceled out and ignored. Result: Binocular movement thresholds are 2–3× higher than monocular.

whether horizontal or vertical, was presented to either the left eye, the right eye, or to both eyes in opposite directions. This gave six conditions (vertical vs. horizontal and monocular vs. binocular). It is important to note that on binocular trials, the opposite motions in the two eyes tended to cancel out the perceived motion. There were no staircases in this experiment; observers simply reported the target presented, if they were able to, and their percent correct was recorded.

Thus the six conditions were as follows:

#	Left eye Targets/surround	Right eye Targets/surround
1	–	Down/up
2	Up/down	–
3	Up/down	Down/up
4	–	Right/left
5	Left/right	–
6	Left/right	Right/left

3.5.1. Results

Performance was almost perfect in the monocular conditions (95% correct) (mean of three observers). However, percent correct was only 31% for binocular presentation of horizontal motion ($p < 0.05$), and only 20% for binocular presentation of vertical motion ($p < 0.02$). Chance score would be 25%.

Note that in the binocular conditions, the opposite horizontal motions in the two eyes will give a disparity signal which may give the percept of a cross jumping back and forth in depth. On the other hand, the binocular vertical motions will give only a vertical disparity signal, which conveys no depth information and will probably be averaged out and ignored (Howard & Rogers, 2002). This may explain why the binocular motion threshold was lower (better) for horizontal than for vertical motion. But the main conclusion is that the monocular performance was two or three times better than the binocular performance. Tyler (1971) showed binocular suppression of the threshold for stereomotion relative to monocular motion, which included the observation of complete stationarity for amplitudes below a ratio of a factor of 6. Tyler and Foley (1974) made further measurements of the suppression of stereomotion compared to monocular motion. Qian et al. (1994) extended these findings to alternating apparent motion, reporting that when two nearby non-transparent dots move in opposite directions, the visual system can average the two motions together and the dot pair looks stationary. In our experiment, we

found a similar motion averaging or cancelation occurring across the two eyes.

3.6. Experiment 6: afterimages from unseen colors

Experiments 2–4 showed that monocular information about color from each eye, once fused together binocularly, is no longer accessible to consciousness. But we shall now show that it is still there and can be brought into awareness if the visual system is interrogated in the right way.

Moutoussis and Zeki (2002) used this same technique of dichoptic color fusion to make identical monocular stimuli of opposite color contrast “disappear” at the binocular level and thus become “invisible” as far as conscious visual perception is concerned. They measured brain activity during this invisible stimulation, and found that house-specific and face-specific brain areas were always activated in a stimulus-specific way regardless of whether the stimuli are perceived. Absolute levels of cortical activation, however, were lower with invisible stimulation compared with visible stimulation.

3.6.1. Procedure

The eyes binocularly fused a stereogram on a Macintosh monitor screen via a mirror stereoscope at a viewing distance of 31 cm (Fig. 5). Each eye saw two blurred spots, each 3.67° in diameter and positioned respectively 3.67° above and 3.67° below a small fixation cross. For the left eye, the upper spot was magenta (6.5 cd m⁻², CIE x = 0.386, y = 0.264) and the lower spot was green (10.6 cd m⁻², CIE x = 0.311, y = 0.417). For the right eye the upper spot was green and the lower spot was magenta. A sharply defined grid of black horizontal and vertical lines, spaced 0.6° apart, was superimposed over the spots in each eye. This provided contours that encouraged binocular fusion and prevented binocular rivalry. At the beginning of each trial, the fields behind the grids were a uniform mid-gray of luminance 9.3 cd m⁻². The four colored spots then faded in gradually over a period of 12 s. By making the spots blurred, fading in gradually, and complementary in color to the two eyes, we were able to ensure that the binocularly fused images were gray and no adapting colors were ever seen. After a further adapting period of 4 s, the fields were briefly switched to black

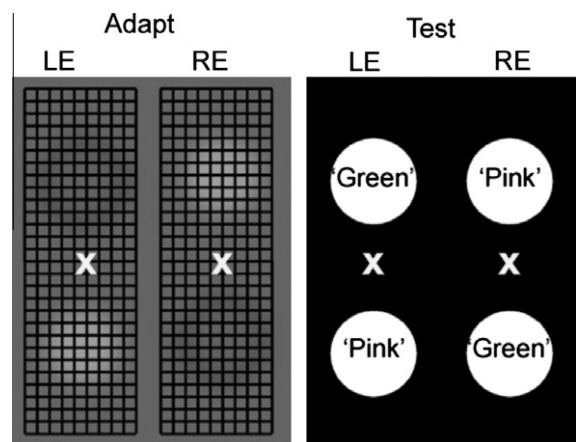


Fig. 5. Observers adapted to blurred colored spots that faded up gradually. Above the fixation spot, the left eye saw a magenta spot (here dark gray) and the right eye saw a green spot (here light gray), and vice versa below the fixation spot. The superimposed black grid aided fusion and prevented binocular rivalry. Observers did not notice any colors. Then white test disks were flashed up in one of four positions. Observers named the color of the perceived afterimage, “pink” or “green” in the positions shown. Result show that unseen colors could produce negative colored afterimages, showing access to stored monocular information.

for both eyes and a white test disk was flashed up for 1 s *in one* [eye only], above or below the fixation point, and in the position of one of the four spots. Five observers reported the perceived hue of any afterimage by hitting one of two computer keys to indicate “pink” or “green”. The colored adapting stimulus was then restored for a topping-up period of 4 s. This cycle continued, with the white test disk flashing up in random order in the four possible positions (left-eye or right-eye, vs. upper or lower), every 5 s for 20 trials per test-position (a total of 80 presentations). All responses were recorded for later analysis.

3.6.2. Results

Observers never perceived any of the colors in the adapting blurred spots. However, they reported the predicted colors on the white test disks (*left eye*: upper afterimage green, lower afterimage pink. *Right eye*: upper afterimage pink, lower afterimage green) on 100% of trials. The false alarm rate was zero. The probability of these “100% correct” results happening by chance over the total of 400 trials (80 trials \times 5 observers) was $2^{-400} \approx 10^{-120}$. This handsomely exceeds $p < 0.0001$.

These results indicate that although observers could not report the adapting colors, they did consistently see the resulting afterimages. *Conclusion*: The opposed adapting colors in the monocular visual pathways were averaged together binocularly to give an achromatic grey, making the monocular colors inaccessible to consciousness. It was as though information was taken in but then wastefully discarded. However, the color information was still available at a monocular level when interrogated by a monocular white flashed disk (provided that the other eye saw only black, which ruled out binocular color averaging). We conclude that color information can be stored at a monocular level (for at least long enough to generate an afterimage), and is subsequently averaged together binocularly with the input from the other eye. Usually the monocular information is unavailable to consciousness, but we have shown here that it can be made available by the afterimage technique.

3.7. Experiment 7: flicker-defined shapes

This experiment, unlike all the previous ones, is designed to show that two eyes can be better, not worse, than one. All spots were now grey and flickering, with targets defined by opposite (counterphase) flicker in the two eyes and the surround defined by the same (in-phase) flicker in the two eyes.

3.7.1. Procedure

All spotted tiles were now grey, and they flickered up and down between randomly chosen luminance levels (anywhere between 0 and 255) at a rate of 5 changes/s. All background pixels flickered in-phase to the two eyes ($I_L = I_R$), so that each corresponding pair of pixels always had the same luminance. But all spots that defined a target flickered in counterphase in the two eyes, so that when any given spot was light to one eye it was dark to the other eye ($I_L = 255 - I_R$). There was no correlation between the luminances of spatially different tiles within one eye. Three conditions were run: the stimuli were presented to the left eye only, right eye only, or to both eyes. As before, three randomly interleaved staircases homed in independently on the contrast thresholds for the left eye, right eye, and both eyes. Note that the targets did not exist within one eye's view on its own, but existed only as a correlation in the flicker between the two eyes. The logic is that same as for Julesz' (1971) random-dot stereograms. The binocular condition was the item of interest. We predicted that if binocular fusion were successful, then the background pixels would show relatively strong flicker, since each spot had the same luminance in both eyes (correlation across the eyes = 1), but the targets would show much

weaker flicker, since corresponding spots were light in one eye and dark in the other (correlation = -1).

3.7.2. Results

All seven observers could readily identify the binocular targets on the basis of their weaker perceptual flicker compared to the surround. Their mean Michelson contrast thresholds were calculated as $(L_{\max} - L_{\min}) / (L_{\max} + L_{\min})$, where L_{\max} and L_{\min} were the average values of the light and dark phases of the flicker. (These max and min values were randomly modulated on each cycle of flicker). We found contrast thresholds of 0.375 for monocular, 0.18 for binocular viewing ($p < 0.001$). Thus, loosely speaking, two eyes performed twice as well as one.

Our results are somewhat at variance with those from earlier authors. Sherrington (1904) and Thomas (1954) measured the flicker thresholds for a binocularly fused flickering disk, and found that the relative phase of the flicker in the two eyes made almost no difference to the thresholds. Sherrington concluded that binocular perception results from the combination of “already elaborated unocular sensations contemporaneously proceeding”. He suggested that the phenomena of binocular fusion take place psychically and are not based on a low-level physiological mechanism.

These authors found little or no effect of flicker phase when measured at or near threshold. We found pronounced phase differences in our suprathreshold experiment; but our results do not necessarily contradict theirs, since our binocular fusion could well happen at a higher (“psychic”) rather than lower (“physiological”) level.

Even though our Experiment 7 showed that two eyes could be better than one, it still relied upon the same principle as the other experiments, in that opposed flickers to the two eyes could, like opposed luminances, colors and motions, cancel out in the binocularly fused percept. So once again monocular information did not reach conscious awareness, whereas the binocular information did.

Our results suggest that cross-eye correlations are not detected only by some module specialized for processing binocular disparity (Julesz, 1971), but involve a more versatile process that can distinguish in-phase from counterphase dichoptic flicker, which unlike binocular disparities are unlikely to occur in nature.

4. Discussion

4.1. Let us summarize our findings

Two eyes were worse than one in Experiments 1–5, in which the regions of monocular stimulus differences were dichoptically opposed. The hidden information could be revealed by addition of a monocular mask in Experiment 6. Two eyes were better than one in Experiment 7, in which the dynamic flickering texture was identical in the target and surround regions monocularly but differentiated dichoptically.

Experiment 1: Opposed brightness, using light grey and dark grey spots to define targets and surround: the Michelson contrast thresholds were 0.173 for monocular viewing, 0.377 for binocular ($n = 3$, $p < 0.005$).

Experiment 2: Opposed colors, using lime and orange spots: The threshold color separation, in CIE coordinates, was 6.5 times greater for binocular than for monocular viewing ($n = 8$, $p < 0.0001$).

Experiment 3: Percent correct scores, using a fixed-hue version of Experiment 2, were 91% for monocular but only 25% for binocular viewing – a 3.6-fold ratio ($n = 4$, $p < 0.001$).

Experiment 4: Opposed colors, using yellow targets on orange/lime surrounds: The threshold color separation was 4.7 times

greater for binocular than for monocular viewing ($n = 4$, $p < 0.0001$).

Experiment 5: Opposed back-and-forth motions. Percent correct was 95% monocular, 31% for binocular horizontal motions ($p < 0.05$), and 20% for binocular vertical motions ($p < 0.02$) ($n = 3$).

Experiment 6: Afterimages from unseen monocular colors. Although the monocular colors disappeared in the binocularly fused view, they could still be accessed as monocular afterimages ($n = 5$, $p \ll 0.0001$).

Experiment 7: Opposed flickers – two eyes were better than one. The Michelson contrast thresholds were 0.37 monocular, 0.18 binocular ($n = 7$, $p < 0.001$).

In round numbers, putting opposed signals into the two eyes approximately doubled the contrast thresholds, increased color thresholds four- to six-fold, and reduced percent correct scores for color two- to three-fold. Clearly information from the individual eyes is being discarded wholesale, such that only the average values from the two eyes are retained (Harris & Rushton, 2003) and the individual values from each eye are lost. However, the afterimage experiment showed that some monocular information is retained and can be retrieved, although in the real world it never is. Conversely, in Experiment 7 on flicker, the visual system combined the different monocular flickers to retrieve a correlated visual object, although such objects never occur in the real world.

The issue of dichoptic summation of different colors was reviewed by Helmholtz (1909/1924), who in many conditions failed to get it. In this paper, we have studied the path followed by the lost color information. The monocular information must exist prior to the site of binocular combination, and the (linear) binocular combination of the monocular neural signals is the mechanism of its loss. This view corresponds to the Juleszian view (1971) of the cyclopean retina. Our Experiment 6 shows that the monocular information can be retrieved or revealed, by using a monocular mask to avoid the dichoptic summation. We have no direct information about neural locations, but the monocular colors that are unmasked in Experiment 6 must persist at least as far as the monocularly driven neurons in V1, while the earliest site for binocular combination would be the binocularly driven neurons that are also in V1.

What are the evolutionary implications of our findings? Why have these recondite and probably useless monocular and binocular phenomena not evolved out of existence? It is important to view our results through a “stereoscopic” lens. The goal of stereopsis is to recover the information about the 3D positions of objects in the world, which requires the dual images of the objects on the two retinas to be combined as well as possible into single percepts. Thus, it is evolutionarily advantageous to suppress the dichoptic differences between near-corresponding images of the same object (which is a fair description of most of the stimuli in the present paper), especially in cases of small shiny objects that may appear very different in the two eyes. To the extent that civilization creates more shiny objects than does the natural environment, this functionality may even be still evolving.

Also, the fact that we decided to oppose target and surround regions of different character in unnatural stimulus configurations is not a comment on the need for such a functionality in the natural environment (and, indeed, one might imagine conditions when peering through dense foliage or looking at for the “catpaw” footprint of wind squalls on the sunlit surface of the sea on a windy day that would come close to mimicking some of the experimental paradigms). At the very least we might argue that these obscure abilities to combine dichoptic stimuli have survived because, like the appendix and the coccyx, they might not do us any good but they usually do us no harm.

Acknowledgments

Supported by grants to S.A. from the Academic Senate and the Department of Psychology, UC San Diego. We are grateful to C.W. Tyler for valuable suggestions and discussions.

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